Facultative nest modification by Rock Wrens (*Salpinctes obsoletus*) Rock Wrens, nest site modification, goaldirected beh

1. INTRODUCTION

While many bird nests are structurally complex, the underlying cognitive requirements of nest-building behaviour have been debated (Lefebvre *et al.*, 2004; Hansell and Ruxton, 2008; Healy *et al.*, 2008). Recent laboratory studies have comprehensively demonstrated that nest-building behaviours are heavily reliant on the cognitive skill of the building birds (Muth and Healy, 2011; Moreno, 2012; Bailey *et al.*, 2014). It is informative, therefore, to measure not just nest construction behaviour, but facultative adjustments that animals make to their nest construction behaviours. Such adjustments provide evidence of behavioural complexity and potential cognitive demands (Healy *et al.*, 2008; Walsh *et al.*, 2013; Biddle *et al.*, 2015). Flexible nest construction behaviours have been shown to compliment simple fixed action patterns, to change according to experience, and to require learning, multitasking, and retention of information (Yeh *et al.*, 2007; Walsh *et al.*, 2011, 2013). These combined lines of evidence suggest that nest building and nest placement often does require advanced awareness and processing of nest site conditions.

Many birds augment their nests with additional external materials that can improve nest success through various means. Examples include: camouflage, *i.e.* lichens, colour-matched paper (Hansell, 1996; Bailey *et al.*, 2014),

thermal conductors or insulators; Afik *et* [redacted]

et al, 2002; Bentley-Condit and Smith, 2010). These definitions have been debated in the literature, but are grounded on the fundamental idea that tools are non-self objects used to manipulate the environment in a goal-directed manner (St. Amant and Horton, 2008; Seed and Byrne, 2010). Here we examine how birds may use stones as tools during a unique nest construction strategy; augmenting a nesting cavity by placing stones both within and around it. Facultative usage of environmental materials (tools) around the nest by birds supports the idea that nest construction is not confined to simply building a structure which contains eggs (Leader and Yom Tov, 1998). Some argue that tool use has been assigned a privileged designation, stressing that tool use *per se* does not presume cognitive ability (Hansell and Ruxton 2008; Arbib 2012), but other work suggests that tool use and environmental manipulation may be seen as evidence for complex processing of the nesting environment (Soler *et al.*, 1996; Leader and Yom-Tov, 1998).

[redacted]ock Wren[redacted] ([redacted]*alpinctes* [redacted]*oletus*) build[redacted] cup [redacted] out of grass and twigs, which they situate within natural rock cavities (Bent, 1964; Lowther *et al.*, 2000). Prior to and during nest construction, Rock Wrens alter the form of those cavities by placing stones below the nest cup and around the cavity entrance. Studying Rock Wren nests goes beyond typical “nest-building” behaviour, because the added stones are not part of the nest itself. Rather, their use is a structural modification of the nesting environment (Warning and Benedict, 2014). The stones that Rock Wrens place around nests can be used as quantifiable units with which to examine the relationship between nest structures, nest-building behaviour, and nest cavity properties. Rock Wrens can and do occasionally nest successfully without using stones, yet stones are an integral part of the nesting strategy of this species (Merola, 1995; Lowther *et al.*, 2000).

Rock Wrens exhibit high variation in the size and type of nest cavities, and in the amount of stones that they add to nest cavities, which has led to much speculation as to the function(s) that the stones serve (Bailey, 1904; Smith 1904; Brewer 2010). Our previous work has

3. RESULTS

Rock Wren nest stones were consistently thin throughout the study area, with stone thickness and weight showing less variability than length, and width (Table 1). Stones ranged in weight from 0.2 to 12.6 g (mean = 3.03 g, or ~ 20% of average body mass). Nests sampled in New Mexico *versus* Colorado contained stones that were slightly longer on average ($t_{5.72} = 2.66$, $P = 0.032$), but did not differ in width ($t_{5.7} = 1.41$, $P = 0.21$), thickness ($t_{5.7} = -0.28$, $P = 0.79$), or weight ($t_{7.0} = 0.87$, $P = 0.41$) (Table 1).

The original cavity opening areas of nests were circularity. We suggest that flat stones have increased stacking and wedging properties relative to round stones, and therefore improve the stability of nest structures which is important as fragile structures may fall and expose the nest. Additionally, Rock Wrens may maximise the size of stones which they can carry in their bills by preferentially selecting flat stones. Alternatively, flat stones may be prevalent in the wider environments of the study areas that we compared. It is notable that several key nest stone features were remarkably consistent across relatively large geographic areas: Rock Wren nests separated by 1000 km contained stones with almost identical widths, thicknesses and weights. Longer stones in New Mexico compared to Colorado probably reflect differences in underlying geology. Nest sites in New Mexico contain limestone and dolomite formations (Stark, 1956; Osleger, 1998), while the Colorado study area is located in fluvial sandstone and Miocene sedimentary lithology (Izett, 1975; Madole, 1995). Further research could usefully elucidate the differences in stone selection among different Rock Wren populations. Overall, however, stone shape preferences seem to vary little geographically. If flat stones are a key requirement for nesting, then their absence could perhaps limit geographical range. Appropriate selection of materials with particular properties is an important indicator of tool use in animals; our results suggest that Rock Wrens meet this criterion (Chappell and Kacelnik, 2004).

We also found that Rock Wrens adjust the amount of stones that they place in nest structures according to the cavity opening size. Rock Wrens placed more stones at large cavity openings, sometimes blocking up to 100 cm^2 of the cavity entrance (see Appendix). In our study, Rock Wrens did not place stones throughout the cavity, as is evidenced by the lack of a relationship between cavity depth and stone use. This suggests that they are not merely filling empty space within the cavity, but are instead minimising the size of the nest cavity entrance by constructing precise stone structures, using more stones in openings that were larger prior to stone placement. Despite this relationship, the nests in our study did not have consistently sized entrances when stones were in place (mean ± SD [range], 61.2 ± 40.1 [12.2–189] cm^2; see Appendix), reflecting both variability in cavity selection and limitations to the size, especially the height, of constructed structures. As nest cavity entrances increase in size, they likely become more difficult to occlude, even with the addition of more stones. Variation in completed nest entrances also suggests that other factors, such as nest stability, drainage, and predator avoidance may be driving stone use at nests. Facultative placement and assembly of stones suggests flexibility and greater cognitive complexity than is sometimes attributed to nest construction behaviours (Lefebvre *et al.*, 2004; Raby and Clayton, 2009). This flexible approach to cavity modification likely improves nest protection, and allows Rock Wrens to nest in a wide variety of cavity types and sizes (Bailey, 1904; Warning and Benedict, 2014).

Other species are flexible when building nests. Stanback *et al.* (2013) showed that Eastern Bluebirds (*Sialia sialis*) adjust the height of nests according to cavity depth, and Britt and Deeming (2011) demonstrated that Blue Tits (*Cyanistes caeruleus*) used less (non-scarce) nesting material as ambient air temperatures warmed leading up to nest construction. There has been less direct evidence, however, for birds modifying the microenvironment into which nests are placed (Howlett and Stutchbury, 1997; Leader and Yom-Tov, 1998). Although nest and abode construction is not typically included in tool use definitions since nests are fixed structures, modifications to the environment around nests may be an important bridge between typical nest-building behaviour and more commonly acknowledged tool use (Hansell and Ruxton, 2008; Bentley-Condit and Smith, 2010). More research will be needed to determine the amount of memory and learning that Rock Wrens use during nest construction, and to evaluate the decision-making processes used to select and amend nesting cavities, but our data provide an initial suggestion that Rock Wrens do use higher-order cognitive processes when building nests (Healy *et al.*, 2008; Bailey *et al.*, 2014). Here we provide an example object or substance" (Seed and Byrne, 2010) through a specialised nesting behaviour. Such behaviours require complex nest site manipulation and dynamic interactions between nest builders and their environments.

5. ACKNOWLEDGMENTS

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Nest ID	Location	County, State[a]	Cavity entrance area with stones (cm^2)	Cavity entrance area without stones (cm^2)	Area occluded by stones (cm^2)	Number of stones	Total stone weight (g)
001	Horsetooth Reservoir	Larimer, CO	40	66	26	216	477
002	Horsetooth Reservoir	Larimer, CO	52	120	68	371	1140
003	Pine Ridge NA	Larimer, CO	44	120	76	558	1204
004	Pine Ridge NA	Larimer, CO	49	169	120	514	1292
005	Pine Ridge NA	Larimer, CO	60	78	18	106	282
006	Pine Ridge NA	Larimer, CO	66	84	18	104	268
007	Pine Ridge NA	Larimer, CO	153	258	105	42	111
008	Pine Ridge NA	Larimer, CO	21.9	21.9	0	0	0
009	Red Mountain OS	Larimer, CO	126	168	42	554	1442
010	Cherokee Park SWA	Larimer, CO	56.2	56.2	0	0	0
011	Coyote Ridge NA	Larimer, CO	18	112	94	214	439
012	Coyote Ridge NA	Larimer, CO	63	67.5	4.5	265	557
013	Blue Sky OS	Larimer, CO	168	256	88	306	736
014	Blue Sky OS	Larimer, CO	30	36	6	258	335
015	Horsetooth Reservoir	Larimer, CO	36	40	4	37	45
016	Horsetooth Reservoir	Larimer, CO	50	72	22	130	360
017	Horsetooth Reservoir	Larimer, CO	50	50	0	32	67
018	Horsetooth Reservoir	Larimer, CO	35	38.5	3.5	39	79
019	Arthur's Rock	Larimer, CO	32.5	48	15.5	117	306
020	Arthur's Rock	Larimer, CO	19.5	29.3	9.8	121	366
021	Arthur's Rock	Larimer, CO	35	42	7	230	583
022	Arthur's Rock	Larimer, CO	31.5	65	33.5	230	610
023	Arthur's Rock	Larimer, CO	28.5	44	15.5	291	762
024	Lory State Park	Larimer, CO	47.3	102	54.7	152	435
025	Lory State Park	Larimer, CO	189	300	111	439	879
026	Lory State Park	Larimer, CO	94.5	169	74.5	290	757

Nest ID	Location	County, State[a]	Cavity entrance area with stones (cm^2)	Cavity entrance area without stones (cm^2)	Area occluded by stones (cm^2)	Number of stones	Total stone weight (g)
050							