

# Effect of nest characteristics on thermal properties, clutch size, and reproductive performance for an open-cup nesting songbird

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## ABSTRACT

Maintaining avian eggs and young at optimum temperatures for development can increase hatching success and nestling condition, but this maintenance requires parental energetic demands. Bird nests, which often provide a structure to safely hold the eggs and nestlings and protect them from predators, can additionally be designed to help maintain eggs' optimum temperatures by minimising heat loss, especially in climates where eggs cool rapidly when unattended. We collected and measured Prairie Warbler (*Setophaga discolor*) nests in western Massachusetts, U.S. in 2009 and conducted a climate-controlled, nest-cooling experiment to determine how nest characteristics affect thermal properties for small, open-cup nesting birds. We then assessed if nests with better insulation properties resulted in any fitness benefits, and also tested if nest structural characteristics affected birds' fitness. We found that nest characteristics influenced their thermal properties, with thicker, heavier, and larger nests having slower cooling rates and higher predicted equilibrium egg temperatures. Both nest cup depth and clutch size significantly declined over the breeding season, and we observed a trend, although non-significant, that nests with shallower cups had smaller clutches. Contrary to studies on cavity-nesting birds, we found no significant effects of nest thermal properties or nest structure on hatching and fledging success, nestling condition, brood parasitism, or nest survival. Prairie Warblers in our study site may already be adapted to build nests within a range that maximises their fitness. Furthermore, studies have shown that open-cup nests of other species are relatively thicker and more insulated in colder environments at higher latitudes than our study. Instead of building nests to solely minimise heat loss, open-cup nesting birds in temperate climates may also be driven by opposing selection pressures when building their nests, such as to prevent nestlings from overheating during hot days.

**Keywords:** heat loss, insulation, nest design, nest structure, Prairie Warbler

## 1. INTRODUCTION

Incubation by birds, like other stages in avian life history, has energetic and fitness tradeoffs (Stearns, 1992; Conway and Martin, 2000; Nord and Williams, 2015). The costs and benefits of incubation span multiple generations; costs for the incubating parents, such as investing energy and reducing foraging time to maintain eggs at an optimum temperature, can subsequently lead to benefits for the offspring in the nest, such as better nestling condition and immune response, and potentially increased survival (Reid *et al.*, 2000; Pérez *et al.*, 2008; Ardia *et al.*, 2010; Hepp and Kenamer, 2012). To minimise the parental energetic costs and to maximise fitness benefits, nests are often constructed to reduce heat loss (Deeming and Mainwaring, 2015), especially when incubation is intermittent in relatively cooler climates (Calder, 1971; Lombardo *et al.*, 1995; Mainwaring *et al.*, 2012). Embryo

development for birds is optimal at high temperatures (36.5–38.5 °C), and development is suspended below cold temperatures (24–26 °C) (Webb, 1987; DuRant *et al.*, 2013). Ambient temperatures in cold climates, and even in temperate climates, are often well below optimal for embryo development (Haftorn, 1988; Weathers and Sullivan, 1989). Therefore, in these climates, a well-insulated nest is important to reduce heat loss through the nest walls and maintain egg temperatures when a parent is on the nest (Heenan, 2013; Deeming and Mainwaring, 2015). Moreover, during off-bouts, nest insulation may be important in reducing egg-cooling rates thereby minimising the time and energetic demands needed to re-warm the eggs (Vleck, 1981), although convective heat loss through the nest opening may also be influential during off-bouts, especially in open-cup nests during windy conditions (Hilton *et al.*, 2004; Heenan and Seymour, 2012).

Nest thermal properties can be influenced by nest structural characteristics, including size, thickness, mass, and cup volume (Whittow and Berger, 1977; Windsor *et al.*, 2013). For many species, nests that are thicker, heavier, and constructed with more insulating materials are better at reducing heat loss (Møller, 1991; Hilton *et al.*, 2004; Szentirmai *et al.*, 2005; Pinowski *et al.*, 2006). For instance, Tree Swallow (*Tachycineta bicolor*) cavity nests that are relatively larger, deeper, and have more insulating feathers are better at maintaining egg temperatures within the nest (Windsor *et al.*, 2013). However, interspecific variation exists and nest thickness and size does not always affect nest insulation. For example, Kern (1984) observed that wall thickness (not including floor thickness) did not affect the thermal conductance of open-cup nests in certain subspecies of White-crowned Sparrows (*Zonotrichia leucophrys*).

In addition to examining nest characteristics and their effect on insulation, some studies have examined if nest characteristics and thermal properties subsequently affect various aspects of birds' reproductive performance (e.g. clutch size, hatching and fledging success, number of young, nestling condition; Wiebe, 2001; Álvarez and Barba, 2011; Álvarez *et al.*, 2013). In temperate climates in Michigan, Tree Swallow nests that had insulating feathers experimentally removed from the nest box produced relatively fewer fledglings of smaller size compared to control nests with feathers (Lombardo *et al.*, 1995). In Spain, Álvarez and Barba (2008) observed hatching and fledging success in Great Tits (*Parus major*) increased with nest size, and larger nest cups had larger clutch sizes. In Poland, Gładalski *et al.* (2016) found that Blue Tit (*Cyanistes caeruleus*) nests with heavier nest linings had higher hatching success, while heavier Great Tit nests had higher fledging success. In natural nest cavities, Acorn Woodpeckers (*Melanerpes formicivorus*) in California preferred nest cavities with warmer microclimates, and these cavities fledged relatively higher numbers of young (Hooge *et al.*, 1999). Overall, many studies on cavity-nesting birds in temperate climates have observed that larger and more insulated nests increase some aspect of birds' reproductive performance.

Despite recent research on cavity-nesting birds, there are few studies on the effect of nest insulation on reproductive performance for open-cup nesting birds (Mainwaring *et al.*, 2014a; Deeming and Mainwaring, 2015). This is a considerable knowledge gap, since selection pressures on open-cup nests are inherently different than cavity nests and this could influence the design of nests and their effect on birds' fitness (Mainwaring *et al.*, 2014b). For instance, compared to cavity nests, open-cup nests are more exposed to the thermal environment and more subject to heat loss (Lamprecht and Schmolz, 2004). As a result, nest characteristics may influence heat loss and birds' fitness differently in open-cup nests. Also, open-cup nests often have higher predation rates than cavity nests (Martin and Li, 1992), so in addition to being well-

insulated, open-cup nests need to be compact and well-concealed (Nolan, 1978; Møller, 1990; Antonov, 2004). Moreover, unlike nests in natural cavities or nest boxes that provide structural support, open-cup nests are often built on branches or grasses, and must be well-constructed to support eggs and nestlings (Coon *et al.*, 1981; Heenan and Seymour, 2011; Biddle *et al.*, 2015) while also providing adequate space for nestlings (Heenan, 2013; Møller *et al.*, 2014). Open-cup nests can be more insulated due to the combination of being larger, heavier, and thicker (Crossman *et al.*, 2011), yet thicker nests may also have less space inside the nest for the eggs and young (Suárez *et al.*, 2005). Nest cup space likely evolved in a dynamic interplay with clutch size, with the possibility that smaller nests might constrain clutch size (Álvarez and Barba, 2008; Møller *et al.*, 2014). In addition, a lack of cup space can result in nestlings being accidentally pushed out of nests by siblings (Slagsvold, 1982, 1989a). Alternatively, nestlings in cups with a narrow diameter can be pushed downward in the nest and become smothered by their siblings or have less of an opportunity of being fed (Slagsvold, 1982, 1989b). Because of more complex selection pressures, the structure of open-cup nests may not have evolved to maximise thermal benefits due to tradeoffs with other factors.

To address knowledge gaps in our understanding of relationships between nest characteristics, thermal properties, and reproductive performance in open-cup nesting birds, we conducted a study on Prairie Warblers (*Setophaga discolor*), which are open-cup nesting songbirds. As a starting point for our study, our first objective was to assess correlations among nest structural characteristics to determine how nest size, thickness, mass, and space inside Prairie Warbler nests are integrated together. Because the effect of nest structural characteristics on nest insulation can vary among species and nest type (Kern, 1984; Windsor *et al.*, 2013), our second objective was to determine which characteristics of Prairie Warbler nests influence their thermal properties. To accomplish this, we conducted climate-controlled, nest-cooling experiments to measure nest thermal properties. Lastly, because open-cup nests are subject to multiple and different selection pressures compared to cavity nests, our final objective was to assess if nest characteristics and thermal properties influence clutch size, hatching and fledging success, brood parasitism, nest survival, and nestling condition for an open-cup nesting bird.

## 2. METHODS

### 2.1 Study site and nest measurements

We conducted our research in the Montague Plains Wildlife Management Area, an approximately 600 ha Pitch Pine-Scrub Oak (*Pinus rigida-Quercus ilicifolia*) barren located in western Massachusetts, northeastern

U.S. (42°34'N, 72°31'W; see maps in Akresh *et al.*, 2015; Akresh and King, 2016). A weather station located at the study site recorded temperature and precipitation during the breeding season from May to July 2009. The average daily mean temperature was 14.2 °C in May, 17.6 °C in June, and 19.3 °C in July, and the total amount of precipitation was 11.7 cm in May, 16.3 cm in June, and 24.3 cm in July. Prairie Warblers in the study site occupied habitat with dense understory vegetation and a low percentage of tree canopy cover, nesting primarily in woody shrubs and saplings (e.g. *Quercus* sp. and *Spiraea* sp.) that were 0.5–3 m in height (King *et al.*, 2011; Akresh, 2012).

From May to July 2009, nests were located by observing the behaviour of parents and conducting systematic searches in territories (Martin and Geupel, 1993). Once located, we monitored nests every 2–3 days until nestlings fledged or the contents of the nest disappeared (Martin and Geupel, 1993). We determined nest initiation dates (first-egg laid) by either finding nests during the building stage, or estimating first-egg dates based on hatch dates (Nolan, 1978). We were able to confidently age young nestlings (0–2 days old) based on their size, amount of down, presence of feather sheaths, and behaviour (Nolan, 1978). When nestlings were eight days old, we banded nestlings, measured their tarsus length ( $\pm 0.1$  mm) and weighed them with a digital scale ( $\pm 0.1$  g). For nests that were found empty on day 8 (nestlings typically fledge when 9–10 days old, but can fledge on day 8; Nolan, 1978), we determined nest failure by systematically searching for fledglings in the territory during visits every 2–3 days (Akresh *et al.*, 2015).

After young fledged or nests failed, we measured nests while still attached to nest substrates. We determined nest visibility by positioning ourselves 1 m away from the nest with our eyes at nest height, and visually determining the percentage of the nest that was visible (Martin and Roper, 1988). We did this in each cardinal direction, and then also looking down from 1 m above the nest. We then averaged these five percentages as our measure of nest visibility. By placing a small ruler horizontally on the top of nests in the north–south direction, we measured ( $\pm 1$  mm) the outer diameter. We did this measurement again along the east–west direction, and averaged the two measurements to obtain the average nest diameter. In a similar fashion, we measured the inner cup diameter along north–south and east–west directions, and averaged these two values to obtain the average inner cup diameter. By noting the outer edge and inner edge of the nest walls on the ruler, we also obtained the wall thickness on four sides of the nest, and averaged these to obtain the average wall thickness.

We then placed the ruler vertically on the side of the nest, and measured the height of the nest ( $\pm 1$  mm). Lastly, we placed the ruler vertically in the middle of the nest cup, and measured the cup depth ( $\pm 1$  mm). We obtained the floor thickness by subtracting the nest height from the cup

depth. An estimate of cup volume was calculated as half of an ellipsoid, using the equation  $\text{volume} = (4/3\pi abc)/2$ , where  $a$  is the cup depth,  $b$  is the north–south cup radius (the measured north–south cup diameter/2), and  $c$  is the east–west cup radius (Lombardo, 1994). We then carefully removed nests from the attached branches, placed them individually in partially open plastic bags and allowed nests to dry for 4–5 months (depending on when the nest was collected). Lastly, we measured the dry mass of all the nests on the same day (during a time span of 3 h) using a digital scale ( $\pm 0.1$  g).

We excluded nests damaged by predators (*i.e.* a hole in bottom or side of the nest;  $n = \sim 5$ ) or nestlings (*i.e.* walls frayed and torn;  $n = 2$ ). We were unable to measure or collect some predated nests that were deconstructed and the nest material quickly moved to a new nest by the female nest builder. This resulted in fewer predated nests measured and collected compared to the overall sample of nests ( $n = 90$ ) located during the study in 2009 (Akresh, 2012). Because we did not record nest measurements during incubation, we note that nests with nestlings could have stretched, so the presence of nestlings could have affected our nest measurements (Watt and Dimberio, 1990; Palomino *et al.*, 1998; Powell and Rangen, 2000). However, the presence of nestlings likely only affected certain nest characteristics (see Section 2.3), and we therefore believe that most of our results (with noted exceptions) were not affected by the timing of our nest measurements (Palomino *et al.*, 1998).

## 2.2 Cooling trials

We measured the thermal properties of dried nests in a climate-controlled room maintained at 15 °C, which is similar to temperatures that often occur on spring mornings at our study site. Each nest was held by three vertical plastic rods in a custom-built apparatus, such that the nest was held upright as if in the fork of a branch and was surrounded by ambient air. In each nest, we placed four 13.1 mm wide and 17.9 mm long plastic eggs in the nest cup, which mimics the average clutch size and egg size in Prairie Warblers (Nolan, 1978). Each egg was filled with wire pulling lubricant (Clear Glide, Ideal Industries, Sycamore, IL, U.S.) that mimics the thermal properties of albumen (Ardia, D., unpublished data). The eggs were wrapped in a hot, dry rice-filled cloth that heated them to 38.5–39.8 °C just before each trial. The eggs were then placed in the nest within 1 min of the start of each cooling trial. Cooling rates were measured using a 36 g PFA-insulated type-K thermocouple (Omega, Stamford, CT) inserted into the centre of one egg. The thermocouple was connected to a Hobo U12-14 (Onset Computer, Bourne, MA), that recorded temperature (°C) every second. We covered the top of nests with 2.1 cm thick Styrofoam insulation to minimise heat loss and recorded changes in temperature for 30 min. Each nest was cooled twice



to measure repeatability (Lessells and Boag, 1987). Nests were allowed to return to ambient temperatures before being used in subsequent trials.

### 2.3 Statistical analyses

We estimated cooling rates using an iterative sums-of-squares minimisation approach, using the equations of Voss and Hainsworth (2001) to build a program in Mathematica Version 7.0 (Wolfram Research, Inc., 2008). Before running cooling rate analyses, we first removed any data spikes (temperature data irregularities due to the thermocouple) and smoothed data files using local regression (LOESS). We then calculated the thermal properties  $k_2$  and  $T_{eq}$ .  $k_2$  is the second order cooling constant and measures the cooling rate of the nest/egg thermal mass against the thermal gradient of 15 °C (Windsor *et al.*, 2013), while  $T_{eq}$  is the equilibrium temperature estimated after 60 min of predicted cooling based on the rate of cooling (Voss and Hainsworth, 2001). Cooling trials were repeatable for  $k_2$  ( $P < 0.001$ ;  $R^2 = 0.87$ ) and  $T_{eq}$  ( $P < 0.001$ ;  $R^2 = 0.90$ ).

We assessed relationships between nest characteristics by conducting Pearson correlations for every pair of nest characteristics. We note that nestlings in nests may have potentially influenced our measurements of certain nest structural characteristics; examining this with simple linear models, nests with hatched nestlings ( $n=43$ ) compared to nests that failed before hatching ( $n=17$ ) did have wider cup diameters (difference in means, 5.2 mm;  $T=3.2$ ,  $P=0.002$ ), more cup volume (difference in means, 9.6 cm<sup>3</sup>;  $T=2.9$ ,  $P=0.006$ ), and slightly thinner nest walls (difference in means, 1.8 mm;  $T=-2.3$ ,  $P=0.03$ ), but nest height, cup depth, floor thickness, nest diameter, and nest mass did not differ in nests with and without nestlings ( $P>0.1$ ). Unfortunately, we cannot rule out the possibility that the measured nests with nestlings were just built differently than the measured nests without nestlings, because we did not measure individual nests before and after hatching. Still, given the above findings, we conducted an additional multiple linear regression analysis to examine the relationship between cup diameter

and wall thickness, taking into account that nestlings may have affected nest cup diameters. In this analysis, cup diameter was the response variable, and the predictor variables were wall thickness, whether or not there were nestlings in the nest, and an interaction term between these two variables. We used the program R version 3.2.1 (R Core Team, 2015) for all statistical analyses unless noted otherwise. For single-variable, fixed-effect models, degrees of freedom were  $n-2$ .

To examine nest thermal properties as a function of nest characteristics, we first conducted a principal component analysis (PCA) of the nest characteristics. We decided to present the first three principal components because these respective eigenvalues were above one and explained most of the variation in the data. However, because the third PCA component (PC3) was largely just a measure of cup depth (Table 1), in all our analyses we chose to examine cup depth rather than PC3 to conduct more straightforward analyses. We conducted six separate univariate linear regressions, with PC1, PC2, or cup depth as the predictor variable, and one of the nest thermal indexes,  $k_2$  or  $T_{eq}$ , as the response variable. Notably, PC1,  $k_2$ , and  $T_{eq}$  did not differ in nests with hatched nestlings compared to nests that failed before hatching ( $P>0.1$ ), although PC2 values were greater in nests with nestlings ( $T=3.5$ ,  $P<0.001$ ). The lack of an effect of nestling presence on  $k_2$  and  $T_{eq}$  in our Prairie Warbler nests is also consistent with findings in Cruz *et al.* (2016), who found that thermal properties in the same individual Great Tit nests measured during incubation and again after fledging were significantly correlated.

We used MARK version 8.0, run through the R package 'RMark' (White and Burnham, 1999; Dinsmore *et al.*, 2002; Laake, 2013) to determine if daily nest survival was affected by nest thermal properties. We examined single-variable models with  $k_2$  or  $T_{eq}$  as the predictor variable. Because more insulated nests could also be larger and more visible to predators, we also tested if nest survival was affected by nest size (PC1; see Results). We excluded abandoned nests from the analyses because we were interested in examining effects on daily nest predation rates. For successful nests, we included observation days until the last active nest check (the last day nestlings were

**Table 1** Summary statistics (mean  $\pm$  SD) and principal component analysis loadings of eight nest characteristics from 60 Prairie Warbler nests

	Mean $\pm$ SD	PC1	PC2	PC3
Nest height (mm)	63 $\pm$ 12	-0.858 <sup>a</sup>	-0.311	0.154
Cup depth (mm)	33 $\pm$ 5	-0.262	0.424	0.812 <sup>a</sup>
Floor thickness (mm)	30 $\pm$ 12	-0.77 <sup>a</sup>	-0.513 <sup>a</sup>	-0.207
Average wall thickness (mm)	10 $\pm$ 3	-0.577 <sup>a</sup>	-0.448	0.364
Average cup diameter (mm)	45 $\pm$ 6	-0.311	0.854 <sup>a</sup>	-0.401
Average nest diameter (mm)	65 $\pm$ 7	-0.766 <sup>a</sup>	0.391	-0.054
Nest cup volume index (cm <sup>3</sup> )	36.1 $\pm$ 12.4	-0.403	0.902 <sup>a</sup>	0.08
Nest mass (g)	5.6 $\pm$ 1.5	-0.775 <sup>a</sup>	-0.155	-0.337

<sup>a</sup>High loadings ( $> |0.5|$ ) for each component.

seen in the nest; Dinsmore *et al.*, 2002). We determined if predictor variables significantly affected nest survival by examining the 95% confidence intervals of the parameter estimates. The effect was deemed insignificant if the 95% confidence interval included 0. Like nest predators, Brown-headed Cowbirds (*Molothrus ater*) might parasitise Prairie Warbler nests that are larger and more insulated. We tested this using generalised linear models (GLM) fit to a binomial distribution, with nest size (PC1) or nest insulation ( $k_2$  or  $T_{eq}$ ) as the predictor variable and whether or not the nest contained a cowbird egg as the binary response variable. Using a simple linear model, we also examined if nest size (PC1) affected nest visibility.

In addition to providing insulation and concealment from predators, nests must also provide enough space for eggs and young (Slagsvold, 1982; Møller *et al.*, 2014). Clutch sizes often decrease during a breeding season for temperate passerines (Nolan, 1978). To test if clutch size also decreases temporally for our study population, we conducted a GLM with all nests found in 2009 with a known clutch size and first-egg date. Because 96% of nests examined had three or four eggs, we converted the clutch size data into a binomial variable: nests having two or three eggs *versus* nests with four eggs. We then fit this clutch size response variable to a binomial distribution, and used first-egg date as the predictor variable. Next, using simple linear models, we tested if space inside the nest (PC2) or cup depth followed a similar pattern and decreased temporally with a predictor of first-egg date. Finally, in a more direct comparison using a GLM fit to a binomial distribution, we examined if clutch size was directly a function of space inside the nest (PC2 or cup depth as the predictor). For all analyses with clutch size, we excluded nests with Brown-headed Cowbird eggs/nestlings. We were also interested in comparing any temporal changes in nest cup space with any temporal changes in nest size or insulation, to assess if birds built larger (PC1) or more insulated ( $k_2$  or  $T_{eq}$ ) nests earlier in the season when temperatures in the study site were colder (Britt and Deeming, 2011). We tested this using linear models with PC1,  $k_2$ , or  $T_{eq}$  as the response variable, and first-egg date as the predictor variable.

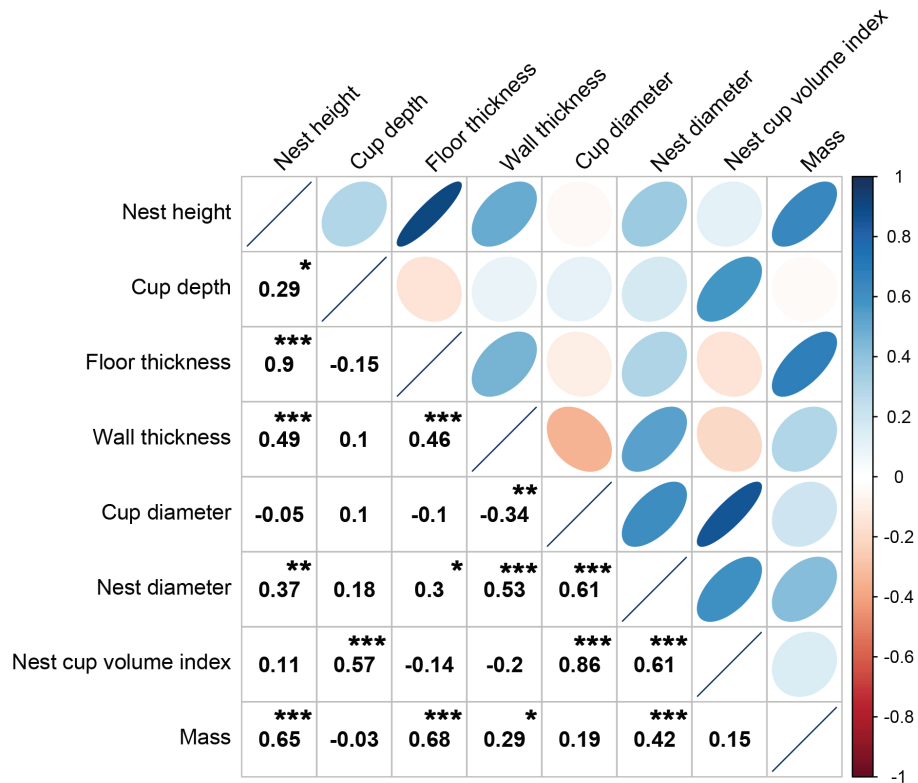
For nests that fledged at least one young Prairie Warbler, we examined hatching and fledging success as a function of  $k_2$  or  $T_{eq}$ . Nests had a range of 0–2 eggs that did not produce fledglings out of a total of 2–4 eggs, and we fit the proportional response data (number of fledglings/number of eggs) to a binomial distribution (Crawley, 2007). In this analysis, we chose to combine hatching success (probability of an egg hatching) and fledging success (probability of the nestling fledging), due to small sample sizes of both eggs that failed to hatch and nestlings that failed to fledge. We only included nests with a known clutch size and number of fledged young, and excluded nests with cowbird eggs. Using a similar analysis, we also tested hypotheses that nest size (PC1), cup space (PC2) or cup depth affected hatching and fledging success. In the analysis with cup depth, one nest was a highly influential outlier, and as a result we chose to discard this nest in that analysis.

We conducted linear mixed models using the ‘nlme’ package (Pinheiro *et al.*, 2015) to determine if nest thermal properties affected nestling condition, and also tested the hypothesis that nest structural characteristics influenced nestling condition. We calculated a size-corrected nestling body condition index by taking the residuals from a linear relationship of tarsus length regressed over mass ( $r=0.43$ ,  $P<0.001$ ). We then examined  $k_2$ ,  $T_{eq}$ , PC1, PC2, or cup depth as the main predictor variable, and separately tested their effect on nestling body condition. In each of these five separate models, we assigned individual nestlings as our sample unit, and accounted for variation among nests by including a fixed effect of brood size and a random effect of individual nest. We also included fixed-effect covariates of date and time of measurement in the models. We did not include nests with cowbird nestlings in our analysis. We presented results from models including the random effect of individual nest, but we note that we found very similar results testing simpler, fixed-effects models without the random effect.

### 3. RESULTS

We measured and conducted thermal experiments with 60 Prairie Warbler nests. Certain nest characteristics were highly correlated with each other (Figure 1). Nest size measurements were highly correlated with nest thickness measurements; nests greater in height had thicker floors ( $T=15.9$ ,  $P<0.001$ ) and nests with wider diameters had thicker walls ( $T=4.8$ ,  $P<0.001$ ). Heavier nests were greater in height ( $T=6.4$ ,  $P<0.001$ ) and wider in diameter ( $T=3.6$ ,  $P<0.001$ ), and had thicker floors ( $T=7.1$ ,  $P<0.001$ ) and walls ( $T=2.4$ ,  $P=0.02$ ). Nests with wider diameters also had wider cup diameters ( $T=5.9$ ,  $P<0.001$ ) and more volume inside the nest cup ( $T=5.8$ ,  $P<0.001$ ). Interestingly, nests with thicker walls also had smaller cup diameters ( $T=-2.8$ ,  $P=0.007$ ). However, in a more detailed analysis, we found a significant interaction between the presence of nestlings in the nest and wall thickness in their effect on cup diameter ( $T=-2.1$ ,  $P=0.04$ ). Partitioning the data into two separate groups and conducting simple linear models, nests that contained nestlings had a significant, negative relationship between wall thickness and cup diameter ( $n=43$ ,  $T=-2.8$ ,  $P=0.008$ ,  $R^2=0.16$ ), but this relationship was not significant for nests without nestlings ( $n=17$ ,  $T=0.1$ ,  $P=0.89$ ).

The first three PCs explained 85% of the variation in nest characteristics (PC1: 40%, PC2: 31%, and PC3: 14%). PC1 (hereafter nest size) was negatively related to nest size, thickness and mass, with high negative loadings for nest height, nest diameter, wall thickness, floor thickness, and mass (Table 1). PC2 (hereafter cup space) reflected space inside the nest cup, with high positive loadings for cup diameter and cup volume index. PC3 was also a measure of space inside the nest cup, with high positive loadings for cup depth.



**Figure 1** A Pearson correlation matrix of eight nest characteristics from 60 Prairie Warbler nests. Correlation coefficients ( $r$ ) appear on the bottom triangle, and a graphical display of these values appears on the top triangle. The number of asterisks denote the significance of the correlation: \* denotes  $0.05 < P < 0.01$ , \*\* denotes  $0.01 < P < 0.001$ , \*\*\* denotes  $P < 0.001$ . Blue-tinted ellipses represent positive correlations, while red-tinted ellipses represent negative correlations. The boldness of the colour and shape of the ellipse represent the strength of the relationship between variables, with stronger correlations having bolder colours and narrower ellipses.

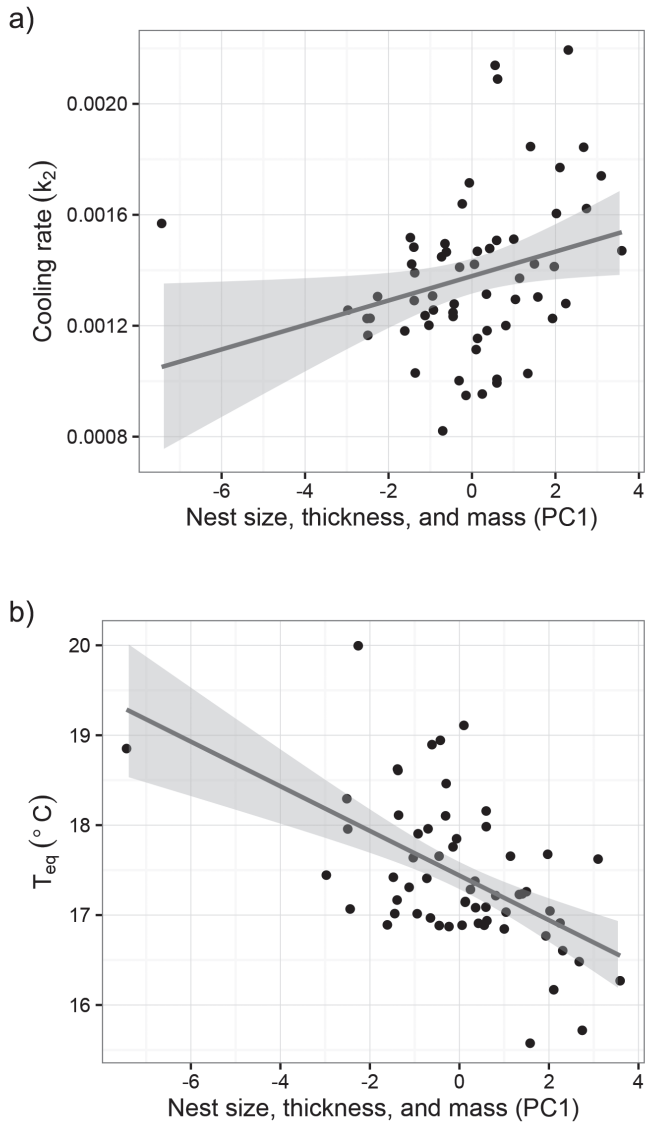
Larger and thicker nests (lower PC1 values) had significantly slower cooling rates ( $k_2$ :  $T=2.2$ ,  $P=0.03$ ,  $R^2=0.08$ ; Figure 2a); this relationship was more significant ( $T=3.2$ ,  $P=0.002$ ,  $R^2=0.15$ ) excluding an influential outlier in the analysis (a very large nest for which  $PC1=-7.44$ ).  $T_{eq}$ , the predicted equilibrium temperature of the eggs, was significantly higher for larger and thicker nests (lower PC1 values:  $T=-4.9$ ,  $P<0.001$ ,  $R^2=0.30$ ; Figure 2b). There were no significant relationships between  $k_2$  and either nest cup space (PC2:  $T=-0.2$ ,  $P=0.80$ ) or cup depth ( $T=-0.3$ ,  $P=0.76$ ), or between  $T_{eq}$  and nest cup space ( $T=0.3$ ,  $P=0.79$ ) or cup depth ( $T=1.6$ ,  $P=0.12$ ).

Of the 60 nests measured, young fledged from 30 (50%), 21 (35%) were predated, and 9 (15%) were abandoned. Excluding abandoned nests and for a total of 757 observation days,  $k_2$ ,  $T_{eq}$  and nest size (PC1) did not have a significant effect on daily nest survival (95% CI of  $\beta$  for  $k_2=-1519$  to 1297; 95% CI of  $\beta$  for  $T_{eq}=-0.704$  to 0.393; 95% CI of  $\beta$  for  $PC1=-0.067$  to 0.484). Of the 60 nests, 11 (18%) were parasitised by Brown-headed Cowbirds. There were no significant relationships between whether or not a nest was parasitised and  $k_2$  ( $Z=-0.8$ ,  $P=0.43$ ),  $T_{eq}$  ( $Z=0.5$ ,  $P=0.60$ ), or nest size (PC1:  $Z=0.5$ ,  $P=0.62$ ). Moreover, larger and thicker nests (PC1) were not more visible ( $T=-0.8$ ,  $P=0.41$ ).

For nests where young fledged, we found no relationship between hatching and fledging success and  $k_2$  ( $n=24$ ,  $Z=-0.1$ ,  $P=0.94$ ) or  $T_{eq}$  ( $Z=-0.9$ ,  $P=0.39$ ). Additionally, there was no relationship between hatching and fledging success and either nest size (PC1:  $Z=0.5$ ,  $P=0.62$ ) or cup depth ( $Z=-1.6$ ,  $P=0.11$ ), although there was a non-significant trend in which nests with less cup space (PC2) had a higher proportion of eggs that produced fledged young ( $Z=-1.7$ ,  $P=0.08$ ).

Nests where egg laying began earlier in the season had a higher probability of having a larger (four egg) clutch ( $n=55$ ,  $Z=-3.7$ ,  $P<0.001$ ; Figure 3a). Interestingly, cup depth also had a significant relationship with first-egg date, with deeper cups earlier in the season ( $n=58$ ,  $T=-3.8$ ,  $P<0.001$ ,  $R^2=0.20$ ; Figure 3b). Also, there was a non-significant trend for a direct effect: nests with deeper cups had a slightly higher probability to have a larger (four egg) clutch ( $n=41$ ,  $Z=1.7$ ,  $P=0.086$ ). We found no relationship between cup space (PC2) and first-egg date ( $T=-0.4$ ,  $P=0.69$ ), and no direct effect of cup space (PC2) on clutch size ( $Z=1.1$ ,  $P=0.27$ ). Additionally, nests with earlier first egg-dates were not larger and thicker (PC1:  $n=58$ ,  $T=0.7$ ,  $P=0.47$ ) and did not have lower  $k_2$  values ( $T=-0.2$ ,  $P=0.84$ ) or higher  $T_{eq}$  values ( $T=-0.2$ ,  $P=0.81$ ).

We measured 68 nestlings from 23 successful nests. Taking brood size, date, and time of measurement into account, we

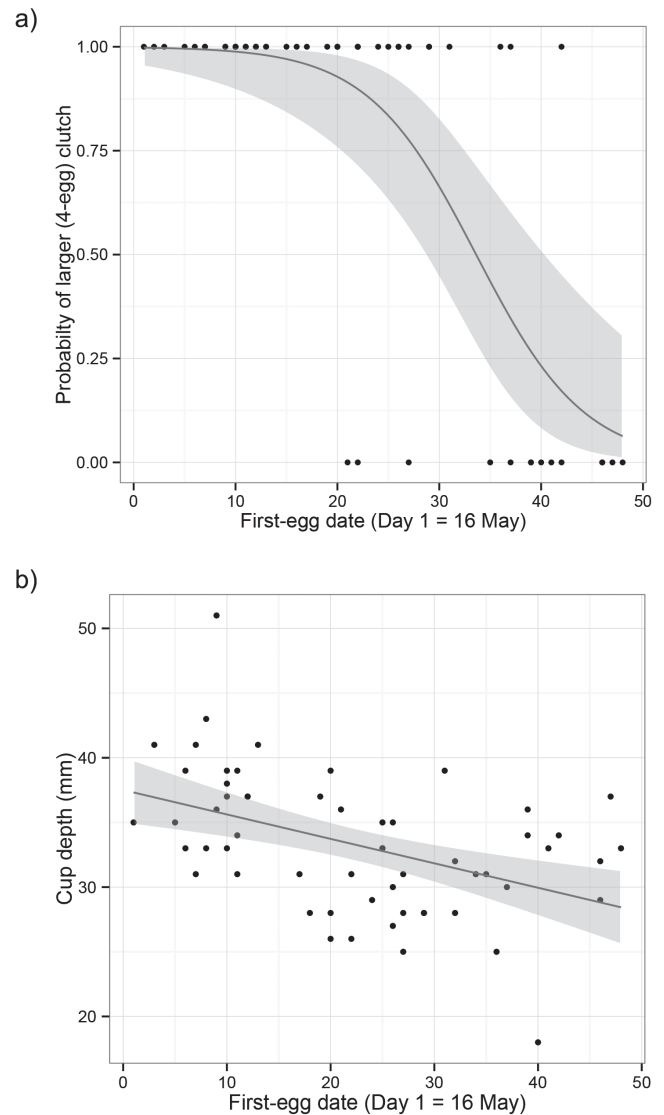


**Figure 2** (a) The effect of nest size, thickness, and mass (PC1) on the cooling rate ( $k_2$ ), and (b) on the equilibrium temperature ( $T_{eq}$ ). Grey lines and shading represent regression curves and 95% confidence intervals. Note larger, thicker, and heavier nests have lower PC1 scores.

did not find any significant relationships between nestling body condition and the thermal properties ( $k_2$ :  $T=1.1$ ,  $P=0.30$ ;  $T_{eq}$ :  $T=0.3$ ,  $P=0.79$ ), or between nestling condition and nest structural characteristics (PC1:  $T=-0.6$ ,  $P=0.55$ ; PC2:  $T=-0.9$ ,  $P=0.37$ ; cup depth:  $T=0.3$ ,  $P=0.78$ ).

#### 4. DISCUSSION

We found that the characteristics of Prairie Warbler nests influenced their thermal properties. Larger nests as indicated by a composite of nest size, thickness, and



**Figure 3** (a) Predicted probability of a nest having a larger four egg clutch (compared to a two or three egg clutch) as a function of first-egg date for Prairie Warbler nests in 2009. Grey line and shading represents regression curve and 95% confidence interval. Points represent clutch size of individual nests (four egg nests on the top, two or three egg nests on the bottom of the figure). (b) Cup depth as a function of first-egg date in 2009.

weight had slower cooling rates ( $k_2$ ) and higher predicted equilibrium temperatures ( $T_{eq}$ ) in controlled cooling trials. In a similar cooling experiment with Penduline Tit (*Remiz pendulinus*) nests, Szentirmai *et al.* (2005) found that thicker nests had significantly slower cooling rates and higher 'terminal temperatures' (similar to  $T_{eq}$ ), although Penduline Tit nests are domed and structurally different than the small open-cup nests in our study. In White-crowned Sparrow open-cup nests, increased floor thickness, mass, and size, and decreased wall porosity, significantly increased nest insulation, but wall thickness had less of an effect (Kern, 1984). In open-cup nests of Common Blackbirds (*Turdus merula*), insulation



significantly increased with the mass of dry grasses, but nest insulation was not affected by structural characteristics including wall thickness (Mainwaring *et al.*, 2014b). Investigators have also found that open-cup nesting birds build bigger, thicker, and heavier nests at higher latitudes and higher elevations, presumably to better insulate nest contents from colder temperatures (Kern and Van Riper, 1984; Crossman *et al.*, 2011; Mainwaring *et al.*, 2012; Heenan *et al.*, 2015). Specifically, Rohwer and Law (2010) observed that thicker and larger Yellow Warbler (*Setophaga petechia*) nests were built at higher latitudes, and these nests lost heat at slower rates in nest-cooling experiments compared to thinner, smaller nests built at lower latitudes. Overall, most studies' findings are similar to ours, in that thicker, heavier, and larger nests are more thermally insulated, but for some open-cup nesting species certain structural characteristics may not influence thermal properties (Kern, 1984; Mainwaring *et al.*, 2014b). This interspecific variation might be due to different nest designs and materials used among species and locations, as well as differences in which nest structural characteristics and thermal properties were measured and how they were quantified (Deeming and Mainwaring, 2015; Deeming and Gray, 2016a).

We found that larger Prairie Warbler nests (in height and diameter) were heavier and had thicker walls. Other studies of open-cup nests, such as nests of American Robins (*Turdus migratorius*), Yellow Warblers, and Tawny Pipits (*Anthus campestris*), have revealed similar relationships with nest diameter, weight, and wall thickness (Suárez *et al.*, 2005; Crossman *et al.*, 2011). Prairie Warbler nests with thicker walls were larger in diameter and had smaller cup diameters, but the relationship between wall thickness and cup diameter was primarily observed in nests with nestlings. Nests that had wide cup diameters and thin walls could have been the result of nestlings stretching the nest cup and compacting the nest walls (Kern, 1984; Slagsvold, 1989b; Watt and Dimberio, 1990). Nevertheless, in open-cup nests of Tawny Pipits, Suárez *et al.* (2005) found a significant negative correlation between wall thickness and cup diameter in nests measured during incubation before nestlings were present. Thus, when open-cup nesting birds build relatively thick nest walls, in addition to building outwards to make the nest diameter wider, there is a chance that they also build inwards, creating a nest cup with a smaller diameter. Birds may not solely build their nests outwards because of selection pressures against building a very wide nest, including increased visibility (Møller, 1990). Also, nest cups can stretch when nestlings become larger (Slagsvold, 1989b), mitigating potential effects of building narrower nest cups.

In relation to providing space in nests for the eggs and nestlings, we did not observe an effect of cup diameter on clutch size. This differs from studies on cavity-nesting birds that have found clutch size can decrease with nest cup space (Lombardo, 1994; Álvarez and Barba, 2008). In our study, the influence of nestlings stretching the nests

may have obscured any relationships between clutch size and cup diameter. We did observe a non-significant trend for deeper nest cups to have larger clutches, and found significant relationships in which cup depth, as well as clutch size, declined over the breeding season. Therefore, female Prairie Warblers may construct nests with shallower cups later in the season as they decrease clutch size, but do not directly match nest cup depth to clutch size on each breeding attempt. Building taller nests with deeper cups could be energetically costly and time consuming (Mainwaring and Hartley, 2013). As a result, females may build shallower nests later in the season if deeper cups are not needed to contain the eggs and young. In contrast to findings of Slagsvold (1982, 1989b), we did not observe that nests with a larger cup diameter or deeper cups had greater hatching and fledging success or nestlings in better condition. More research examining nest cup space, wall thickness, clutch size, and reproductive performance would be useful to further test the relationships among these factors in open-cup nesting birds.

We did not find any significant effects of nest thermal properties on reproductive performance (*i.e.* hatching and fledging success, nest survival, and nestling condition), which contrasts with other studies on cavity-nesting birds, such as with Tree Swallows (Lombardo, 1994), Great Tits (Álvarez and Barba, 2008, 2011), and Blue Tits (Gładalski *et al.*, 2016). Our study was conducted during a relatively cooler and wetter breeding season, which had later leafing phenology, compared to other breeding seasons in our study site (Akresh, 2012). Thus, although our study was only conducted during one breeding season and we did not take into account variation in environmental conditions among years, we would have expected to observe significant effects of nest insulation on reproductive performance during this colder year. In open-cup nests, eggs are likely to lose more heat due to convection during female off-bouts compared to cavity nests (Lamprecht and Schmolz, 2004; Heenan and Seymour, 2012). The differing roles of conduction and convection between open-cup and cavity nests may therefore explain the contrasting effects of nest insulation on reproductive performance between open-cup and cavity nests, at least in temperate climates. Strong effects of convection on heat loss might have outweighed any effects of Prairie Warbler nest insulation on birds' fitness in our study.

There are few studies on open-cup nesting birds to compare with our study that have specifically examined nest thermal properties and reproductive performance (Deeming and Mainwaring, 2015). Consistent with our study's findings, in open-cup nesting Rufous Bush Robins (*Cercotrichas galactotes*), floor thickness and wall density were not related to hatching success and nest mass did not influence the number of young fledged; however, this was in a hot, Mediterranean climate (Palomino *et al.*, 1998). Also, similar to our findings, Lent (1992) observed that nest height, nest diameter, and cup depth had no effect on nest survival, the number of young fledged, or nestling mass for open-cup nesting Gray Catbirds (*Dumetella carolinensis*), but nest weight and insulation were



not measured in this study. Unlike cavity-nesting birds, open-cup nesting birds in temperate climates may not build nests to directly maximise thermal benefits because of opposing selection pressures, such as the pressure to build smaller, less visible nests. However, in our study, larger nests were not more likely to be predated, parasitised, or more visible. Therefore, we did not find support for the hypothesis that the nests' structure was built smaller to better conceal nests from predators, although this has been observed for other open-cup nesting species (Møller, 1990; Antonov, 2004; Wysocki *et al.*, 2015).

Besides the opposing selection pressure of nest predation, there could also be an opposing selection pressure to promote some heat loss in open-cup nests in temperate climates (Mertens, 1977; Ardia, 2013; Rodríguez and Barba, 2016). Over-heating eggs on hot days can be lethal to embryos, which are already close to lethal temperatures during incubation (Webb, 1987; DuRant *et al.*, 2013). In contrast, under-heating the eggs for short periods of time often has less drastic consequences than a complete failure of the clutch (Webb, 1987). Furthermore, well-insulated nests could possibly lead to hyperthermia of nestlings on hot days, especially nestlings exposed to direct sunlight (Mertens, 1977; Nolan, 1978; Lombardo, 1994). Therefore, minimising heat loss in nests may not be as important in temperate climates (Heenan *et al.*, 2015) and, in these climates, our results suggest that nest thermal properties may have a negligible impact on reproductive performance for open-cup nesting birds, at least for our study population. In our study site, there were a few days during the breeding season in which maximum temperatures exceeded 32 °C. It is also noteworthy that we conducted our study in a Pitch Pine-Scrub Oak barren, which is subject to relatively more extreme temperatures (at certain times up to  $\pm 5$  °C) than the surrounding areas (Motzkin *et al.*, 2002). In this environment, although relatively colder temperatures might have put selective pressure on birds to build insulated nests, relatively hotter temperatures may be more lethal to nestlings, and thus may have put greater pressure on birds to build nests that allowed for some heat loss. Regardless of our local study area, nest insulation is likely more important for birds' fitness in very cold climates, and as a result, studies have observed relatively thicker and more insulated open-cup nests in very cold climates (e.g. northern Manitoba and northern Great Britain) compared to more temperate climates (Rohwer and Law, 2010; Crossman *et al.*, 2011; Mainwaring *et al.*, 2014b). These studies show the potential for open-cup nesting birds to build larger nests in lower latitudes, but due to tradeoffs with other factors or to disperse some heat from the nest during hot days, nests are built relatively smaller and less insulated in more temperate zones (Mainwaring *et al.*, 2014b).

Despite our findings, it is possible that in our study there were other biological or methodological reasons for why we did not observe a significant effect of nest insulation on birds' reproductive performance. Besides the nest-cooling experiment, our study was mostly observational and experimental manipulation of nests may have increased our

ability to make inferences. In our study population, birds could have already selected to build nests in the optimal range of nest structure and thermal insulation for reproduction, such that there was not enough variation to have an observable effect on birds' fitness. Furthermore, although nest thermal properties can play a role in hatching and fledging success (e.g. Lombardo *et al.*, 1995), hatching and fledging success can also be affected by food availability and parent age (Nol and Smith, 1987). It is possible that parents increased their time incubating (e.g. took shorter off-bouts), or increased their feeding rate of nestlings, at less insulated nests to diminish any negative effects on eggs or nestling condition due to heat loss from the nest (Conway and Martin, 2000; Álvarez and Barba, 2014; Deeming and Gray, 2016b); however, we have no data to support this hypothesis. Furthermore, if nests were built in different microclimates (*i.e.* due to the placement of the nest within vegetation or the location in the study site; Motzkin *et al.*, 2002), this may have also obscured the relationship between nests' thermal properties and reproductive performance.

As global warming continues and ambient temperatures change locally and globally, birds may respond to these changes by altering and adapting the size and characteristics of their nests (Møller and Nielsen, 2015). However, our results suggest that nest structural design for small open-cup nesting birds in temperate climates may be more driven to perform other functions, rather than to insulate the eggs and nestlings (Heenan and Seymour, 2011; Wysocki *et al.*, 2015). Indeed, Deeming (2016) has proposed that nests work in concert with incubating birds as a bird–nest incubation unit and as a result, other factors likely influence passerine nest design. Specifically, nests must also allow for incubating females to regulate humidity and promote respiratory gas exchange for the eggs, in addition to keeping the eggs at an optimal temperature (Deeming and Biddle, 2015; Deeming, 2016). More studies on open-cup nests' characteristics, thermal properties, tradeoffs with regulating gas exchange, and relationships with reproductive performance in a variety of species will be beneficial in understanding the key functions of open-cup nests and how birds in different climatic zones will respond to current and future changes in climate (Deeming and Mainwaring, 2015; Deeming, 2016).

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