

GEOGRAPHIC VARIATION IN NESTS OF YELLOW WARBLERS BREEDING IN CHURCHILL, MANITOBA, AND ELGIN, ONTARIO

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Abstract. Nesting structures are important for successful reproduction in most birds, and, because of this, geographic variation in nest morphology and composition are usually interpreted as adaptations to breeding in different environments. We compared the structure of nests of Yellow Warblers (*Dendroica petechia*) breeding in Churchill, Manitoba, and Elgin, Ontario, Canada. Churchill is subarctic in habitat and typically much colder during the breeding season than Elgin. We compared temperature, rainfall, and wind speed at these two sites and then tested whether differences in nest structure corresponded to different environments. Yellow Warblers breeding in Churchill built larger, less porous nests that retained heat better but also absorbed more water and took longer to dry than Yellow Warbler nests from Elgin. We suggest that differences in the structure of Yellow Warbler nests represent adaptations to breeding in different environments because the differences in nest morphology and properties of heat retention and water loss correspond to differences between the sites in environmental challenges.

Key words: *adaptation, arctic breeding, Dendroica petechia, geographic variation, nests, Yellow Warbler.*

Variación Geográfica de los Nidos de *Dendroica petechia* que se Reproducen en Churchill, Manitoba, y en Elgin, Ontario

Resumen. Para la mayoría de las especies de aves, las estructuras de anidación son importantes para la reproducción exitosa y, debido a esto, las variaciones geográficas en la morfología y la composición de los nidos son generalmente interpretadas como adaptaciones a la reproducción en diferentes ambientes. Comparamos la estructura de los nidos de individuos de *Dendroica petechia* pertenecientes a poblaciones reproductivas de Churchill, Manitoba y de Elgin, Ontario, Canadá. La localidad de Churchill presenta un hábitat subártico en que el clima durante la época reproductiva es típicamente más frío que el de Elgin. Comparamos la temperatura, la precipitación y la velocidad del viento en estos dos sitios y luego probamos si las diferencias en la estructura del nido se correspondieron con las características de los dos ambientes. Los individuos de Churchill construyeron nidos mayores pero menos porosos que retuvieron más el calor pero que también absorbieron más agua y por eso demoraron más en secarse que los nidos de los individuos de Elgin. Sugerimos que las diferencias en la estructura de los nidos de *D. petechia* representan adaptaciones a la reproducción en ambientes diferentes, porque las diferencias en la morfología y en las propiedades de retención del calor y en la pérdida de agua del nido se corresponden con diferencias en los desafíos ambientales de los dos ambientes.

INTRODUCTION

Different breeding sites pose distinct environmental challenges for breeding birds (Collias and Collias 1984, Hansell 2000). Parents, in songbirds typically the incubating female, must maintain their eggs at temperatures 36–38 °C for optimal embryo development (Drent 1975, Webb 1987), but maintaining such stability can be difficult in regions of extreme temperatures and precipitation (Grant 1982). Similarly, in areas that receive heavy rainfall, keeping the nest dry or constructing a nest that does not absorb and retain water helps maintain optimal gas exchange between the developing embryo and the environment and helps prevent hypothermia of the embryo and nestling (White and Kinney 1974).

Because of the importance of nests to birds' reproduction, differences in nest morphologies between geographically separated populations are often interpreted as adaptations to different breeding environments. One method for breeding birds to overcome environmental challenges is by building nests of different sizes and/or materials to match local conditions (Hovarth 1964).

At least three studies have examined variation in nest morphology and breeding environment among a diversity of birds (Palmgren and Palmgren 1939, Wagner 1955, Collias and Collias 1971), and all suggest that species breeding in colder habitats build larger, better-insulated nests. Although these studies described how birds may construct their nests in response to different environments, none examined geographic variation in nests within a single species.

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We know of only five studies that have compared geographic variation in bird nests within a single species (Schaefer 1976, Kern 1984, Kern and van Riper 1984, Kern et al. 1993, Briskie 1995). Of these, the studies of the Hawaii Amakihi (*Hemignathus virens*) (Kern and van Riper 1984), and Yellow Warbler (*Dendroica petechia*) (Briskie 1995) provide strong support that individuals breeding in colder locations build larger, better insulated nests than those breeding in warmer, wetter locations. The studies examining geographic variation in nests of the White-crowned Sparrow (*Zonotrichia leucophrys*) (Kern 1984) and Song Sparrow (*Melospiza melodia*) (Kern et al. 1993) have found less robust geographic patterns of nest morphology; both of these species often nest on the ground, making the microclimate of the nest site possibly more important than the nest structure (Kern et al. 1993).

We examined and quantified differences in nests of the Yellow Warbler at two locations where the species breeds in Canada: Churchill, Manitoba, and Elgin, Ontario. Qualitative differences in Yellow Warbler nests were first described by Briskie (1995), who found that nests from northern Manitoba were larger than nests from southern Manitoba. We expand on Briskie's work by bringing Yellow Warbler nests from two widely disparate sites into the laboratory and testing their properties under different environmental conditions. The habitat at our more northern site of Churchill is subarctic, with a mosaic of tundra, willow thickets, stunted spruce (*Picea mariana* and *P. glauca*), and larch (*Larix laricina*) trees. The habitat at our southern site of Elgin is mixed deciduous forest with scattered marshes and waterways. At both locations, Yellow Warblers typically, but not always, place their nests low (<2 m) to the ground in short deciduous shrubs, usually in the crooks of forked branches. Because nests are not placed on the ground and rarely placed near tree trunks, presumably they have little buffer from cold temperatures, rain, and wind. To assess how the different conditions at Churchill and Elgin may favor different nest morphologies, we measured differences between the study sites in three environmental variables: temperature, precipitation, and wind speed. Churchill is colder, drier, and windier than Elgin, and nests from Churchill are larger and typically made of materials that provide good thermal insulation (Briskie 1995). Therefore, we predicted that nests from Churchill should be better suited to cold environments and should lose heat at rates slower than do nests from Elgin. Because Churchill nests are typically constructed with fluffy materials that likely absorb much water, we predicted that they should be poorly suited to wet environments and thus absorb more water and dry more slowly than nests from Elgin. We tested these predictions by examining differences in (1) nest morphology and nest-wall porosity, (2) heat loss, and (3) water absorption and drying rates.

METHODS

STUDY SPECIES

The Yellow Warbler is a small (~10 g) migratory songbird that breeds throughout temperate North America and winters

from Mexico to South America (Lowther et al. 1999). On the basis of plumage and morphology, Browning (1994) recognized 43 subspecies of the Yellow Warbler. He assigned those breeding at Churchill to *D. p. parkesi* and those breeding at Elgin to *D. p. aestiva*. Only females build nests, and away from the northern extremity of the breeding range, including Elgin, females readily renest if early nests are destroyed or depredated. Once a pair successfully fledges young, it typically does not attempt to raise additional broods within that season (Lowther et al. 1999).

NEST COLLECTION

During the breeding seasons of 2008 and 2009, we collected Yellow Warbler nests at the Churchill Northern Studies Centre (58° 40' N, 94° 25' W; elevation 20 m) about 20 km west of Churchill, Manitoba, and from the Queen's University Biological Station (44° 30' N, 76° 19' W; elevation 125 m) near Elgin, Ontario. We searched for Yellow Warbler nests by following females that were carrying nesting materials and by searching appropriate habitat. We monitored all nests found during building and laying so that we could be sure when nest construction and laying were completed. Nearly all active Yellow Warbler nests that we found were included in this study, reducing any potential bias in our selection of nests. Nests were collected immediately after being completed and prior to egg laying, in the early stage of laying, or during early incubation. We excluded nests that fledged nestlings from our analyses because nestlings change the shape of nests considerably (Holcomb and Twiest 1968, Calder 1973; V. G. Rohwer, pers. obs.).

We have observed no differences between Yellow Warbler nests built early in the breeding season and those built later, and female Yellow Warblers appear to build multiple nests with very consistent morphologies (Patrick 2009). Nonetheless, we collected all nests early in the breeding season to control for any unmeasured variation through the breeding season in nest composition or morphology.

CLIMATE DATA

We compiled weather data from Environment Canada's online database (Environment Canada 2010) for Churchill and Ottawa, Ontario. Ottawa is about 100 km northeast of our study site in Elgin, but it is the closest weather station with consistent, long-term data; environmental conditions at Ottawa and Elgin are similar. For each location, we plotted monthly averages (\pm SD) of temperature, precipitation (rain only), and wind speed for May, June, and July. Yellow Warblers do not reach Churchill until June (Briskie 1995, Jehl 2004), so in our analyses of environmental data we do not include the month of May as part of the breeding season at Churchill. We plotted the average values for each month from 1978 to 2009, with minor exceptions; precipitation data for Churchill were missing for 1999–2001, 2008, and 2009, and wind-speed data from both locations are from years 1989–2009.

MORPHOLOGY OF NESTS

We took five measurements from each nest: nest-wall thickness, exterior cup diameter, inner cup diameter, exterior nest depth, and inner cup depth; all measures were taken in the laboratory after the nest was collected. Because nests vary in their shape and size, we followed Kern and van Riper (1984) in measuring nest-wall thickness by taking the average of eight evenly spaced measures of the nest wall. Measures of exterior and inner cup diameters are the average of the maximum and minimum diameters. Exterior nest depth is the distance from the solid bottom of the outside of the nest (material dangling below the solid bottom not included) to the top rim of the nest walls, and cup depth is the distance from the bottom of the nest cup (where eggs are placed) to the top rim of the nest walls. We measured a total of 110 nests, 63 from Churchill and 47 from Elgin.

NEST POROSITY

Under the assumption that the more light penetrates the nest walls, the more porous the nest (Kern and van Riper 1984), we used light penetration to measure nest-wall porosity. In a dark room, we placed the nests with the cup inverted over a light bulb (General Electric #44 incandescent bulb, 2 watts, 6.3 volts). Each nest was photographed five times: one photo of the bottom of the nest (taken from above) and four photos of the nest wall, each separated by 90° of rotation around the circumference of the nest. For all photos, we placed over the nest a cubic box 17 cm on a side and constructed with thin, white paper sides. The box provided a standardized area over which escaping light could be photographed, and it also prevented us from photographing escaping light in multiple photos, which would overestimate nest-wall porosity. All photos were taken with a Nikon D40 digital camera from a tripod with a 50-mm lens and fixed photographic settings (F-stop 2.5, ISO 400, shutter speed 0.2 sec). This technique for estimating nest-wall porosity is similar that described by Kern and van Riper (1984). We standardized photos by ensuring that all sides of the box were of equal distance from the light bulb and by maintaining the camera at a consistent distance of 45 cm from the box.

To calculate the amount of light that passed through the nest walls, we used ImageJ software, version 1.41. Because the brightness of light that passed through the nests varied from a faint glow to a bright beam, we set a threshold for brightness and considered pixels of light above the threshold to have penetrated the nest wall. We set our brightness threshold to one half of the maximum possible brightness emitted from the light bulb. We calculated maximum brightness by photographing our experimental set-up with the light bulb on and covered by the box. We converted each photo to an 8-bit black-and-white image and counted the number of light and dark pixels. We excluded photos of the bottom of the nests because, regardless of location, light penetration through the bottom of every nest was <0.001%; for each nest, counts of light pixels are averaged

from the four photos of the nest's sides. We converted all pixel counts into percentages to account for nests of different sizes and used percentage of light pixels per nest in our analysis of light penetration. All nests included in our analysis of porosity are from 2008 only (Churchill $n = 18$, Elgin $n = 16$).

HEAT LOSS

To estimate how quickly nests from Churchill and Elgin lost heat, we randomly chose 10 nests (five from each location) from our assortment of 40 nests collected in 2008 and brought them into a climate-controlled room (4 °C). We chose 4 °C because at Churchill Yellow Warblers commonly experience this temperature during cold periods, so it should provide a low but biologically realistic temperature for our tests. In each trial, we used four Yellow Warbler eggs filled with 100% silicone caulk (DAP, Canada) to simulate a clutch. All eggs came from nests with incomplete clutches collected at Elgin; no eggs showed signs of development (blood or small embryos) when contents were blown from the eggshell, indicating that they were freshly laid. We measured heat loss from inside the egg by placing the wire tip of an electronic thermometer (Barnant thermocouple thermometer, type T) in one egg. In all 10 trials, we placed the thermometer into the same egg to control for possible differences among silicone-filled eggs. Using a light bulb that fit into the nest cup, we heated both eggs and nest to 37 °C. When the temperature reached 37 °C, we quickly removed the lamp and fitted a cotton ball snugly into the nest cup to prevent all heat from dissipating through the top of the open cup. We used the same cotton ball for each nest to control for any differences in heat loss that resulted from the cotton. The diameter of the inner cup of nests from Churchill and Elgin was similar (Table 1), so the cotton ball fit well in all nests. We allowed eggs to cool to room temperature between trials before heating them again, and all nests were placed in the cold room over night to ensure that they reached room temperature (4 °C) prior to each trial. We took temperature readings every 30 sec for 30 min but restricted our analysis to a 6-min interval between minutes 2 and 8 of each trial,

TABLE 1. Morphological variation in Yellow Warbler nests between Churchill, Manitoba and Elgin, Ontario; nests from Churchill are typically larger than nests from Elgin. Table provides mean values (in mm) \pm SE.

	Churchill, Manitoba	Elgin, Ontario	<i>P</i>
Nest-wall thickness	13.4 \pm 1.7 ($n = 63$)	9.4 \pm 1.9 ($n = 47$)	<0.001
Exterior cup diameter	76.6 \pm 3.8 ($n = 63$)	65.2 \pm 4.4 ($n = 45$)	<0.001
Inner cup diameter	48.3 \pm 2.3 ($n = 63$)	47.9 \pm 3.1 ($n = 45$)	0.4
Inner cup depth	35.1 \pm 3.1 ($n = 63$)	36.2 \pm 3.3 ($n = 46$)	0.1
Exterior nest depth	77.4 \pm 15.5 ($n = 63$)	63.8 \pm 10.8 ($n = 46$)	<0.001

because temperatures often continued to rise for the first minute after the light was removed and because 6 min is a realistic period for a female Yellow Warbler to be off the nest during incubation (V. G. Rohwer, unpubl. data).

WATER ABSORPTION AND NEST-DRYING RATES

To measure differences between nests from Churchill and Elgin in water absorption and drying rates, we submerged nests in water and measured the change in mass over time. We first took the dry weight of each nest, and then submerged the nest in water at room temperature for 2 min and reweighed the saturated nest. Subtracting the nest's dry mass from its wet mass allowed us to quantify the amount of water absorbed. We then placed randomly chosen pairs of nests (one from Churchill and one from Elgin) in a climate-controlled chamber with temperature set to 20 °C and relative humidity set to 35%. We used paired trials to control for the increase in the humidity in the chamber while the nests were drying. For the first 2 hr of the experiment we weighed nests every 15 min, for the following 2 hr, every half hour. If a nest was still not dry, we weighed it 24 hr after the initial time of saturation. We then plotted nest mass on time to calculate the rate of water loss for each nest. For our trials of water absorption and nest drying, we used the same 10 nests that we used in the heat-loss experiment, and all 10 of these nests were used in our analysis of nest-wall porosity.

STATISTICAL ANALYSIS

We used Wilcoxon tests to assess differences between Churchill and Elgin in average temperature, rainfall, and wind speed; no environmental data fit the assumptions of normality. Analyses for Elgin were based on data for May, June, and July, those for Churchill, on data for June and July only. To account for excluding May from the Churchill breeding season, we compared environmental data for each month separately for each location. All data on morphological variation in nests were normally distributed, and we tested for differences by using a two-tailed *t*-test. We tested for differences between locations in nest-wall porosity by using a Wilcoxon test of light-penetration values (before converting them to percent light-penetration values). For our heat-loss and water-absorption trials, we log-transformed all data prior to analysis and used two-tailed *t*-tests to analyze differences between locations. For our drying-rate trials with paired nests, we used our measures of the nests' mass through time to calculate the rate of water loss for each nest and tested for differences in drying rates with a paired *t*-test. We report all results as means \pm SD unless these data are in Table 1.

RESULTS

CLIMATE DATA

Churchill is significantly colder (Churchill, 9.6 °C \pm 3.4; Elgin, 17.5 °C \pm 3.5; $z = -9.3$, $P < 0.001$), windier (Churchill, 17.9 km hr⁻¹ \pm 1.6; Elgin, 12.0 km hr⁻¹ \pm 1.9; $z = 8.4$, $P < 0.001$),

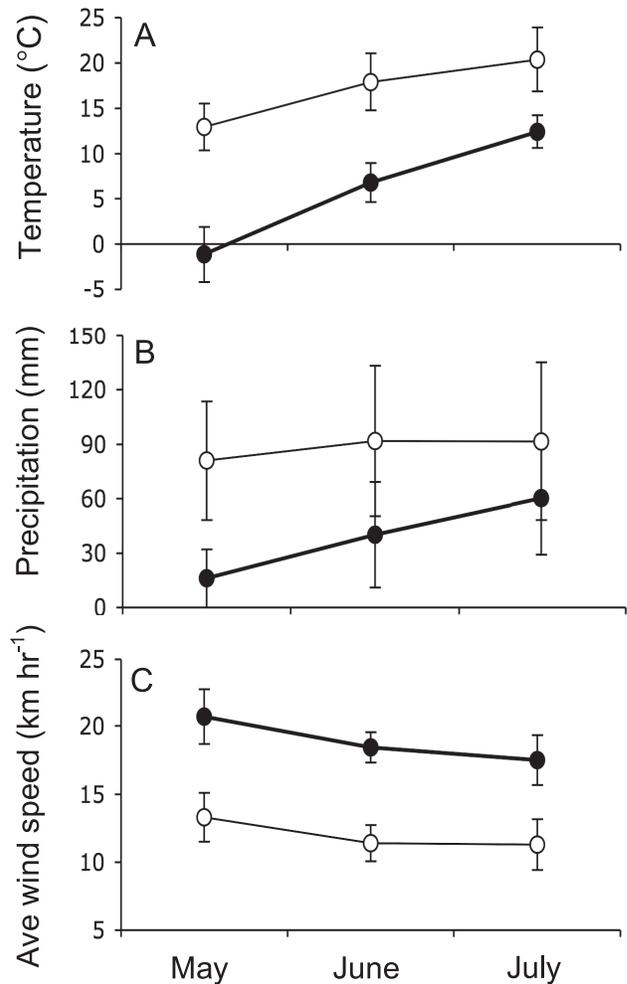


FIGURE 1. (A) Temperature, (B) precipitation (rain only), and (C) wind speed at Churchill, Manitoba (filled circles) and Elgin, Ontario (unfilled circles) during the Yellow Warbler's breeding season. Points represent average daily values \pm SD for May, June, and July for years 1978–2009; see text for exceptions. Note that in May Yellow Warblers are absent at Churchill but present and breeding at Elgin.

and receives less rainfall (Churchill, 50.2 mm \pm 31.5; Elgin, 88.1 mm \pm 39.5; $z = -6.0$, $P < 0.001$) than Elgin during the Yellow Warbler's breeding season (Fig. 1). Excluding environmental data from Churchill for the month of May had no effect on our analysis because differences between the locations in temperature, rainfall, and wind are consistent in all three months, May, June, and July (Fig. 1). At Churchill, the summer of 2009 was cold with average monthly temperatures much lower than normal (May, -6.7 °C; June, 3.7 °C; July, 8.9 °C), but this did not appear to affect nest size (V. G. Rohwer, unpubl. data).

MORPHOLOGICAL DIFFERENCES OF NESTS

We found three differences in morphology between nests from Churchill, Manitoba, and those from Elgin, Ontario (Table 1). Nests from Churchill had thicker walls (Churchill, 13.4 mm;

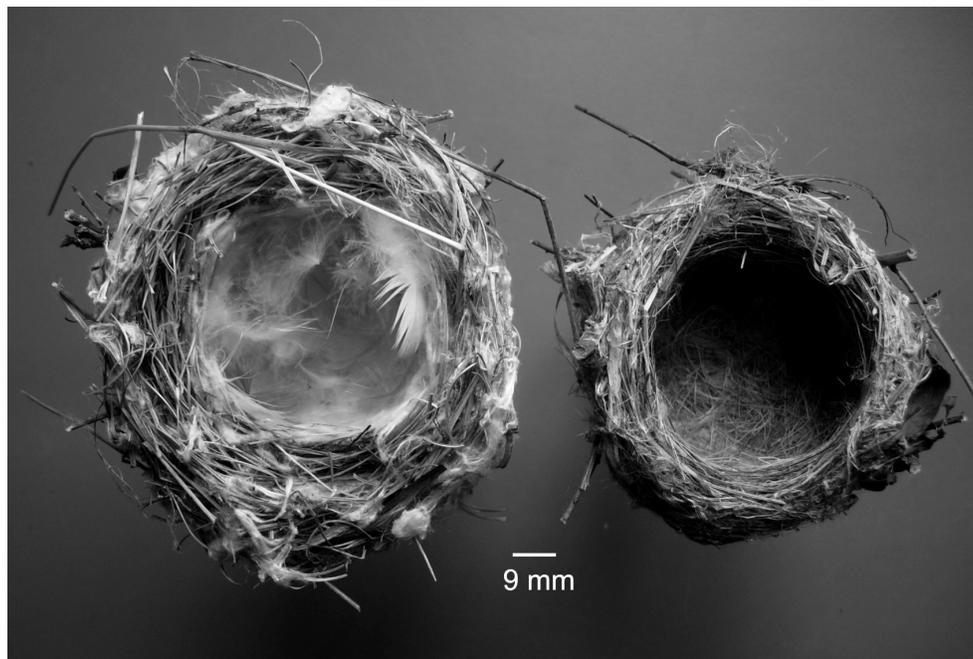


FIGURE 2. Representative Yellow Warbler nests from Churchill, Manitoba (left) and from Elgin, Ontario (right).

Elgin, 9.4 mm; $P < 0.001$), the exterior diameter of their cup was wider (Churchill, 76.6 mm; Elgin, 65.2 mm; $P < 0.001$), and they were deeper (Churchill, 77.4 mm; Elgin, 63.8 mm; $P < 0.001$) than nests from Elgin. The 4-mm difference between locations in nest-wall thickness is not enough to explain the 13.6-mm difference in external depth and the 11.4-mm difference in external diameter, even when nest-wall thickness is doubled (as it must, because external diameter includes measures of two nest walls). Overall, nests from Churchill were larger and much deeper externally than nests from Elgin (Fig. 2). We found no difference between nests from Churchill and Elgin in the diameter (Churchill, 48.3 mm; Elgin, 47.9 mm; $P = 0.4$) or depth (Churchill, 35.1 mm; Elgin, 36.2 mm; $P = 0.1$) of the inner cup (Table 1).

In addition to differences in nest size, we noticed striking differences between the sites in nest materials. At Churchill, Yellow Warblers constructed their nests primarily of dry grasses, feathers, and fluffy plant materials such as the coma of fireweed (*Epilobium* spp.) and willows (*Salix* spp., primarily *S. brachycarpa* or *S. glauca*). At Elgin, in contrast, Yellow Warblers frequently constructed their nests of fine strips of bark from milkweed (*Asclepias* spp.) and dry grasses (C. Crossman, unpubl. data).

NEST POROSITY

Nests from Churchill were less porous (allowed less light to pass through the nest walls) than nests from Elgin (Wilcoxon $z = 3.9$, $P = 0.0001$; Churchill $n = 18$, Elgin $n = 16$; Fig. 3). Churchill nests typically had zero percent light penetration,

while the average percent light penetration for nests from Elgin was $2.0 \pm 3.8\%$ light pixels nest⁻¹.

HEAT LOSS

Nests from Elgin lost heat faster than did nests from Churchill (t -test: $t_8 = -6.0$, $P < 0.001$; $n = 5$ for both locations; Fig. 4). Heat loss was most rapid at the start of each trial and slowed progressively as eggs and nest approached room temperature (Fig. 4).

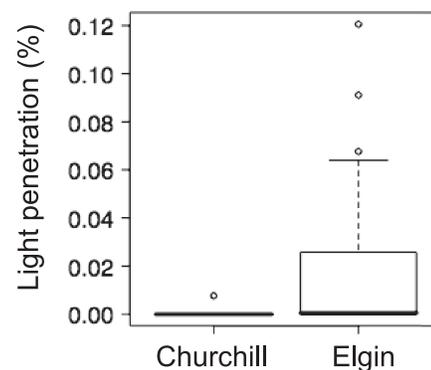


FIGURE 3. Percent light penetration through Yellow Warbler nests from Churchill, Manitoba ($n = 18$) and Elgin, Ontario ($n = 16$). The middle line in box plots represents the median, upper and lower edges of the box represent 75th and 25th percentiles, whiskers show maximum and minimum values, and outliers are marked with dots. On average, nests from Elgin have more porous walls than do nests from Churchill.

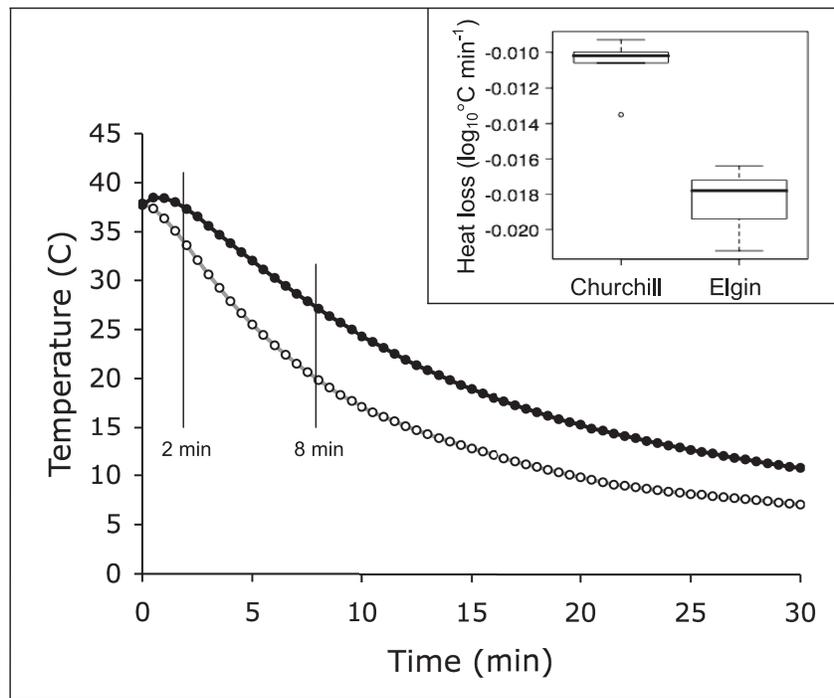


FIGURE 4. The average rate of heat loss ($^{\circ}\text{C min}^{-1}$) from Yellow Warbler nests from Churchill, Manitoba ($n = 5$, filled circles) and from Elgin, Ontario ($n = 5$, unfilled circles). The two vertical lines between minutes 2 and 8 encompass the 6-min interval we used for our heat-loss analysis shown in the insert. Box plots show the median, 75th and 25th percentiles, maximum and minimum values (whiskers), and outliers (dots). Nests from Churchill lost heat at slower rates than did nests from Elgin.

WATER ABSORPTION AND NEST-DRYING RATES

Nests from Churchill absorbed more water (Churchill, $42.0 \text{ g} \pm 12.4$; Elgin, $24.6 \text{ g} \pm 6.6$; t -test: $t_8 = -2.7$, $P = 0.01$; $n = 5$ for both locations; Fig. 5) and dried more slowly (paired t -test: $t_4 = -3.5$, $P = 0.02$, $n = 5, 5$; Fig. 6) than did nests from Elgin. After 4 hr of drying, nests from Churchill were on average

47% dry, those from Elgin were 52% dry. Unfortunately, we did not weigh nests frequently enough to examine how drying rates change with time.

Nests from Churchill were larger and heavier than those from Elgin (Churchill, $9.7 \text{ g} \pm 3.2$; Elgin, $6.3 \text{ g} \pm 1.5$; t -test: $t_8 = -2.4$, $P = 0.02$; $n = 5$ for both locations). To examine the

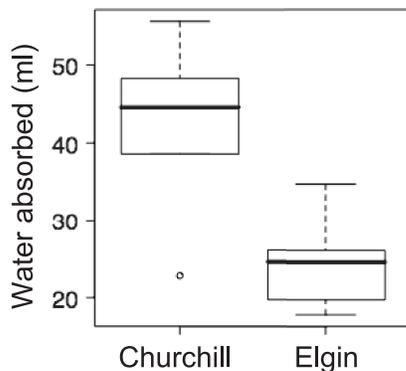


FIGURE 5. The amount of water absorbed by nests from Churchill, Manitoba ($n = 5$), and from Elgin, Ontario ($n = 5$). Plot shows the median, 75th and 25th percentiles, maximum and minimum values (whiskers), and outliers (dots). On average, nests from Churchill absorb more water than do nests from Elgin.

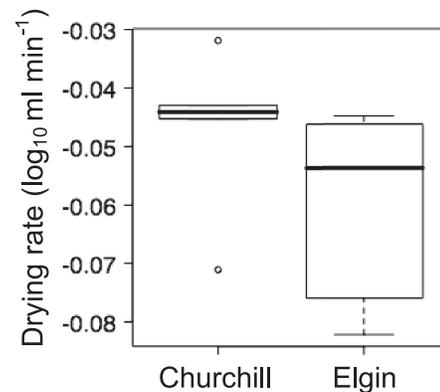


FIGURE 6. Rates of drying of nests from Churchill, Manitoba ($n = 5$), and from Elgin, Ontario ($n = 5$). Box plot shows the median, 75th and 25th percentiles, maximum and minimum values (whiskers), and outliers (dots). On average, nests from Churchill dry at rates slower than do nests from Elgin.

relationship between nest size and water absorption, we combined the nests from each location and regressed the amount of water absorbed on the dry mass of each nest. Larger nests (those with heavier dry masses) absorbed more water than smaller nests ($r^2 = 0.68$, $P = 0.003$, $y = 3.6x + 4.1$).

DISCUSSION

Temperature is perhaps the most important climatic variable that affects the reproductive success of birds. The colder, drier, and windier environment of Churchill likely favors the larger, better insulated nests characteristic of Yellow Warblers breeding there. In contrast, nests from our warmer, wetter, more southerly site of Elgin are smaller, lose heat faster, and also absorb less water. Because Yellow Warblers appear to build nests that are well suited to the environments in which they breed, we suggest, as did Briskie (1995), that different nest morphologies represent adaptations to different environments.

CLIMATE AND VARIATION IN NESTS

In cold environments, such as Churchill, nests that lose heat quickly will likely lead to measurable reductions in the fitness of incubating females, eggs, and nestlings. In several species of birds, incubating females increase their basal metabolic rates (likely to maintain eggs at optimal temperatures) as temperatures decrease (Vleck 1981, Haftorn and Reinertsen 1985). In cold temperatures, females with thin nests likely face a trade-off between the need to incubate and brood young and the expense of self maintenance. Trade-offs in nestling care and self maintenance have been confirmed in at least one species. Female Tree Swallows (*Tachycineta bicolor*) nesting in experimentally heated boxes maintained better body condition, fed their nestlings at higher rates, and their nestlings grew faster (Pérez et al. 2008). Similar studies in nest-building rodents have found correlations between nest size and energy expenditure; rodents that build larger nests use less energy to maintain a warm nest than rodents that built small nests (Pearson 1969, Lynch and Hegmann 1973). These studies suggest that the thick nests built by Yellow Warblers at Churchill help to conserve energy both for the incubating female and nestlings.

At arctic or subarctic sites like Churchill, weather patterns are less predictable, and cold fronts can occur during the middle of the breeding season (Briskie 1995, Jehl 2004). Although these cold fronts are sporadic, they likely select for thick-walled nests. The 2009 breeding season was much colder than average, yet we noticed no difference in nest-wall thickness or nest size and observed only minor differences in nest materials (V. G. Rohwer, unpubl. data). Surprisingly, in 2009 nests did not appear to be constructed with larger quantities of fluffy, insulating materials, but this lack of difference may be an artifact of the availability of materials rather than the female's preference.

Differences between Churchill and Elgin in wind speed and precipitation may further help explain differences in Yellow

Warbler nests. Especially in cold environments, strong winds and precipitation can be costly for breeding birds because both typically reduce egg and nestling temperatures or cause the incubating female to increase her metabolic rate in an effort to compensate for colder nest temperatures. Churchill is windier than Elgin, and nests from Churchill had thicker, less porous nest walls. Strong winds likely favor larger, less porous nests through which airflow is reduced and in which warmer temperatures can be maintained. That Churchill receives less rain than Elgin likely allows Yellow Warblers breeding in Churchill to build nests of fluffy materials that provide good thermal insulation but that also absorb more water and take longer to dry, making them poorly suited to wet environments. However, because incubating females can shield the nest from rain and prevent water from entering the nest cup (V. G. Rohwer, unpubl. video data), we think precipitation may have less of a role in explaining differences in the size and composition of Yellow Warbler nests.

PREDATION AND COWBIRD PARASITISM AND VARIATION IN NESTS

In addition to differences in climate, predation pressure and parasitism from Brown-headed Cowbirds (*Molothrus ater*) may also select for differences between our study sites in nest structure. If nest predators and cowbirds use visual cues to find and locate nests, as some studies suggest (Møller 1990, Eichholz and Koenig 1992, Clotfelter 1998, Mullin and Cooper 1998), then larger nests should be more conspicuous and suffer from rates of predation and parasitism higher than do smaller nests. Predation rates are thought to be higher at lower latitudes (Schemske et al. 2009, McKinnon et al. 2010), a pattern consistent with our study sites (V. G. Rohwer, unpubl. data). Not only do predation rates appear higher at Elgin, but predators are more diverse and abundant; Brown-headed Cowbirds and snakes (especially of the genus *Elaphe*) are absent at Churchill but common at Elgin (Godfrey 1986, Ernst and Barbour 1989). Lower predation rates from fewer nest predators and the absence of cowbirds farther north likely allow Yellow Warblers to build thicker, bulkier, more conspicuous nests. This, however, does not mean that warblers that build large conspicuous nests will not suffer from high predation but that at Churchill predation may be a weaker selective agent than climate on nest morphology.

ECTOPARASITISM AND VARIATION IN NEST MORPHOLOGY

A third possible adaptive explanation for different nest morphologies could be differences between Churchill and Elgin in assemblages of ectoparasites. Comparative studies suggest that ectoparasites are more diverse and abundant at lower latitudes (Schemske et al. 2009). If our two sites differ in this way, and if ectoparasites affect Yellow Warblers, birds breeding at Elgin should use greater quantities of green plants and

aromatic materials that are thought to inhibit ectoparasite growth (Wimberger 1984). However, we have noticed no differences between the locations in the amount of parasite-inhibiting nest materials. We think ectoparasites have far less influence on nest morphology than does climate, but this alternative explanation awaits further study.

NONADAPTIVE EXPLANATIONS OF VARIATION IN NEST MORPHOLOGY

There seem to be two obvious nonadaptive alternative explanations for the differences we found in Yellow Warbler nests. The first is availability of nesting materials. Although nests at these two sites are constructed of different materials, differences in Yellow Warbler nests are unlikely to be caused by differences in access to materials. At Elgin, insulating materials, similar to those found at Churchill, such as the fluff from cattails (*Typha* spp.) and various poplars (*Populus* spp.) are widely available to Yellow Warblers but are used infrequently.

A second nonadaptive alternative is that geographic variation in Yellow Warbler nests is a product of random chance rather than adaptation. This seems unlikely for three reasons. First, differences in nest morphology correspond well with multiple environmental variables that are known to challenge nesting birds. Second, similar patterns of geographic variation in nests have been suggested for several European (Palmgren and Palmgren 1939) and North American birds (C. Crossman, unpubl. data). Third, patterns of geographic variation in the nests of deer mice (*Peromyscus* spp.; King et al. 1964) and of the Southern Flying Squirrel (*Glaucomys volans*; Muul 1974), are similar. In all cases, birds and rodents build thicker, larger nests in colder (usually more northern) locations than do conspecific individuals or closely related species breeding in warmer regions. These parallel similarities in nest morphology within a diversity of birds and rodents suggest that building larger nests in colder regions is an adaptation rather than a chance event.

Yellow Warblers breeding in colder, harsher environments face a much greater challenge in maintaining a warm nest and in meeting their daily energetic requirements. Cold nest temperatures can lower fitness by reducing the hatchability of eggs, increasing the incubating female's metabolic rate, or reducing nestlings' growth rates. Likely in response to the challenges of subarctic breeding, at Churchill Yellow Warblers build large, well-insulated nests that help maintain warm nest temperatures in a cold, northern climate. Given that Yellow Warblers appear to build nests that are well suited to local conditions, how do Yellow Warbler nests from the southern extreme of the breeding range compare with mid-latitude and northern nests? Do females preferentially choose nesting materials that match the challenges of local conditions? These questions are important because, among the North American wood warblers, the Yellow Warbler has one of the broadest breeding ranges (Lowther et al. 1999), and its ability to change its nest morphology and

composition in relation to its environment likely permits it to breed in such a diversity of habitats.

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