Repeatability of an extended phenotype: causes and consequences of nest variation in a free-living songbird

Running Title: Repeatability of nest construction

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HIGHLIGHTS

- Repeatability of construction behaviours in the wild is understudied
- House wrens are highly variable in their nest morphology
- Female house wrens are highly repeatable in cup composition
- House wren nests are unrelated to nestling survival or parental condition
- Differences in individual preferences likely explains nest variation

ABSTRACT

Construction behaviour is an aspect of the extended phenotype that allows organisms to build structures that alter their environments in potentially beneficial ways. Although individuals vary in the expression of this extended phenotype (e.g., structure morphology), the repeatability of construction behaviour remains understudied, especially among free-living populations. Many oviparous taxa construct nests, making them of particular interest because variation in nest architecture may directly affect fitness. Using a free-living, cavity-nesting songbird, the northern house wren (*Troglodytes aedon aedon*), as our model, we estimated the contribution of the primary builder (the female) to nest variability by measuring the repeatability of nest morphology between successive clutches. We further examined whether nest morphology was related to the dimensions of the nesting cavity, breeding date, or nest success. We found the composition of the cup lining to be a highly repeatable behaviour for the nesting female, although the size and composition of the structural platform appeared more related to the dimensions of the cavity. Despite the expectation that construction effort would show a seasonal decline, similar to clutch size in this species, nest morphology remained incredibly variable throughout the breeding season and was unrelated to the survival of the offspring. Our study suggests that variation in construction behaviours is a product of multiple factors including the preferences of the builder and physical constraints. The absence of any clear links between construction behaviour and fitness indicates that nest morphology is not under strong selection. As a result, diverse female building preferences may explain the extreme among-individual variation in nest structure in this species.

INTRODUCTION

Alfred Russel Wallace (1865) once stated: "…so great is the tendency to vary that it is difficult to find two individuals exactly alike." Phenotypic variation is both ubiquitous and a fundamental requirement for evolution (Darwin & Wallace 1858). As such, a considerable amount of research has been devoted to understanding the causes and consequences of among-individual variation. The interaction between an organism's phenotype and the environment determines its success, and selection can push populations toward one or more optimal phenotypes (van Rijssel et al. 2018, LeGrice et al. 2019). However, the relationship between the phenotype and the environment can be bi-directional, allowing individuals to reshape their environments in ways that affect their fitness (i.e., "niche construction"; Laland et al. 1999). This bi-directional interaction can bias the direction of selection in favour of the individual, and often leads to reduced spatial and temporal variation in phenotypes (Clark et al. 2020).

Construction behaviour is a unique behavioural phenotype where the product of the construction acts as both an extension of the builder's phenotype (i.e., "extended phenotype"; Dawkins 1982) and an artificial environment more beneficial for the builder. Construction behaviours may enhance the builder's fitness by providing protection from predators (Beebe 1953, Hermes, 2013, Sugiura 2016) and environmental exposure (Zeibis et al. 1996, Korb & Linsenmair 2000, Korb 2003, Rosell & Campbell-Palmer 2022), as well as increasing access to resources such as food (Hölldobler & Wilson 1990, Miyashita & Shinkai 1995, Blamires et al. 2010) and mates (Borgia 1985, McKaye et al. 1990). As a result, construction behaviour has become taxonomically widespread across both vertebrate and invertebrate species (Hansell 2005). Eusocial insects build colonial shelters (e.g. termite mounds), some mammals dig burrows, most spiders spin webbed traps, and certain species of fishes and birds construct

bowers. However, despite the clear potential for construction behaviour to benefit the fitness of an individual, trade-offs often occur between investment in the construction process and other behaviours that affect fitness, such as foraging, which can result in negative effects on both the builder (Madden 2002, Bailey et al. 2015) and the structure (Ellendula et al. 2021, Parthasarathy et al. 2022).

It is well established that the products of construction behaviours exhibit among-individual variation, but the extent and cause of variation *within* an individual's construction behaviour is less clear (DiRienzo & Aonuma 2018). For example, an individual's construction behaviour might be static, plastic, or some combination of the two as its experience and environment changes. Many organisms build multiple versions of the same structure throughout their lifetimes, which provides an opportunity to evaluate the consistency of this behaviour. Repeatability estimates, calculated as intra-class correlation coefficients, can be used to assess how much of the variation observed among individuals can be explained by variation within individuals (Hayes & Jenkins 1997). When among-individual variation is high and within-individual variation is low, then the repeatability estimate will be high and that trait will be considered repeatable. Repeatability estimation can be used to understand the extent to which phenotypic traits are the product of static characteristics, such as heritability ("upper level of heritability"; Bell et al. 2009, Møller 2006) and preferences (Mennerat et al. 2009, Järvinen & Brommer 2020), or plastic characteristics, such as experience (DiRienzo et al. 2019, Whittaker et al. 2023). For this reason, the repeatability of a large variety of behaviours have been examined across taxa (Bell et al. 2009), but there are few studies examining the repeatability of construction behaviours. Most of these studies have focused on spider web structure (Fisher et al. 2019, DiRienzo et al. 2020, DiRienzo & Montiglio 2016) or nest

87 morphology (Whittaker et al. 2023, Muth & Healy 2011, Rushbrook et al. 2008), but few have
88 examined the behaviour exclusively in the wild (Møller 2006, Järvinen et al. 2017).
89 Nest building is a very common construction behaviour among oviparous taxa that serves
90 the primary function of providing a safe, hospitable space for eggs or altricial young to develop
91 (Mainwaring et al. 2014a). With few exceptions (e.g., brood parasites), bird species produce an
92 incredible array of nests that can be structurally complex or simple, but must contain at least
93 one of four zones: an outer nest layer, an attachment to the environment, a structural layer, and
94 a lining (Hansell 2000). Zones are often discernible from one another by the materials used,
95 with zone composition being largely species specific (Biddle et al. 2018). Nests can be built by
96 the male, female, or both with some division of labour by zone (Hansell 2000). The
97 morphology of the nest, structure, size, and composition, can be important for providing the
98 same benefits of niche construction observed for other structures by protecting the young from
99 predators (Hays et al. 2022, Møller 1990) and environment exposure (Medina et al. 2022,
100 Perez et al. 2020, Cerezo & Deeming 2016, Mainwaring et al. 2014b, Franklin 1995), as well
101 as potentially playing a role in mate attraction for some species (Jelínek et al. 2016,
102 Mainwaring et al. 2008, Ueda 1985).
103 Here, we investigated the causes and consequences of the variation and repeatability of
104 northern house wren (*Troglodytes aedon aedon*) nest morphology and composition. House
105 wrens are secondary cavity nesters that raise two to three clutches a season, often reusing the
106 same nest throughout (Johnson 2020). They will, however, build a new nest when the previous
107 nest is stolen, destroyed, or experimentally removed (Alworth 1996), making them an ideal
108 model for the examination of repeatability in construction behaviour. House wren nests
109 arguably contain 2 to 3 zones: sometimes an outer layer consisting of spider egg sac material, a

structural zone made of various types of sticks, henceforth referred to as the "stick platform," and a cup defined as a simple depression, at the top of the stick platform, lined with grasses and feathers (McCabe 1965). Although the layout and composition of the zones are standard, house wren nests are highly variable in their morphology. For example, in some nests the stick platform may be built so large that it covers the entrance hole of the box (McCabe 1965). While establishing a territory, unmated males place a variable number of sticks (range: <10 to >400; Johnson 2020) into potential nesting cavities. After pairing, the female completes the stick platform (Alworth & Scheiber 2000, Johnson 2020) and creates a lined cup either before or during egg laying. Considering the collective effort of the female in both completing the stick platform and constructing the nest cup during the construction phase, we defined the female as the primary nest builder in our study.

Despite the benefits of nest construction observed among other bird species (Mainwaring et al. 2014), house wren nest architecture appears to be unrelated to the mate selection process, the survivability of offspring (Alworth 1996, Eckerle & Thompson 2005), or the limiting of brood parasitism (Pribil & Picman 1997). Thus, the available evidence suggests that nest architecture in this species has limited effects on fitness, and so it remains unclear why house wren nests exhibit such extreme variation among individuals. The absence of selective pressure on nest construction could be one explanation for the amount of variability observed. Some research suggests that constraints imposed by the cavity dimensions and the accessibility of building materials may also drive variation in nest architecture (Stanback et al., 2013). However, no study to date has explored the role of female building preferences as an explanation for the variation.

We sampled house wren nests across an entire breeding season to assess the contribution of the female builder, the box cavity, and seasonal timing to nest architecture. We also examined how variation in nest dimensions and composition correlated with offspring survival. Unlike most construction behaviour research that often relies on coarse measures of structure like nest weight (Mainwaring et al. 2008, Walsh et al. 2010, Adreani et al. 2022), we used a finer approach of directly quantifying the individual building materials (e.g., exact count of sticks) used in nest construction. We predicted that nests would have high variability among individuals but that there would be low within-individual variability, specifically that the female identity would be the best predictor of nest dimension and composition as measured by a repeatability estimate. Based on previous data, we predicted that the architecture of the nest would not relate to the survivability of offspring, but may relate to the dimensions of the cavity in which it was built.

METHODS

Study System

We monitored northern house wren (*Troglodytes aedon aedon*) breeding behaviour in 160 nest boxes across six sites in Delaware and Union counties in Ohio, U.S.A., between May 9 and August 25 of 2022. Of those 160 boxes, 79 produced at least one nest with a complete clutch, which was the threshold for inclusion in our study. We measured nest box dimensions with digital callipers (nearest 0.001 mm). Nest boxes were rectangular wooden cuboids with internal dimensions of approximately 110 x 115 x 195 mm (Figure 1, see Table 1 for variation in box dimensions). Each box possessed a circular entrance hole with an average diameter of 34 mm and depth of 46 mm, drilled an average of 119 mm from the bottom of the box. Most (*n*

155 = 73/79; 92.4%) boxes also had a rectangular gap separating the top of the front panel from the
156 roof that allowed the panel to swing open. This gap was the same width as the box with a
157 height ranging from 4 mm to 30 mm. Some wrens used this gap as an entrance, particularly
158 when their nest obstructed the primary entrance hole. The variation in box dimensions were
159 due to imperfect construction and the preferences of landowners for slightly different box
160 designs. All boxes were suspended about 1.75 metres off the ground by a greased metal
161 conduit pole to limit predation.

162 We monitored 108 total nests (some boxes were used multiple times), but were unable to
163 visit boxes daily, so exact ageing of nests was not always possible. However, house wrens have
164 predictable rates of egg laying and incubation time, so we were able to estimate first egg dates
165 by counting eggs and incubation start dates by backdating from hatch date (Johnson 2020). In
166 cases where we were not present for hatch day, nestling ages and estimated hatch date were
167 evaluated by measuring nestling weights, wing chord length, and feather tract development as
168 described by Brown et al. (2011).

169 As soon as we discovered a complete clutch, the female was caught in a mist net and
170 banded with a USFWS aluminium leg band and a unique combination of plastic coloured
171 bands for future identification. It was essential to capture and band females to sample repeated
172 nesting attempts, but we chose not to capture males to minimise further disrupting both our
173 experiment and a separate, unrelated study. The female's weight (nearest 0.1 g; Pesola spring
174 scale), tarsus length (nearest 1 mm; ruler), and wing length (nearest 1 mm; ruler) were also
175 measured. While the female was processed, we measured the height of the nest and the width
176 of the "berm" (Stanback et al. 2013), which was defined as the front wall of the cup directly
177 against the entrance hole (see Figure 1), using a dial calliper (nearest 0.1 mm). On day eight of

nestling life, we collected measurements and banded each nestling as described above for adult females. We continued to monitor nests until the clutch fledged or failed, at which point the nest was collected in a large and resealable plastic bag for dissection in the lab and to prevent the nest from being reused or built upon for a successive clutch.

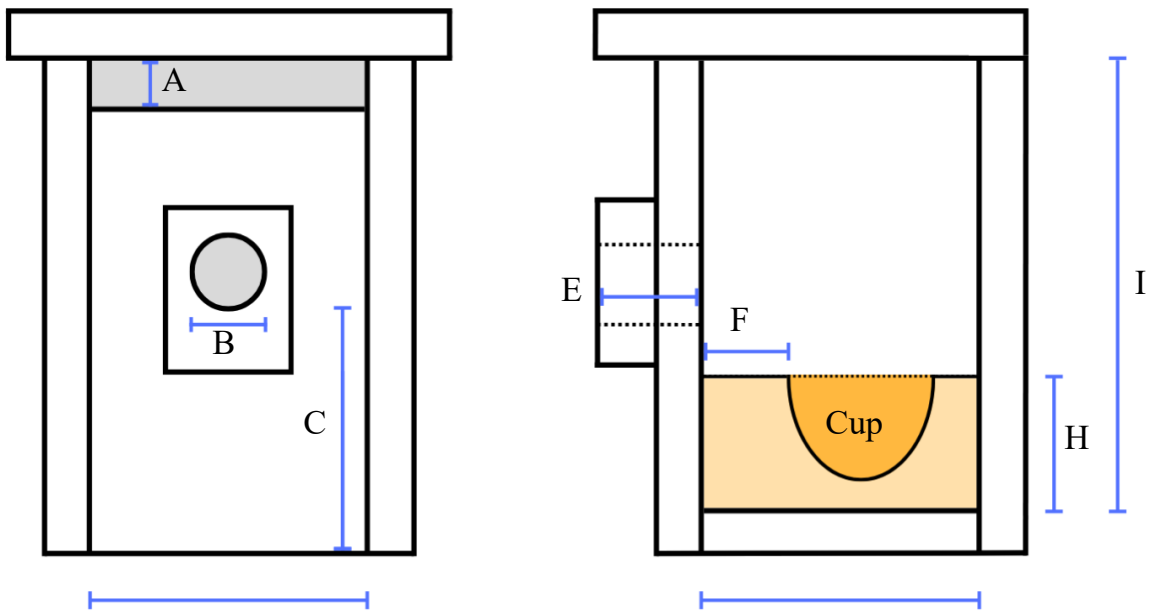

Figure 1 - Model of the nest box and nest (in orange). Both the front (left) and side (right) of the box are shown. A: height of the rectangular gap, B: diameter of the entrance hole, C: distance from the bottom of the box to the bottom of the entrance hole, D: internal length of the box and length of the nest, E: depth of the entrance hole, F: width of the berm, G: internal width of the box and width of the nest, H: height of the nest, I: internal height of the box.

Table 1 - Average, standard deviation, and range of the dimensions of the nest boxes used in this study. See Figure 1 for a model of an average nest box.

	Average (mm)	Standard Deviation (mm)	Range (mm)
Internal Box Height	195.19	14.92	[172.20, 219.90]
Internal Box Volume	2462.20	434.52	[1812.99, 4133.73]
Entrance Diameter	33.60	5.22	[27.90, 44.65]
Entrance Depth	44.11	6.78	[25.00, 56.40]
Height of Entrance	118.94	21.19	[83.10, 151.60]
Gap Height (when present)	14.82	6.11	[4.30, 29.55]

Nest Analysis

After collection, we placed nests in a -20 C freezer for 24 - 48 hours to kill any arthropods. For dissection, nests were placed on a large sheet of white paper and carefully pulled apart to quantify nest materials and characteristics. Most nests were dissected by the lead author, but two assistants were also trained for dissection. We made exact counts of individual sticks, grasses, plumulaceous, and pennaceous feathers. An arbitrary threshold of 4 cm in length was chosen to separate individual sticks and grasses from other debris. Down, contour, and semiplume feathers were categorised as Plumaceous, while wing and tail feathers were categorised as Pennaceous. We used an ordinal scale of 0 to 3 to quantify the amount of faecal material and spider egg sacs present within each nest. Finally, we noted, as a binary yes or no, the presence of snake skin and anthropogenic objects (e.g., plastic).

207

208 *Statistical analysis*

209 Although we sampled 108 nests in total, a small number had to be excluded from our
210 final analysis. One nest was removed during dissection because it contained signs of reuse (i.e.,
211 two individual grass layers separated by a thick stick layer). Two nests were not collected from
212 the field due to reuse or extensive nestling decomposition after predation, and so were unable
213 to be dissected. Due to data loss, the dissection measurements of two additional nests are
214 unaccounted for. Our final sample size was 103 nests.

215 R (version 4.2.3) was used for all analyses. We first assessed whether the observed
216 variation in nest measurements was normally distributed using separate Shapiro-Wilk tests. To
217 test whether nest measurements were repeatable within females, we calculated repeatability
218 estimates (packages: rptR, version 0.9.22) with the nest measurement as the dependent
219 variable, and the identity of the nesting female as the grouping factor. Parametric bootstrapping
220 and permutation, at 10 000 iterations each, were performed to produce confidence intervals and
221 adjusted alpha values for the repeatability estimates, respectively. Significant repeatability
222 estimates were indicated by 1) confidence intervals not overlapping zero (DiRienzo &
223 Aonuma, 2018) and 2) an adjusted alpha value of 0.05. Where nest measurement was binomial,
224 the link-scale approximation (Stoffel et al. 2017) is reported. We used the same approach to
225 test whether the box identity predicted nest measurements. In these models, the nest
226 measurement was the dependent variable, and the identity of the box was the grouping factor.
227 Although there was some overlap in sampling between models with the same female nesting
228 more than once in the same box, the sample size (5/24; 21% of females reused the same box
229 and 6/27; 22% of boxes were used by the same female) was too small to provide a reliable

230 estimate of the effect of these repeated samples on nest measurements. Thus, we chose to avoid
231 a more complex model that included both box and female identity.
232 Linear regressions (Base R Package) were used to test for a relationship between nest
233 measurements and box proportions, date of measurement, and age of the nest, which was
234 defined as the number of days between the first egg and the nest collection date. We used
235 generalised linear models (Base R Package) to analyse the effect of nest measurements on the
236 outcome of the clutch. These models assumed a binomial distribution with nest outcome
237 (fledge/fail) as the dependent variable. Linear models were used to analyse the effect of nest
238 measurement on clutch size and fledge count, assuming a gaussian distribution. Both the
239 generalised linear models and linear models had the nest measurement as the fixed effect, and
240 the date of nest measurement as a covariate to control for seasonal variation in reproductive
241 output.
242
243 *Ethical Note*
244 All procedures were reviewed and approved by the Ohio Wesleyan University
245 Institutional Animal Care and Use Committee (Protocol Number: 05-2021-06), U.S. Federal
246 Bird Banding Lab (Permit Number: 24035), and State of Ohio Department of Natural
247 Resources (Permit Numbers: 23-009, 23-010).
248
249 **RESULTS**
250 *Observed Variability in Nest Architecture*
251 House wren nests were extremely variable (Figure 2). The ratio of the nest height to
252 internal box height ranged from 0.254 to 0.902 (Figure 2A; $\underline{x}$ ±SD: 0.59 ± 0.144). Similarly,

253 the volume of the nest ranges from 655.71 mm^3 to 2776.96 mm^3 (Figure 2B; $\underline{x}$ ±SD: 1437.44 ±
254 409.29). Sticks were the primary contributor to the height and volume of the nest, and we
255 found that stick count exhibited the same variability, ranging from 170 to 1491 sticks in a
256 single nest (Figure 2C; $\underline{x}$ ±SD: 676.14 ± 25.01). The width of the nest berm ranged from 7.00
257 mm to 77.45 mm (Figure 2D; $\underline{x}$ ±SD: 39.62 ± 1.27).

258 We found the number of grass strands within the cup of a single nest ranged from zero to
259 836 (Figure 2E; $\underline{x}$ ±SD: 210.19 ± 16.49). Feather count within the cup was also quite variable,
260 ranging from a singular pennaceous feather to 271 total feathers (Figure 2F; $\underline{x}$ ±SD: 83.79 ±
261 5.70). Plumulaceous feathers were the most common feather found in nests with an average
262 ratio of 5 plumulaceous feathers for every 1 pennaceous. Although the cup is primarily lined
263 with grasses and feathers, other materials such as snake skin (n = 19/103; 18.4%),
264 anthropogenic objects (e.g., plastic; n = 54/103; 52.4%), and hair, noted anecdotally but not
265 quantified, from a variety of mammalian species, including human, were observed. We also
266 consistently found varying amounts of spider egg sac material interspersed throughout the stick
267 platform (n = 88/103; 85.4%).

268 The ratio of the nest height to internal box height (P = 0.74; Figure 2A) and the width of
269 the nest berm (Figure 2D; P = 0.94) were normally distributed across the population. All other
270 continuous nest characteristics showed a right-skewed distribution (P < 0.001).

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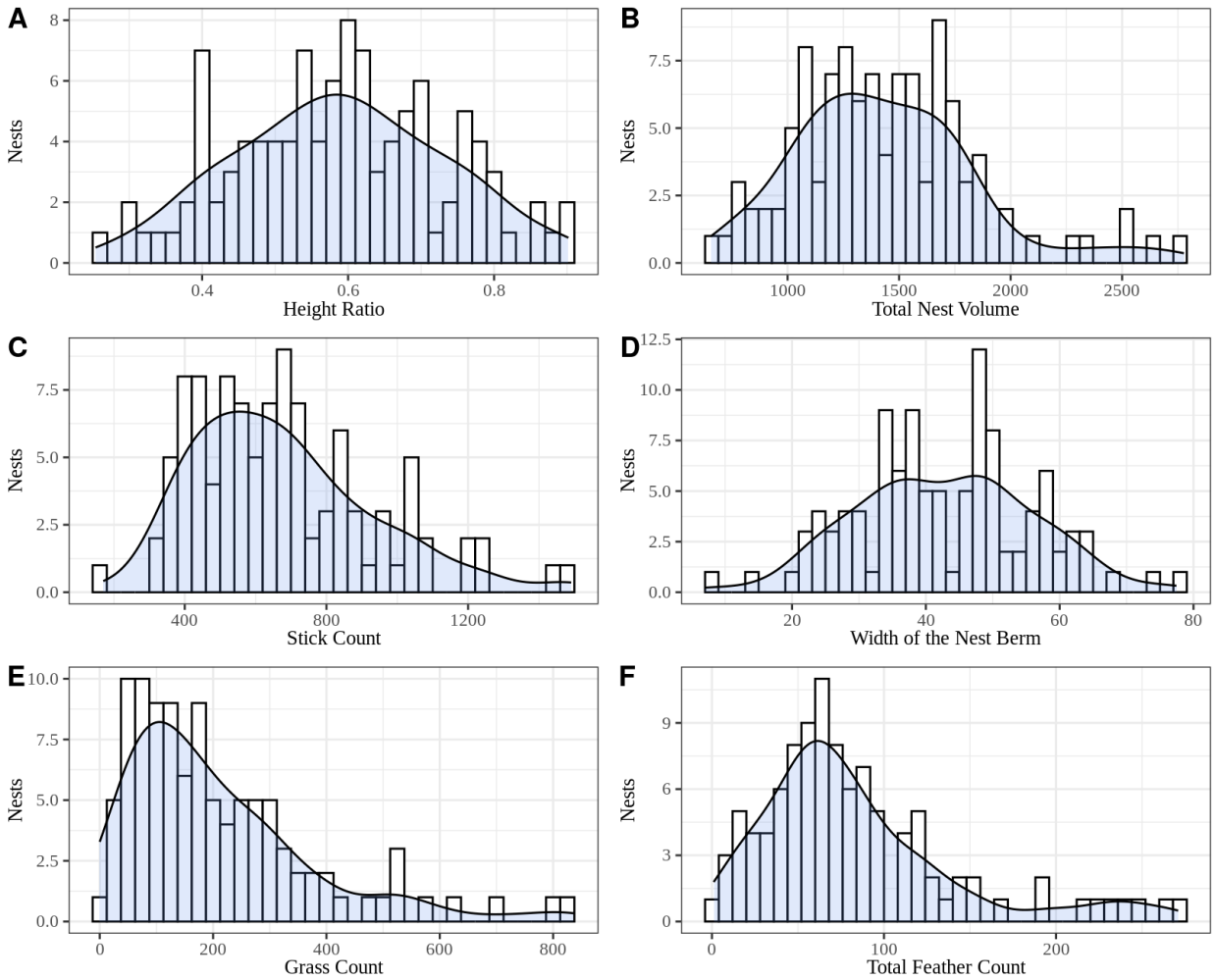

Figure 2 - Histograms showing the number of nests that contained the specified variable. "Height Ratio" (A; P = 0.74) and "Width of the Nest Berm" (D; P = 0.94) exhibit a normal distribution, but other factors show a right-skewed distribution (P < 0.001). The blue plots layered over the histograms represent the outcome of an estimated density distribution.

Variation Explained by Female Builder Identity

Over the course of the nesting season, 24 females renested in our boxes after their initial clutch. Of those females, 19 renested once and 5 renested twice on our study site, and the majority of those females renested in a different box from any previous clutch (22/29 total

renests; 75.9%; Supplementary 1). The identity of the nesting female did not explain the variation in the ratio of the nest height to internal box height ($R = 0 \leq 0.24 \leq 0.56$, $P = 0.08$, Figure 3C), nest volume ($R = 0 \leq 0.22 \leq 0.53$, $P = 0.11$), the width of the berm ($R = 0 \leq 0 \leq 0.34$, $P > 0.99$, Figure 3E), or the number of sticks within the the nest ($R = 0 \leq 0.15 \leq 0.49$, $P = 0.20$, Figure 3A). However, the grass material count was significantly repeatable ($R = 0.23 \leq 0.56 \leq 0.77$, $P = 0.003$, Figure 3B). The total count of feathers in the cup was not repeatable ($R = 0 \leq 0.04 \leq 0.39$, $P = 0.37$), but the pennaceous feather count alone appeared repeatable ($R = 0 \leq 0.33 \leq 0.62$, $P = 0.05$, Figure 3F), although we do note that the confidence interval overlaps with zero. The ratio of pennaceous feathers to plumulaceous feathers within the cup of the nest was significantly repeatable ($R = 0.79 \leq 0.90 \leq 0.95$, $P = 0.002$, Figure 3D). No other measurement was repeatable (Table 2).

Table 2 - Listed nesting materials were not significantly repeatable for both female and nesting box identity. Material specified with "✝" was measured as a simple yes/no presence.

	Box ID		Female ID	
	R & 95% CI	P	R & 95% CI	P
Plumulaceous	$0 \leq 0.03 \leq 0.38$	0.39	$0 \leq 0.02 \leq 0.37$	0.43
Faecal Rate	$0 \leq 0.07 \leq 0.24$	< 0.99	$0 \leq 0.07 \leq 0.25$	< 0.99
Spider Rate	$0 \leq 0.07 \leq 0.24$	< 0.99	$0 \leq 0.07 \leq 0.23$	< 0.99
✝ Snake Skin	$0 \leq <0.001 \leq 0.88$	0.64	$0 \leq 0.14 \leq 0.93$	0.17
✝ Plastic	$0 \leq 0.04 \leq 0.35$	0.32	$0 \leq <0.001 \leq 0.32$	0.48

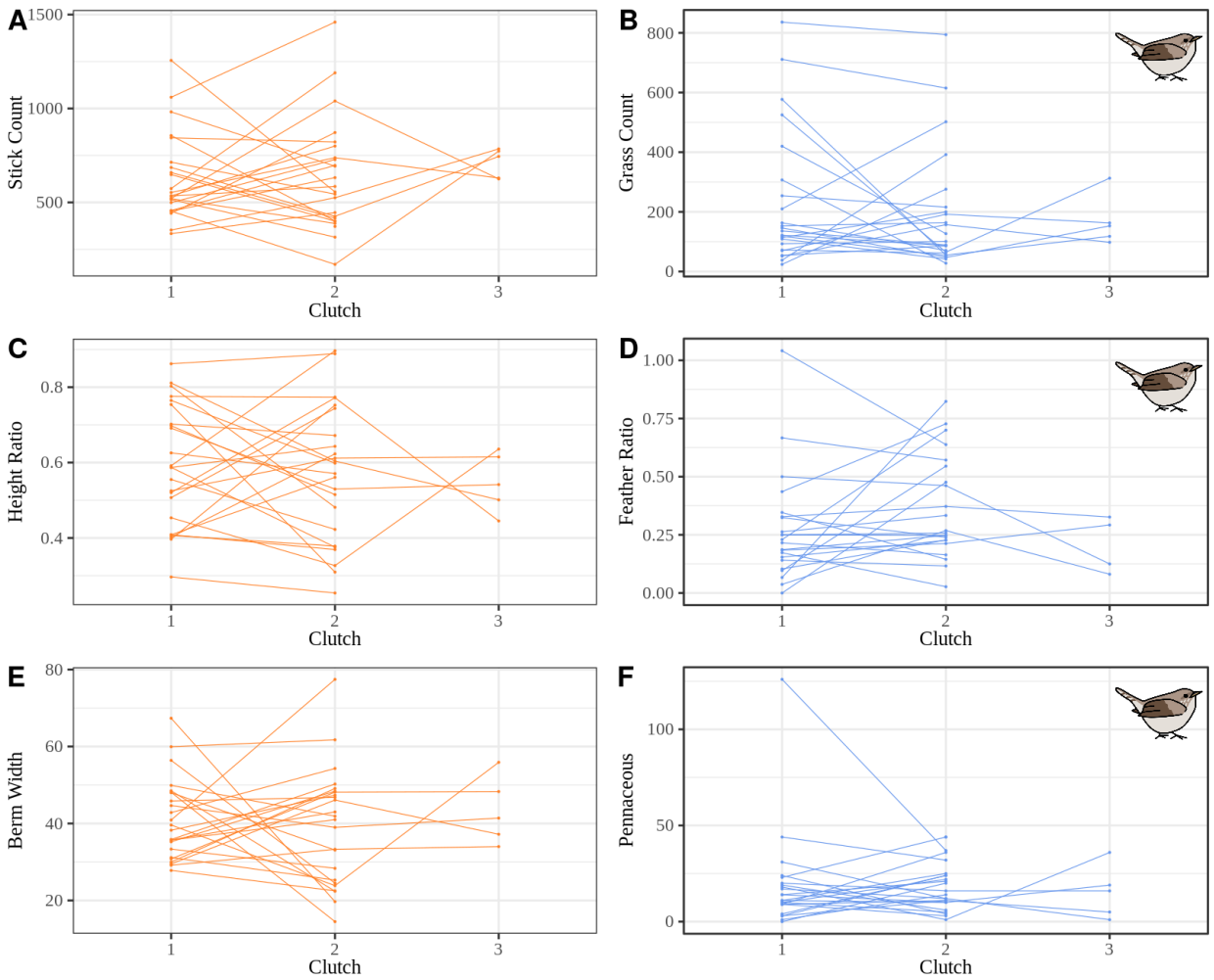

Figure 3 - The repeatability of nest measurements across successive clutches for individual females. Significant repeatability by female identity is indicated by the presence of a house wren drawing. Female house wrens construct similar nest cups across multiple nesting attempts with the grass count (B; P = 0.004), feather ratio (D; P = 0.002), and pennaceous feather count (F; P = 0.05) each indicating significant repeatability for females. However, none of the characteristics of the stick platform showed significant repeatability (P > 0.08). Characteristics of the stick platform are shown in orange (left), and characteristics of the cup lining are shown in blue (right).

Effects of Nest Box Dimensions

The height ($r^2 = 0.06$, $P = 0.006$) and volume ($r^2 = 0.16$, $P < 0.001$, Figure 4A) of the nest platform positively correlated with the internal height of the box. Likewise, the number of sticks within the platform positively correlated with the internal height ($r^2 = 0.12$, $P < 0.001$, Figure 4B) and volume ($r^2 = 0.14$, $P < 0.001$) of the box. The height of the nest was positively correlated with the height of the rectangular gap above the entrance hole ($r^2 = 0.13$, $P < 0.001$, Figure 5A). It is worth noting that within our sample, boxes with taller internal heights tended to have higher rectangular gaps ($r^2 = 0.13$, $P < 0.001$, Figure 5B). The width of the berm positively correlated with the diameter of the entrance hole ($r^2 = 0.03$, $P = 0.05$, Figure 6A), but not the depth of the entrance hole ($P = 0.43$, Figure 6B). The closer the top of the nest was built to the entrance hole (See Figure 1), the larger the width of the berm ($r^2 = 0.09$, $P = 0.001$). No other measurement correlated with box dimensions (Table 3).

Table 3 - P-values of the correlations between nest characteristics and box dimensions. Significant correlations are indicated by bold text.

	Internal Box Height	Internal Box Volume	Gap Height	Entrance Diameter	Entrance Depth
Nest Height	**0.006**	0.86	**< 0.001**	0.63	0.58
Nest Volume	**< 0.001**	**< 0.001**	0.12	0.23	0.85
Nest Berm	0.42	0.053	0.54	**0.05**	0.43
Stick	**< 0.001**	**< 0.001**	0.12	0.81	0.85
Grass	0.20	0.37	0.84	0.19	0.65
Total Feather	0.60	0.88	0.81	0.27	0.08
Pennaceous	0.65	0.69	0.88	0.30	0.16
Plumulaceous	0.64	0.97	0.73	0.33	0.10

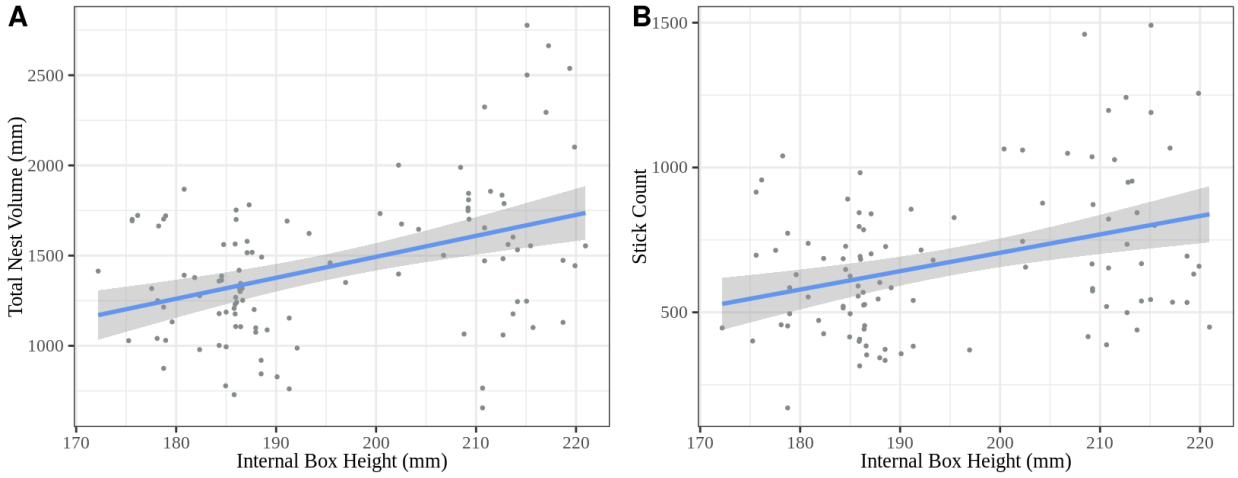

Figure 4 - Significant positive correlations between the internal height of the nesting box and the total volume of the nest (A; P < 0.001) and the stick count (B; P < 0.001).

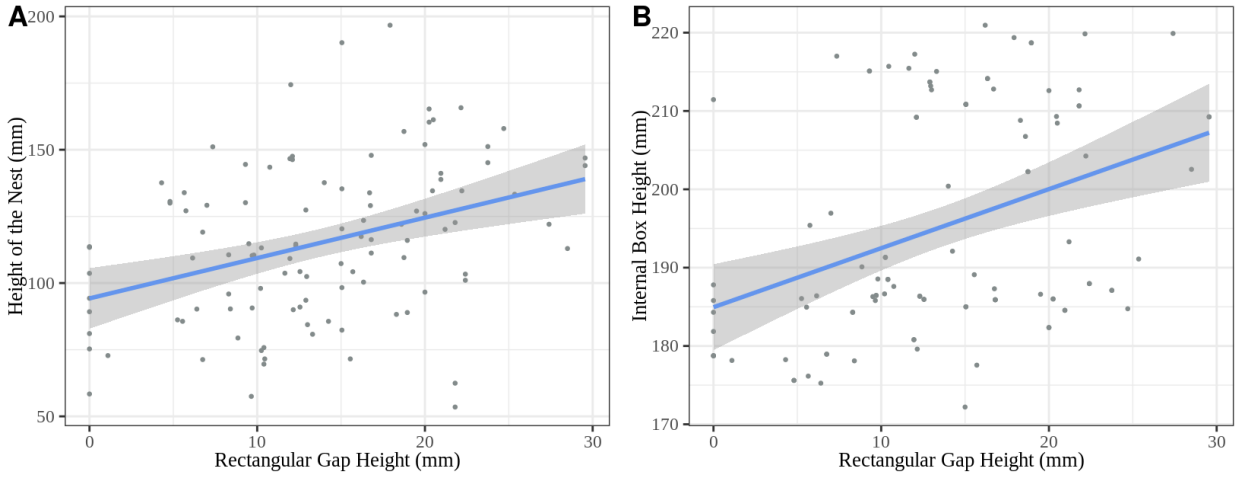

Figure 5 - Significant positive correlations between rectangular gap height and the height of the nest (A; P < 0.001) and internal box height (B; P < 0.001).

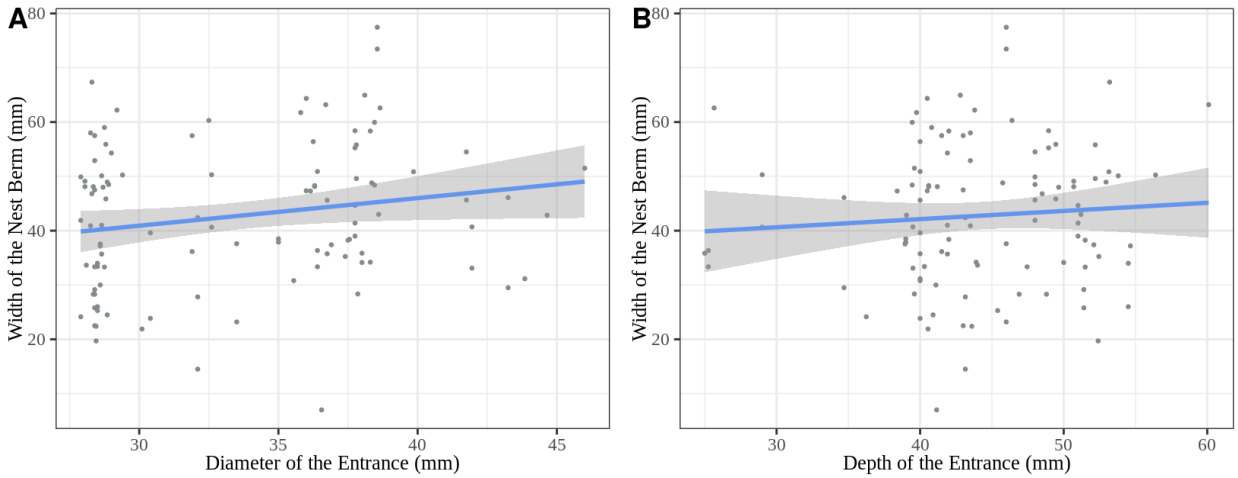

Figure 6 - Relationships between the width of the nest berm and the diameter or depth of the entrance hole. There was a significant positive correlation between the diameter of the entrance hole and the width of the nest berm (A; P = 0.05), but no detectable correlation between the depth of the entrance hole and the width of the nest berm (B; P = 0.43).

Variation Explained By Nest Box Identity

Twenty-six of our boxes were used more than once over the course of the nesting season. Of the boxes, 23 were used twice while 3 were used three times. Of the boxes used more than once, the majority of the nesting attempts were from a different female than any previous attempt (22/29 total reuses; 75.9%; Supplementary 1). The box ID significantly explained the ratio of the nest height to internal box height ($R = 0.25 \leq 0.56 \leq 0.77$, $P < 0.001$, Figure 7C), nest volume ($R = 0.37 \leq 0.65 \leq 0.82$, $P < 0.001$), and the width of the nest's berm ($R = 0.15 \leq 0.49 \leq 0.72$, $P = 0.002$, Figure 7E). Box ID significantly explained the number of sticks within the nest platform ($R = 0.10 \leq 0.45 \leq 0.7$, $P = 0.008$, Figure 7A), but not the grass count ($R = 0 \leq 0.04 \leq 0.38$, $P = 0.38$, Figure 7B), total count of feathers in the nest ($R = 0 \leq 0 \leq 0.34$, $P > 0.99$) or the pennaceous feather count ($R = 0 \leq 0.08 \leq 0.42$, $P = 0.32$, Figure 7F). Box ID

potentially further explained part of the variation in the pennaceous to plumulaceous feather ratio ($R = 0 \leq 0.29 \leq 0.59$, $P = 0.05$, Figure 7D), although the confidence interval overlaps with zero. The box ID did not explain the amount of spider egg sac material in the nest ($R = 0 \leq 0 \leq 0.21$, $P > 0.99$). No other measurements were repeatable (Table 2).

Table 4 - P-values supporting the lack of significant correlations between nest characteristics and the nest age.

	Grass Count	Total Feather	Wing	Body	Age
Nest Height	0.95	0.94	0.69	0.81	0.12
Nest Volume	0.71	0.89	0.49	0.93	0.14
Nest Berm	0.76	0.93	0.37	0.83	0.78
Stick	0.19	0.35	0.32	0.44	*0.052*

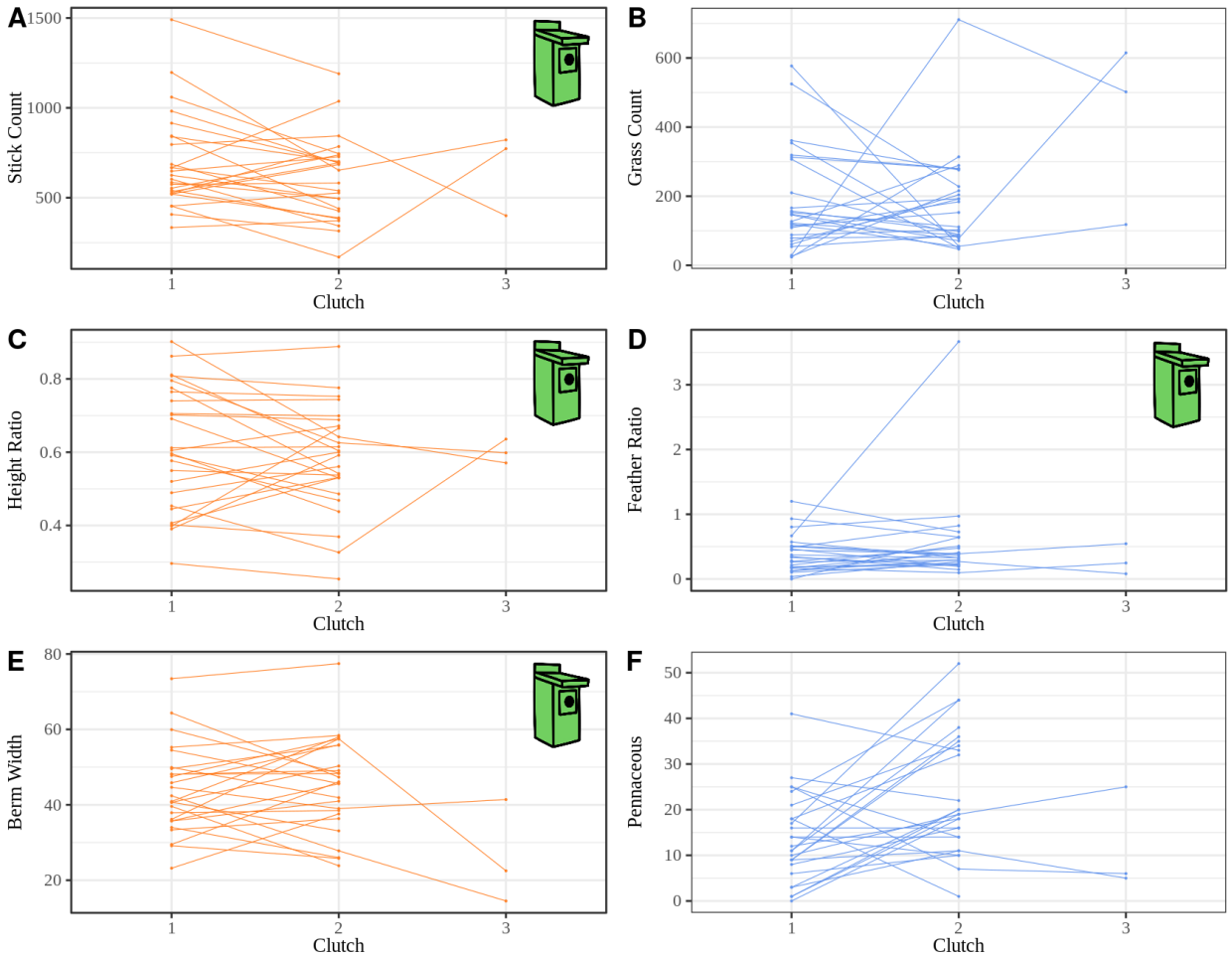

Figure 7 - The repeatability of nest measurements across successive clutches built in the same nest box. Significant repeatability by box identity is indicated by the presence of a nest box drawing. The stick count (A; P = 0.007), height ratio (C; P < 0.001), berm width (E; P = 0.002), and feather ratio (D; P = 0.05) were significantly repeatable traits for the nesting box identity, while grass Count (B; P = 0.39) and pennaceous (F; P = 0.32) were not. Line colours as in Figure 3.

Nest Dimensions and Age

The width of the berm positively correlated with the height ($r^2 = 0.03$, $P = 0.04$), volume ($r^2 = 0.09$, $P < 0.001$, Figure 8A), and stick count ($r^2 = 0.04$, $P = 0.02$, Figure 8B) of the nest.

The stick count positively correlated with the height ($r^2 = 0.37$, $P < 0.001$, Figure 8C) and volume ($r^2 = 0.41$, $P < 0.001$, Figure 8D) of the nest. Total feather count ($r^2 = 0.03$, $P = 0.04$, Figure 8E) and pennaceous feather count ($r^2 = 0.06$, $P = 0.005$, Figure 8F), but not plumulaceous feather count ($P = 0.15$) positively correlated with the grass count. No other correlations were statistically significant (Table 4).

The pennaceous feather count positively correlated with the age of the nest ($r^2 = 0.04$, $P = 0.02$, Figure 9A), but the plumulaceous ($P = 0.43$) and total feather ($P = 0.18$) counts did not. The grass count ($r^2 = 0.03$, $P = 0.054$, Figure 9D) and stick count ($r^2 = 0.03$, $P = 0.052$, Figure 9C) marginally negatively correlated with the age of the nest. As expected, younger nests were also less likely to contain faecal material, with nests older than 20 days almost always containing some amount of faecal material ($t = 5.24$, $P < 0.001$, Figure 9B).

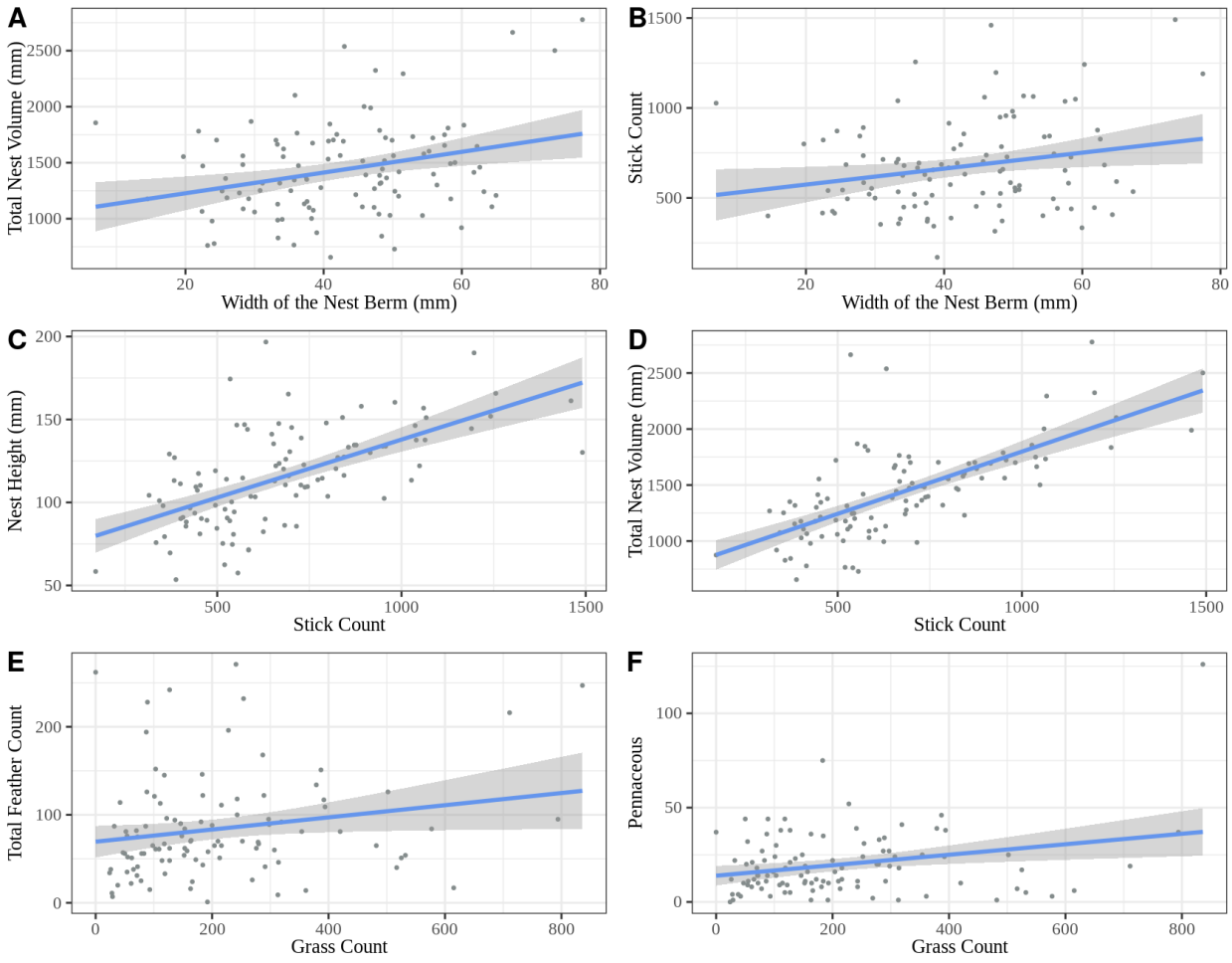

Figure 8 - Relationships between different nest attributes and building materials. The width of the nest berm positively correlated with the total volume (A; $P < 0.001$) and stick count (B; $P = 0.02$) of the nest. The stick count further highly positively correlated with the height of the nest (C; $P < 0.001$) and the total volume of the nest (D; $P < 0.001$). The grass count positively correlated with the total count of feathers (E; $P = 0.04$) and pennaceous feather count (F; $P = 0.005$).

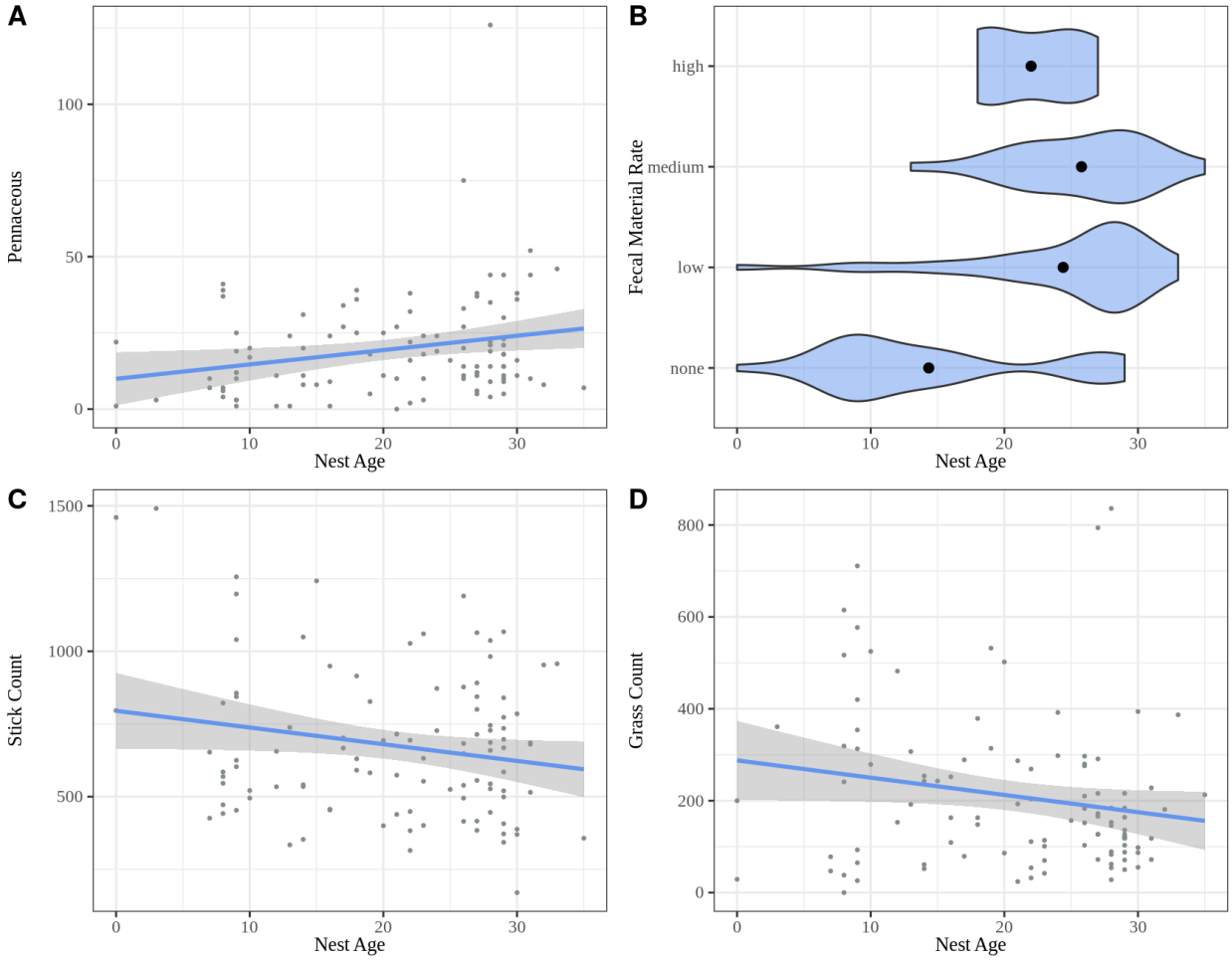

Figure 9 - Relationship between three nest materials and faecal material with the age of the nest at collection. Pennaceous feather count positively correlated with the nest age (A; P = 0.02). Although not statistically significant, the stick count (C; P = 0.052) and the grass count (D; P = 0.054) negatively correlated with the age of the nest. Older nests contained more faecal material than younger nests (B; $P < 0.001$).

Effects of Seasonal Change and Proxies of Fitness

We did not find the ratio of the nest height to internal box height ($P = 0.54$) or the width of the berm ($P = 0.74$) to correlate with the date of measurement. Neither the stick count ($P = 0.72$) or grass count ($P = 0.88$) correlated with the measurement date. A statistical trend was

found with the pennaceous feather count positively correlating with the measurement date (r^2 = 0.02, P = 0.07, Figure 10C), with the result reaching statistical significance with the removal of an extreme outlier (Date of year of outlier: 144; r^2 = 0.09, P = 0.001), but this trend was not found with plumulaceous feathers (P = 0.27) or total feather count (P = 0.15). The amount of spider egg sacs within the nest positively correlated with the measurement date (t = 4.485, P < 0.001, Figure 10D). Nests sampled later in the breeding season were more likely to produce successful clutches than nests built earlier in the season (t = 2.039, P = 0.04, Figure 10A) but also fledged fewer offspring (t = -5.890, P < 0.001, Figure 10B). However, this result is likely due to females laying fewer eggs later in the season (t = -10.26, P < 0.001).

No correlations between the body condition of the female builder, clutch size, or offspring success and nest morphology were observed (Supplementary 2).

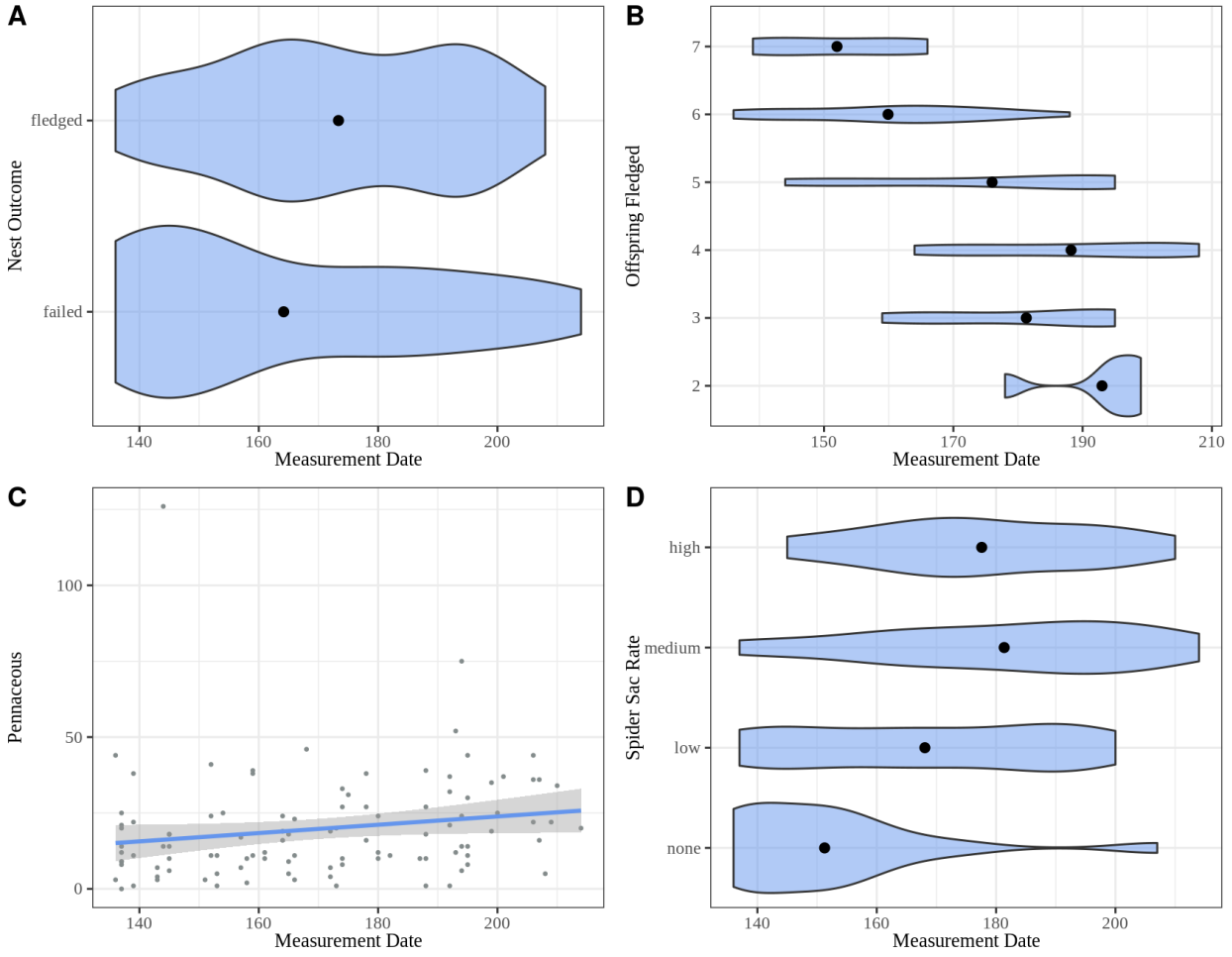

Figure 10 - Significant relationships between nest characteristics and the date of nest measurement (i.e., completion of egg laying). Nests measured earlier in the season were more likely to fail than nests measured later in the season (A; P = 0.04), but also fledged fewer offspring (B; P = 0.002). The pennaceous feather count positively correlated with the measurement date after the removal of the outlier on DOY 144 (C; P = 0.001). Nests measured later in the season also contained more spider sac material than those measured earlier in the season (D; P < 0.001).

DISCUSSION

Extended Phenotypes are Complex

The niche-construction hypothesis argues that construction behaviours should be relatively invariable, both spatially and temporally, because the benefits of the product of the construction should be long term and stable (Clark et al. 2020). However, we found house wren nests to be extremely variable both among-individuals and across the breeding season. Consistent with previous research (Alworth 1996, Eckerle & Thompson 2005), the variation was unrelated to female body condition or the number of offspring fledged, two important proxies of the builder's fitness, suggesting that nest architecture is not under strong selection. We asked: in the absence of strong selection for specific nest characteristics, what explains the observed variability?

Extended phenotypes are a complex bidirectional interaction between the builder and their environment, with builders attempting to express their phenotype within the confines of available space. We found evidence of repeatability for the female builder in multiple components of the cup composition. We also found that nest morphology was affected by the availability of space within the nesting cavity, supported by repeatability in the cavity identity. Our findings suggest a previously unexplored explanation for variation in nest architecture: differences between individual females in their building preferences. Together with the cavity space's ability to constrain or enhance the nest dimensions, these two factors contribute to the complex interplay between the female builder and the environment in the expression of the wren's extended phenotype. We also employed an uncommon method for measuring construction behaviour (i.e., directly measuring individual building materials) leading to the discovery of repeatable characteristics that would have otherwise remained hidden with more

coarse measurements like nest weight. Future research should compare the variation across populations and breeding seasons to fully understand the spatial and temporal variation of nest architecture in this species.

Preferences in Construction behaviour

Our prediction that the nesting female would be the best predictor of variation in nest architecture was only partially supported. The cup composition (i.e., the grass count, pennaceous feather count, and ratio of pennaceous to plumulaceous feathers) was highly repeatable for the female, but female identity did not explain variation in the rest of the nest morphology. This finding reinforces previous conclusions that the female constructs the nest cup independent of the male (McCabe 1965), but implicates other factors in the construction of the stick platform, such as physical constraints. The cup appears largely unaffected by these constraints and similarly unrelated to fitness. We hypothesise that when constraints and selective pressures favouring a specific nest architecture are reduced, the effect of diverse female building preferences on nest variation is enhanced. Female blue tit (*Cyanistes caeruleus*) nests, for example, are also extremely variable in height and this behaviour is moderately repeatable for females (R = 0.40; Järvinen et al. 2017a) despite nest height in this species appearing unrelated to nestling survival or female body condition (Järvinen et al. 2017b). Therefore, variation between individual construction preferences is likely a driving force behind much of the observed variability in nest architecture for cavity nesters.

If much of the nest variation is explained by diversity in individual preferences, it is important to understand what causes builders to differ from each other. Although this study is one of the first to tie the repeatability of an extended phenotype directly to individuals in a

free-living population, lab experiments have implicated differences in experience as a potential factor that affects individual preferences. For example, zebra finch (*Taeniopygia castanotis*) pairs that had previous experience constructing nests built more repeatable nests during experimental trials (Whittaker et al. 2023) and juvenile black widow spiders (*Latrodectus mactans*) exposed to conspecific webs built more repeatable webs in adulthood (DiRienzo et al. 2019). Overall, having prior experiences with construction behaviours tends to result in individuals building more repeatable structures, with experiences being either previous attempts or social interactions.

Some females in our study were more consistent builders than others, but we find it unlikely that experience from prior breeding seasons could have contributed to these differences. Long-term demographic data from multiple northern house wren populations indicate that the majority of individuals only breed in a single season (average lifespan is 1.5 years; interannual return rates ~30%; Johnson 2020) and so are unlikely to provide a sufficient sample size for an analysis of interannual individual differences. The age of individuals could act as a proxy of experience in some species, but we are unable to present an analysis of its effect on repeatability in this study. While moult patterns allow many songbirds to be aged as either in their first breeding season or older, this process is challenging in house wrens (Pyle 1997), and we are not confident in our age assignments.

Individuals are also affected by trade-offs between the construction of the extended phenotype and other behaviours important for fitness. Starved colonies of *Stegodyphus sarasinorum*, for example, invest more in web construction than fed spiders (Ellendula et al. 2021), and immune stressed three-spined stickleback (*Gasterosteus aculeatus*) males construct less compact nests than healthy conspecifics (Barber et al. 2001). Thus, construction

behaviours can be important indicators of the builder's condition. We examined the female body mass and the linear residual between body mass and tarsus length as two measures of female condition as an explanation for among-individual variation, but neither correlated with the observed variability in nest cup composition.

Construction behaviours can also be directly related to reproductive effort and success, particularly in oviparous species, with this relationship often resulting in low among-individual variation (Clark et al. 2020). Zebra finches modify successive nests when the previous clutch fails (Edwards et al. 2020) and male barn swallows (*Hirundo rustica*) who invest more in nest construction also invest more in the food provisioning (Møller 2006). The reproductive effort of female house wrens declines throughout the season (e.g., females lay fewer eggs later in the season), so we expected that pairs would similarly put less effort into nest construction. However, in our study, nest cup composition did not differ between successful or unsuccessful nests or correlate with the number of eggs laid, and remained highly variable throughout the breeding season. Conversely, we found that nests collected longer after the initiation of construction tended to contain more pennaceous feathers than nest collected sooner, and even observed one female returning to her complete clutch of eggs with a feather in her bill, indicating a potential upkeep behaviour in cup composition despite the increasing needs of the offspring. The lack of any apparent reproductive cost to construction behaviour conflicts with the results of other studies on extended phenotypes, but remains consistent with previous literature on northern house wrens (Alworth 1996, Pribil & Picman 1997, Eckerle & Thompson 2005). We discuss potential causes for this lack of fitness-related nest architecture below.

Physical Constraints to Constructions

The box cavity was also a significant predictor of nest morphology and composition. This repeatability supports our prediction that nest architecture would be related to constraints posed by the cavity dimensions. House wrens appeared to be filling the available space and adjusting nest morphology based on differences between box openings. Stanback et al. (2013) suggested that wrens were modulating the nest structure to accommodate for perceived vulnerabilities in the cavity, and our data support this conclusion. For example, the size of the entrance hole is a potential source of vulnerability, as more accessible nests are more likely to be depredated and parasitized (Paclík et al. 2009, Hauber et al. 2024). We found house wrens to have larger berm widths in boxes with larger entrance hole diameters, potentially modulating their nest structure to better protect the contents of the nest. Previous research has suggested that the berm could act as a barrier between the nestlings within the cup and any outside threats (Stanback et al. 2013), however evidence for this relationship is inconsistent (Pribil & Picman, 1997). Despite our support of Stanback et al.'s (2013) finding, the width of the nest berm had no effect on the number of eggs laid or nestling survival. We found a similar correlation between the height of the rectangular gap and the height of the nest, as larger gaps resulted in taller nests. House wrens may be modulating their construction behaviours in response to perceived vulnerability, but our results suggest that this action has little to no effect on nest success.

Evidence from other species suggests that structures can protect inhabitants from predators and environmental threats by the construction of a physical barrier. For example, Eurasian beavers (*Castor fiber*) in the Netherlands, which face lower predation rates and milder climates than their northern counterparts, build lodges with thinner walls (Rosell & Campbell-Palmer 2022). However, cavity-nesters do not need to construct a physical barrier, as

the cavity itself is the barrier between the inhabitants and the outside environment. We hypothesise that the lack of any detectable relationship between nest architecture and fitness in house wrens could be due to selection favouring a better quality cavity rather than specific characteristics of the nest. Observations of platypus (*Ornithorhynchus anatinus*) nests, which are housed inside burrows, are consistent with this hypothesis as the dimensions of the burrow explained offspring production, while effort in nest construction was unrelated (Thomas et al. 2018). Support for this hypothesis in house wrens is more indirect, but males with empty cavities due to experimentally removed nests were just as likely to acquire a mate as control males that initiated nest building (Alworth 1996), suggesting that the cavity rather than the contents are more important in mate choice. Female house wrens also use cavity quantity before male quality when choosing mates (Eckerle & Thompson, 2006) and male house wrens selectively choose nesting boxes with smaller entrances that likely provide superior protection from predators and brood parasites (Pribil & Picman 1997). Collectively, the available data suggest that the reproductive success of house wrens is more related to the cavity itself than the nest.

Limitations

Extended phenotypes become additionally complex when more than one individual contributes to the object of construction behaviour. Both sexes contribute to the nest building in house wrens, so it is important to consider how the male contribution may affect our data and interpretation. Although their contributions are likely not equal, with the female completing the majority of the nest (Alworth & Scheiber 2000), we were unable to directly account for the effect of individual males on construction behaviour because the majority of

555 males were unbanded. Despite this limitation, northern house wren pairs often change between
556 nesting attempts (Baldwin 1921, Drilling & Thompson 1988), so it is rarely the same pair
557 building successive nests. In 2019, we found that out of 31 banded pairs in our population, only
558 6 (19.4%) remained with the same mate for the entire breeding season, with the female being
559 more likely to leave than the male. The fact that females were repeatable in cup composition,
560 despite frequent mate switching, supports our conclusion that the female constructs some
561 aspects of the nest independently of the male. Box identity could potentially be a proxy of the
562 male identity, as cavities are controlled by individual males on their own territories; however,
563 males often control many boxes within the same territory and the rate of movement between
564 these boxes is unknown. Therefore, we are unable to split apart the identity of the male from
565 the identity of the box in this study. Males begin bringing sticks to the cavity before acquiring
566 a mate (Johnson 2020), and so if the box identity is a reliable proxy for male identity, then the
567 male contribution to building could help explain the observed variation in the stick platform,
568 but more research is needed.

569 In most cases, we only measured the construction attempts of individuals twice. House
570 wrens only produce two to three clutches a season, so we are limited by this number and the
571 likelihood the female renested within our nest boxes instead of natural cavities. However, Bell
572 et al. (2009) found no significant effect of the number of observations per individual on
573 repeatability estimates. Instead, the number of observations appears to have a greater effect on
574 the range of uncertainty in the estimate. We provided this range of uncertainty, as a confidence
575 interval, and required the lower end to remain higher than zero for significance. Furthermore,
576 all of our estimates are calculated from a sample size (N = 24 for female identity; N = 26 for

box identity) larger than the median sample size ($N = 22$) of all studies examined by Bell et al. (2009), and so we do not believe that our sample size is a major limitation.

Conclusions

The repeatability of construction behaviours is greatly understudied, particularly in free-living populations. We examined the northern house wren, a species with incredible variation in nest architecture, to estimate the amount of variability in construction behaviour explained by the identity of the female builder and the box identity and its dimensions. We found female northern house wrens to be highly repeatable in the composition of the nest cup, but this behaviour was unrelated to female body condition or nestling survival. The variation in the main structure of the nest, the stick platform, was best explained by the box identity and its dimensions, supporting previous findings that house wrens modify aspects of the nest to compensate for vulnerabilities in the cavity. We hypothesise that the observed variability in nest architecture is due to the nest being under minimal selective pressure, thus allowing the diversity of female building preferences to have a greater effect on the expression of the phenotype. Instead, choosing a protective cavity is likely to be more important for the builder's fitness, with the nest construction process being relatively unimportant for mate selection or nestling survival. However, much of house wren nest construction still remains unclear, including the contribution of the male in constructing the stick platform. Extended phenotypes are complex, requiring an examination of both the environment *and* the builder. The cause of variation in house wren nest morphology has been largely unexplained due to a narrow focus on potential external factors. Studying the repeatability of extended phenotypes across taxa has

provided new insights into the construction behaviours of animals and provides an important method for understanding the causes and consequences of individual preferences.

Data Availability Statement

The data and code that support these findings are available in the Mendeley Data Repository at doi: 10.17632/fnhr5mm99p.1.

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823 **SUPPLEMENTARY**

824 *Supplementary 1 - Individuals examined for Female Identity repeatable traits and Box Identity*

825 *traits. Females with single IDs were unbanded individuals.*

Female Repeatability			Box Repeatability		
Female ID	Clutch	Box ID	Box ID	Clutch	Female ID
288064919	1	3	1	1	288067191
288064919	2	2	1	2	288067191
288067191	1	1	1	3	288067191
288067191	2	1	3	1	288064919
288067191	3	1	3	2	294063102
288064901	1	6	4	1	288064918
288064901	2	4	4	2	288064901
294063102	1	8	9	1	288064920
294063102	2	3	9	2	294063222
288064903	1	19	13	1	288064917
288064903	2	18	13	2	294063155
288067184	1	25	17	1	288064902
288067184	2	24	17	2	294063262
288064906	1	28	19	1	288064903
288064906	2	29	19	2	294063200
288064906	3	29	20	1	288064905
288064947	1	33	20	2	294063294

288064947	2	30
288064905	1	20
288064905	2	21
288064913	1	46
288064913	2	46
288064913	3	54
288064915	1	41
288064915	2	41
294063218	1	47
294063218	2	49
288064991	1	40
288064991	2	39
288064923	1	39
288064923	2	47
288064997	1	56
288064997	2	56
288064939	1	54
288064939	2	55
288067301	1	80
288067301	2	79
288064925	1	68
288064925	2	67
288067007	1	70

29	1	288064906
29	2	288064906
30	1	1
30	2	288064947
33	1	288064947
33	2	294063157
38	1	294063259
38	2	294063453
39	1	288064923
39	2	288064991
41	1	288064915
41	2	288064915
43	1	288064912
43	2	294063461
44	1	288064911
44	2	294063173
46	1	288064913
46	2	288064913
47	1	4
47	2	294063218
47	3	288064923
48	1	5
48	2	288064996

288067007	2	71	49	1	6
288067007	3	65	49	2	294063135
288064916	1	63	49	3	294063218
288064916	2	63	54	1	288064939
288064916	3	62	54	2	288064913
294063101	1	61	56	1	288064997
294063101	2	60	56	2	288064997
294063230	1	76	63	1	288064916
294063230	2	75	63	2	288064916
294063219	1	77	65	1	288067007
294063219	2	66	65	2	7
288064910	1	58	66	1	288064924
288064910	2	59	66	2	294063219
			70	1	288067007
			70	2	294063180

Supplementary 2 - Relationships between the dimensions and components of the nest and various proxies of fitness: Female residual - defined by the correlation between the tarsus length and the body mass, Fledge or Fail - the simply outcome of the nest, Eggs laid - the number of eggs originally laid by the nesting female at the completion of the cup, and Offspring fledged - the estimated number of offspring that fledged the nest (only successful nests examined). ✝️ *Specified material measured as a simple yes/no presence.*

	Female	Fledge or Fail	Eggs laid	Offspring

	residual			fledged
Ratio	t = 1.64, *P* = 0.11	*z* = 0.10, *P* = 0.92	t = -0.77, *P* = 0.45	t = 0.73, *P* = 0.47
Nest Height	t = 0.90, *P* = 0.37	*z* = -0.119, *P* = 0.91	t = -0.81, *P* = 0.42	t = 0.54, *P* = 0.59
Nest Volume	t = 0.46, *P* = 0.65	*z* = -0.132, *P* = 0.89	t = -0.63, *P* = 0.53	t = -0.06, *P* = 0.95
Nest Berm	t = -0.64, *P* = 0.52	*z* = 0.108, *P* = 0.91	t = 0.08, *P* = 0.94	t = -0.35, *P* = 0.73
Stick	t = -0.39, *P* = 0.70	*z* = -0.716, *P* = 0.47	t = -0.03, *P* = 0.97	t = -0.66, *P* = 0.51
Grass	t = 0.67, *P* = 0.50	*z* = -1.564, *P* = 0.11	t = 0.89, *P* = 0.37	t = -1.04, *P* = 0.30
Total Feather	t = 0.03, *P* = 0.97	*z* = 0.310, *P* = 0.76	t = 0.13, *P* = 0.90	t = -1.45, *P* = 0.15
Wing Rate	t = -0.12, *P* = 0.90	*z* = 1.324, *P* = 0.13	t = 0.28, *P* = 0.78	t = 0.12, *P* = 0.91
Pennaceous	t = -1.07, *P* = 0.29	*z* = 1.584, *P* = 0.08	t = -0.01, *P* = 0.99	t = -1.91, *P* = 0.06
Plumulaceous	t = 0.43, *P* = 0.67	*z* = -0.229, *P* = 0.82	t = -0.16, *P* = 0.88	t = -0.95, *P* = 0.35
Spider Sac Rate	t = -0.59, *P* = 0.56	*z* = 0.408, P = 0.68	t = -1.15, *P* = 0.25	t = -0.26, *P* = 0.80
✝️ Snake Skin	χ^2_1 = 0.08, *P* = 0.77	*z* = -0.808, *P* = 0.42	t = 1.202, *P* = 0.23	t = 1.269, P = 0.20
✝️ Plastic	χ^2_1 = 0.002, *P* = 0.96	*z* = -1.567, *P* = 0.11	t = 1.735, *P* = 0.08	t = 0.090, *P* = 0.93

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