TITLE:

Do nest size and shape characteristics affect nest parasitism rates?

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INTRODUCTION

The survival strategy of obligate brood parasitic birds like the Brown-headed Cowbird (*Molothrus ater*) is to lay their eggs in nests of host species and therefore avoid most of the reproductive costs required for raising chicks. Costs transferred to host species include the energy normally required to defend nests, incubate eggs and feed young. Hosts also incur possible reduced hatchling growth due to competition with parasite offspring, eviction of host eggs by earlier hatching parasite chicks, and an increased risk of nest abandonment (Kilner 2005, Servedio and Hauber 2006). To deceive hosts, parasites often choose a host whose eggs they can mimic to ensure a successful incubation without detection (Davies 2000). Not only do cowbirds and other brood parasites synchronize their laying to match the laying time of the host species to further diminish the risk of egg detection, brood parasitic eggs typically have thicker shells than host eggs (Mermoz and Reboreda 1999, Weatherhead 1991).

To successfully parasitize a nest, cowbirds must first be able to locate host nests. Cowbirds detect nests via vocalizations from host species, visual cues during nest building, nest architectural features such as shape, size and structure and overall nest placement in the surrounding habitat (Thompson and Gottfried 1981, Uyehara and Narins 1995, Mclaren and Sealy 2003).

Bird nests serve many purposes including insulation, shelter, and a place to lay eggs and raise young. The nests collected in our study are open cup nests with a distinct concave indention used mainly to hold the eggs, a feature that makes ideal host nests for brood parasitic birds. While larger nests could provide more space for eggs and brood rearing, larger nests are harder to conceal and the prolonged construction time has potential to increase detection of the nest by brood parasites compared to nests that require fewer trips during construction and presumably less materials to build. The idea that bigger nests draw more attention is documented by higher predation rates occurring in larger Blackbird (*Turdus merula*) nests (Møller 1990). Also, larger, bulkier nests tend to attract predators and parasites in higher quantities than do smaller nests of various songbird species (Lopez-Iborra *et al.* 2004, Moreno 2012). In particular, Song Sparrow (*Melospiza melodia*) nests parasitized by cowbirds were significantly heavier in mass when compared to unparasatized nests (McLaren and Sealy 2003). However nest size is not always the predominant factor when determining risk of predation, indicating that nest placement is sometimes a better predictor for predation (Weidinger 2004). Our study addressed how architectural features of Indigo Bunting (*Passerina cyanea*), Yellow-breasted Chat (*Icteria virens*), and Prairie Warbler (*Setophaga discolor*) nests relate to parasitism rates.

HYPOTHESIS

We hypothesized that larger nests would be more likely to be parasitized. Nest features including nest depth, width of the nest and overall nest mass may influence parasitism rates. Nests that are larger in size, depth and mass indicate more construction trips, which equal the possibility of greater attention brought to the nest location. This added attention might signal to brood parasites the location of a host nest which could raise the risk of nest parasitism.

METHODS AND MATERIALS

Study Site

We worked on property managed by Weyerhaeuser Company in Kemper County, Mississippi on sites associated with a research study about how switchgrass (*Panicum virgatum*) intercropping in loblolly pine (*Pinus taeda*) forests affects biodiversity (Loman *et al*. 2013).

Landscapes in the experimental study and the sites of nest collection include those of the Interior Flatwoods Area (Pettry 1997) of the Upper Coastal Plain region in Southeast Mississippi. The habitat was early successional, intensely managed young loblolly pine forests. The management practices on the land were: (1) stands of pine under normal management following traditional Weyerhaeuser site preparation techniques; (2) young pine stands intercropped with switchgrass with site preparation following traditional pine management techniques; (3) older stands of traditionally managed pine intercropped with switchgrass (Loman *et al*. 2013).

Nest Collection

During 2011–2013 as part of the intercropping study, each stand was searched for active nests that were monitored for fate. After nest completion, data on concealment, cover, and surrounding vegetation were recorded in the field for each nest. Once these field measurements were completed, nests were collected, given a number label, bagged and stored in a freezer at the College of Forest Resources on campus at Mississippi State University until ready for use.

Nest Measurements

Before measuring, nests were dried for ≥ 48 hours at 148° F. Nest characteristics measured included total nest mass (g), nest compression (shape), inner and outer cover materials (spider web, flower/inflorescence, animal hair, seed tuft/plant down, narrow graminoids, wide graminoids, fine woody stems measuring less than 5mm, broad leaves, green leaves), the overall visible nest materials that were evident without the need for nest deconstruction, and attachment method (see figure 3.4 in Hansell 2000). Measurements including maximum overall nest width (cm), minimum overall nest width (cm), height (cm), cup depth (cm) and dimensions maximum inner cup width (cm), minimum inner cup width (cm), and a measure perpendicular to the minimum inner cup width (cm) were also recorded for each nest modeled after figure 3.1 in Hansell (2000).

Statistical Procedures

To test the hypothesis that larger, heavier nests have higher parasitism rates, we used general logistic regression models to relate nest architecture and nest dimensions to probability of parasitism for each species studied. Correlated nest dimensions were reduced using principal component analysis. We retained the first component which explained 95.25%, 98.79%, and 97.78% of the variation in Indigo Bunting, Prairie Warbler, and Yellow-breasted Chat nest metrics, respectively. This PC functioned primarily as an index of nest size with Eigen values for Indigo Bunting, Prairie Warbler and Yellow-breasted Chat measuring λ =.83, λ =.67, and λ = .87 for each species respectively. We also included several other covariates and their interactions with the nest size PC. These covariates were nest height, canopy cover and concealment. Best models were identified via AIC model selection.

RESULTS

We used Yellow-breasted Chat, Indigo Bunting and Prairie Warbler nests from 2012 and 2013 with overall nest parasitism rates of approximately 3, 18, and 24 percent, respectively, for the two years combined. The total sample size of all three species of nests that were suitable for testing hypotheses about parasitism and nest architecture was $\approx$ 225.

Model coefficients for the nest size principal component were not different from zero and nest size metrics did not differ between parasitized and unparasitized nests for all species (Tables

1-3). Nest height, canopy cover and concealment did not significantly relate to parasitism rates for the nests in our study area as estimates of each parameter's influence on parasitism centered around zero (Fig. 1). There were slight species variations present between the parameters but none of which were significant enough to affect parasitism rates, suggesting that the relationship between parasitism rates and nest characteristics may vary based on species and study site locations.

CONCLUSION

We found that nest size did not relate to nest parasitism, although nest metrics did vary among species (Table 4). Additionally, none of the nest site characteristics were related to parasitism. This suggests that larger, heavier nests do not have a greater tendency to be parasitized regardless of nest site, which does not support our initial hypothesis. It is possible that suitable nest locations were not a limiting factor for the species of interest at our study site. Likely, there were enough quality shrub nesting areas (which were extremely abundant) for each species to select optimal nesting sites, thus we did not detect any nest size or nest characteristic relationships with parasitism.

Another possible explanation is that our sample does not include damaged nests because they could not be measured. Thus, if parasitized nests were also more likely to be predated (and hence excluded from our sample), this could have biased our analysis against finding nests. Additionally, Brown-headed Cowbirds are known to predate nests they parasitize if the host species rejects the cowbird egg or chick (Hoover and Robinson 2007). While Prairie Warblers are known acceptor species (Rothstein 1975), Yellow-breasted Chats have a tendency to reject foreign eggs found in their nests (Burhans and Freeman 1997), and Indigo Buntings do not presently have an acceptor/rejector species label. Furthermore, overall parasitism rates were relatively low, which could have also precluded us finding nest size – parasitism relationships. Low predation rates could be because other susceptible species available to the Brown-headed Cowbirds such as the Blue Grosbeak (*Passerina caerulea*) were common in the older stands and could have provided better-suited or more easily accessible nests, diverting cowbirds from our study species.

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Table 1. Generalized mixed models with a Bernoulli distributed outcome to test how nest architecture and placement relates to probability of nest parasitism for Yellow-breasted Chat (*Icteria virens*). April-July 2012-2013, Kemper Co., MS.

Model	df	ΔAIC^c	w_i	log likelihood
Intercept	2	0.000	0.215	-17.638
Intercept + Conceal	3	1.009	0.130	-17.091
Intercept + PC1	3	1.475	0.103	-17.325
Intercept + Height	3	1.514	0.101	-17.344
Intercept + Canopy	3	2.093	0.076	-17.634
Intercept + Conceal + PC1	4	2.438	0.064	-16.737
Intercept + Conceal + Height	4	2.891	0.051	-16.964
Intercept + Canopy + Conceal	4	2.915	0.050	-16.976
Intercept + Height + PC1	4	3.073	0.046	-17.055
Intercept + Canopy + PC1	4	3.602	0.036	-17.319
Intercept + Canopy + Height	4	3.622	0.035	-17.329
Intercept + Canopy + Conceal + PC1	5	4.354	0.024	-16.608
Intercept + Conceal + Height + PC1	5	4.432	0.023	-16.648
Intercept + Canopy + Conceal + Height	5	4.692	0.021	-16.778
Intercept + Canopy + Height + PC1	5	5.225	0.016	-17.044
Intercept + Canopy + Conceal + Height + PC1	6	6.283	0.009	-16.467

Table 2. Generalized mixed models with a Bernoulli distributed outcome to test how nest architecture and placement relates to probability of nest parasitism for Indigo Bunting (*Passerina cyanea*). April-July 2012-2013, Kemper Co., MS.

Model	df	ΔAIC^c	w_i	log likelihood
Intercept	2	0.000	0.285	-29.737
Intercept + Height	3	1.658	0.125	-29.468
Intercept + PC1	3	2.039	0.103	-29.658
Intercept + Conceal	3	2.159	0.097	-29.718
Intercept + Canopy	3	2.172	0.096	-29.725
Intercept + Canopy + Height	4	3.643	0.046	-29.326
Intercept + Conceal + Height	4	3.752	0.044	-29.380
Intercept + Height + PC1	4	3.762	0.044	-29.385
Intercept + Conceal + PC1	4	4.234	0.034	-29.621
Intercept + Canopy + PC1	4	4.296	0.033	-29.652
Intercept + Canopy + Conceal	4	4.417	0.031	-29.713
Intercept + Conceal + Height + PC1	5	5.839	0.015	-29.252
Intercept + Canopy + Height + PC1	5	5.882	0.015	-29.273
Intercept + Canopy + Conceal + Height	5	5.893	0.015	-29.279
Intercept + Canopy + Conceal + PC1	5	6.578	0.011	-29.621
Intercept + Canopy + Conceal + Height + PC1	6	8.142	0.005	-29.191

Table 3. Generalized mixed models with a Bernoulli distributed outcome to test how nest architecture and placement relates to probability of nest parasitism for Prairie Warbler (*Setophaga discolor*). April-July 2012-2013, Kemper Co., MS.

Model	df	ΔAIC^{c}	w_i	log likelihood
Intercept	2.0	0.000	0.215	-17.638
Intercept + Conceal	3.0	1.009	0.130	-17.091
Intercept + PC1	3.0	1.475	0.103	-17.325
Intercept + Height	3.0	1.514	0.101	-17.344
Intercept + Canopy	3.0	2.093	0.076	-17.634
Intercept + Conceal + PC1	4.0	2.438	0.064	-16.737
Intercept + Conceal + Height	4.0	2.891	0.051	-16.964
Intercept + Canopy + Conceal	4.0	2.915	0.050	-16.976
Intercept + Height + PC1	4.0	3.073	0.046	-17.055
Intercept + Canopy + PC1	4.0	3.602	0.036	-17.319
Intercept + Canopy + Height	4.0	3.622	0.035	-17.329
Intercept + Canopy + Conceal + PC1	5.0	4.354	0.024	-16.608
Intercept + Conceal + height + PC1	5.0	4.432	0.023	-16.648
Intercept + Canopy + Conceal + Height	5.0	4.692	0.021	-16.778
Intercept + Canopy + Height + PC1	5.0	5.225	0.016	-17.044
Intercept + Canopy + Conceal + Height + PC1	6.0	6.283	0.009	-16.467

Table 4. Modeled parameter estimates influencing Brown-headed Cowbird nest parasitism rates of Indigo Bunting (*Passerina cyanea*), Yellow-breasted Chat (*Icteria virens*), and Prairie Warbler (*Setophaga discolor*). April-July 2012-2013, Kemper Co., MS.

Species	Outer Width (cm)	+/- sd	Dry Mass (g)	+/- sd	Depth (cm)	+/- sd
Yellow-breasted Chat	12.474	1.665	19.623	6.442	7.499	1.209
Indigo Bunting	9.763	1.290	10.019	4.281	6.684	1.124
Prairie Warbler	7.605	0.929	5.581	2.889	5.986	1.173

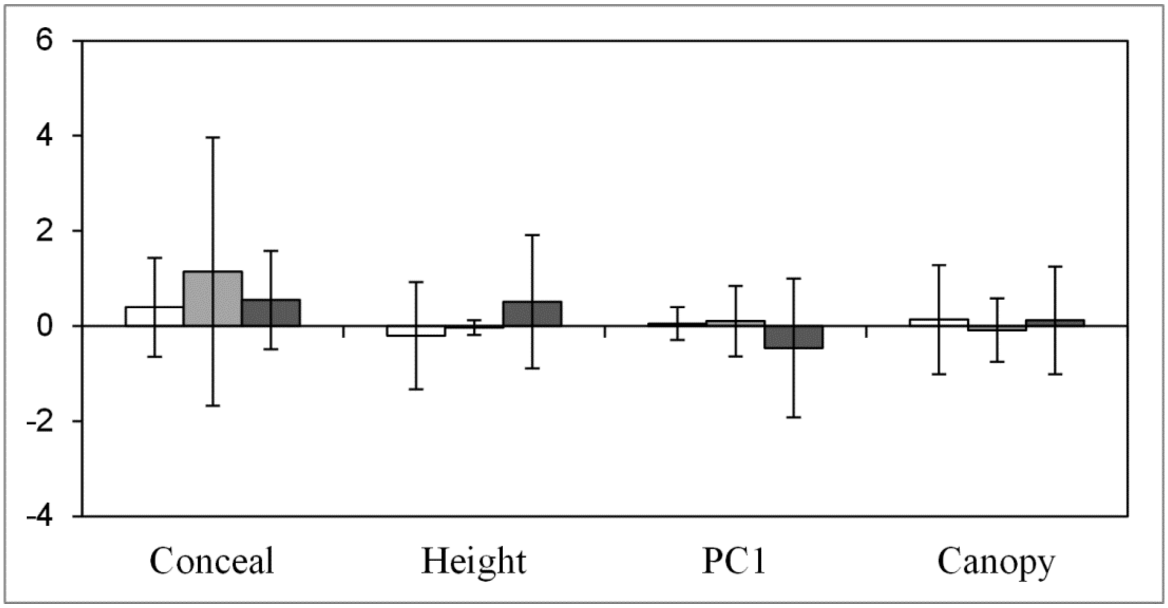

Figure 1. Parameter estimates with 95% confidence intervals. White represents Prairie Warbler (*Setophaga discolor*), light gray represents Indigo Bunting (*Passerina cyanea*), dark gray represents Yellow-breasted Chat (*Icteria virens*). Conceal is a measure of nest concealment, Height is a measure of nest height, PC1 is the principle component representative of nest size, Canopy is a measure of canopy cover. April-July, 2012-2013, Kemper Co., MS, USA.