

Facultative nest modification by Rock Wrens (*Salpinctes obsoletus*)

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ABSTRACT

Dynamic nest-construction behaviours suggest that nest structures can be facultatively adjusted in response to environmental conditions. This is particularly true when nest builders create environmental structures that are supplemental to the nest itself, because these structures can be adapted to nest site conditions. Rock Wrens (*Salpinctes obsoletus*) mechanically alter their nest environments by amending rock-based cavities with stones, which are placed below their soft nest cups and often occlude cavity entrances, and extending out of nest cavities. We measured stones and cavity dimensions in 68 Rock Wren nests to quantify stone form and functional variability in stone use. Nests in our study contained stones with a consistent, flat shape, suggesting that Rock Wrens were selective when choosing stones for use around nests. We found significant positive correlations between the size of the nest cavity entrance, the amount of stones placed in nests, and the occlusion rates of the nest cavity entrances. Our data suggest that Rock Wrens place stones around their nests using selective, goal-directed behaviour with the objective of approaching an optimal cavity entrance size. Stone use at nests reflects high behavioural flexibility, and can be considered tool use during nest construction.

Keywords: Rock Wrens, nest site modification, goal-directed behaviour, stone measures

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), prey attraction (*i.e.* mammal dung; Smith and Conway, 2007), or improvements to nest microclimate (*i.e.* thermal conductors or insulators; Afik *et al.*, 1991; Heenan, 2013). For cavity nesters, modification of cavities can

increase the number of suitable nesting sites by making previously unsuitable cavities suitable nest sites, and may allow breeding habitat expansion (Von Haartman, 1957; Martin and Li, 1992; Eberhard, 1998). When outside objects are brought in to alter the cavity environment, some researchers would consider those objects to be tools (Pierce, 1986; Mather, 1994; Levey *et al.*, 2004), while others would not consider these objects to be tools if they remain fixed to the environment as part of the completed nest (Lefebvre *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).

Rock Wrens (*Salpinctes obsoletus*) build soft cup nests 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 shown that stones occlude cavity entrances and alter nest microclimates by keeping them drier during simulated rainfall events (Warning and Benedict, 2014). In addition, we have suggested that Rock Wrens vary stone use according to cavity size and shape (Warning and Benedict, 2014) and here we extend that work by: (1) quantifying the properties of nest stones selected in multiple locations; and (2) examining facultative stone use by quantifying the relationships between nesting cavity properties and the stones placed in those cavities. If Rock Wrens are

using stones as tools that serve specific functions, we predict that they will be choosy about stone form and will preferentially use stones with particular properties (Chappell and Kacelnik, 2004). If this is a species-wide trait then we expect to see similar nest stone properties across the entire species’ range. Furthermore, if stone use by Rock Wrens is modified by discernment of nest site characteristics, we predict that birds will facultatively adjust the number of stones used in relation to cavity size.

2. METHODS

We measured 68 Rock Wren nests on public lands in Colorado, New Mexico, and Nebraska during all years between 2012 and 2015 (Figure 1). Results include new analyses of 46 nests which were included in a previous study by Warning and Benedict (2014), plus 22 more nests that we measured in 2014 and 2015. Four of these nests were located in New Mexico, one in Nebraska, while the rest were from Colorado. We located nests by observing nesting pairs ($n = 42$), or by searching for nests on hillsides and in rock formations ($n = 26$).

To quantify stone use we counted the number of nest stones in each cavity with we counted and weighed stones weighed to the nearest 0.1 g using a portable electronic scale. Using dial callipers, the length, width, and thickness were measured of ~ 15 randomly selected stones (if present) from each nest by blindly drawing stones from a nylon bag ($n = 1133$ stones). We defined length as the longest axis of the stone, width as the second longest axis, and thickness as the narrowest axis. To evaluate possible differences in nest stone selection by Rock Wrens from contrasting locations, we compared mean stone size from nests in northern Colorado ($n = 64$) and New Mexico ($n = 5$), using two-sample *t*-tests.

To document nest cavity dimensions and occlusion by added stones we measured the height (vertical) and width (horizontal) of the cavity entrance (at the smallest entry point) to the nearest 0.5 cm using a flexible ruler, and repeated the measurement in the same location after removing all stones (Figure 2). We measured cavity depth from the entrance plane to the rear wall to the nearest 0.5 cm using a tape measure. All nests were inactive at the time of measurement (post-fledging, failed, or off-season), and we returned all stones to nests after sampling, restoring the original configurations as closely as possible.

Using linear regression, we tested the predictions that birds would use more stones and a greater total weight of stones in at larger (unoccluded) nest entrances, and whether nest occlusion rates correlated with the entrance area and/or depth of nest cavities. We used a paired *t*-test to compare the opening sizes, and a two-sided *F* test for unequal variance to compare the variability of nest cavity entrance dimensions with and without stones present. All statistics were performed in JMP, v.9 (SAS Institute, Cary, North Carolina, USA).

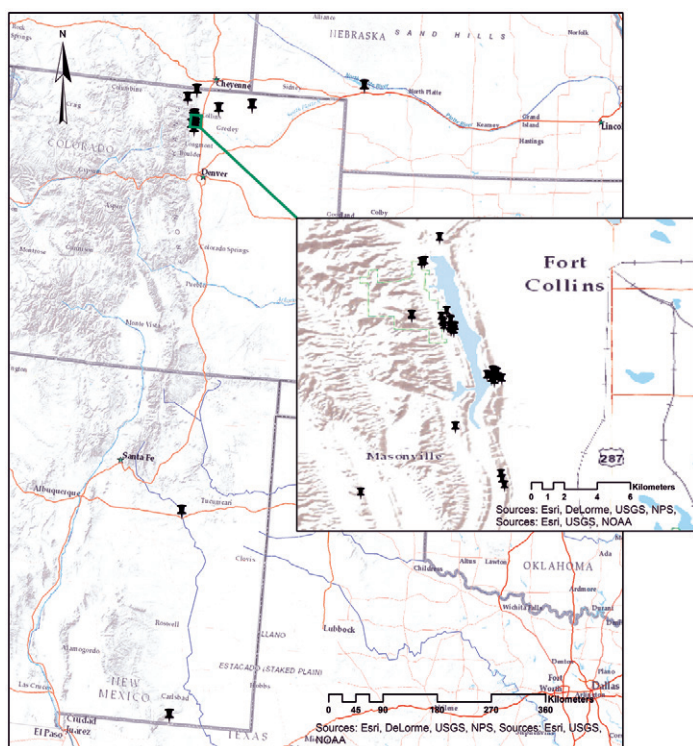


Figure 1 Sampling locations for 68 Rock Wren nests from 2012–2015.

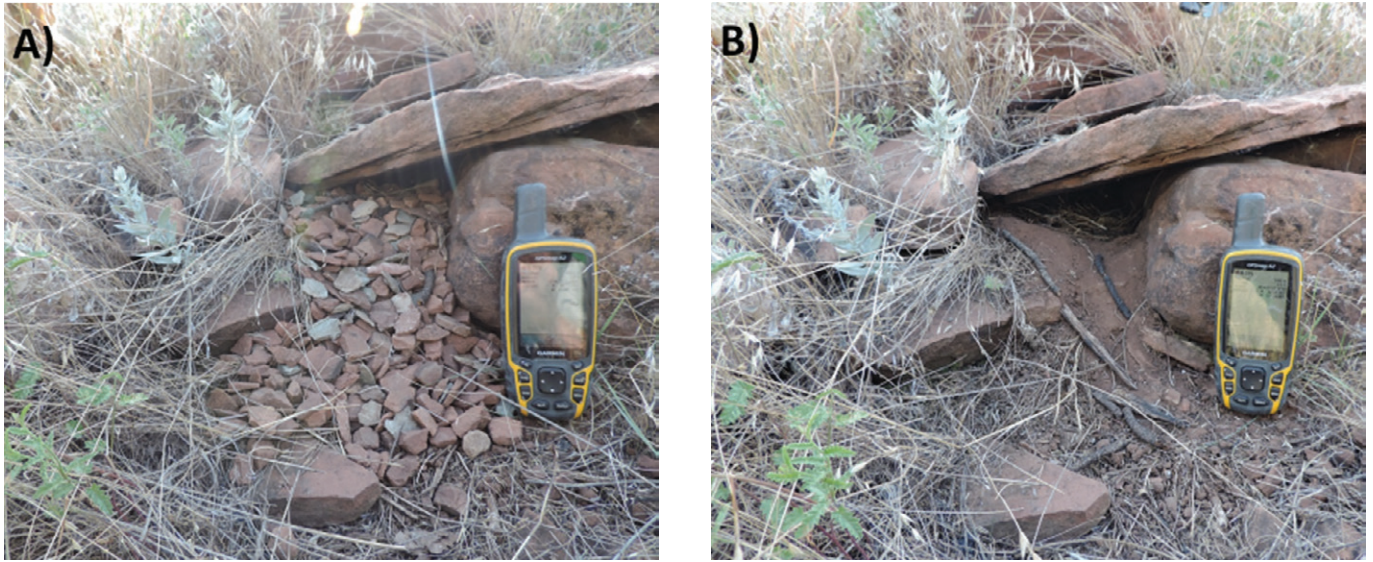


Figure 2 A Rock Wren nest cavity containing 1062 g of stones, shown (A) with stones present, and (B) with stones removed. The GPS unit (14 cm tall) is included for scale. Photos by N. Warning.

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 significantly correlated positively with both the number ($r = 0.52$, $df = 67$, $P < 0.0001$) and weight ($r = 0.52$, $df = 67$, $P < 0.0001$; Figure 3A) of stones added to nests. As a result, the area of the cavity opening occluded by stones correlated tightly with the original size of that opening ($r = 0.84$, $df = 67$, $P < 0.0001$; Figure 3B). Mean cavity opening sizes with stones (61.2 cm²) were significantly smaller than cavity opening sizes without stones (98.2 cm²; $t_{112} = 4.02$, $P < 0.0001$). Further, the variance in cavity opening sizes with stones (SE = 5.0,

SD = 40.1) was significantly smaller than the variance in cavity opening sizes without stones (SE = 7.8, SD = 63.5); $F_{1,66} = 2.44$, $P = 0.0004$). Cavity depth showed no relationship with the weight of stones added to nests ($r = 0.14$, $df = 67$, $P = 0.22$), or with cavity entrance occlusion rates ($r = 0.1$, $df = 67$, $P = 0.37$).

4. DISCUSSION

Successful nests require environmental materials with suitable structural properties (Hansell, 2005; Mennerat *et al.*, 2009; Biddle *et al.*, 2015). These may be materials that make up the nest itself, or, as in the case of the Rock Wren, materials that are used to conceal the nest or alter the environment around the nest. Our data suggest that Rock Wrens choose nest stones according to specialised criteria (Table 1). Rather than taking any available stones, Rock Wrens preferentially select thin, flat stones which they use to occlude cavity entrances. Though we did not sample available stones in the wider environment, observations indicated that the shape of ambient stones near nesting sites showed a wide range of dimensions approaching

Table 1 Summary of Rock Wren nest stone measurements from Colorado and New Mexico

Location	N (stones, nests)	Mean weight (g)	Mean length (mm)	Mean width (mm)	Mean thickness (mm)
Colorado	1037, 64	3.01 ± 1.5 (0.2–12.6)	26.0 ± 6.8 (9.3–59.1)	17.9 ± 4.4 (7.0–37.5)	5.13 ± 1.5 (1.2–10.6)
New Mexico ¹	96, 5	3.18 ± 1.2 (0.4–7.0)	28.2 ± 6.2 (12.0–51.4)	18.7 ± 4.5 (7.4–32.0)	5.14 ± 1.5 (1.8–8.5)
All	1133, 69	3.03 ± 1.5 (0.2–12.6)	26.2 ± 6.8 (9.3–59.1)	18.0 ± 4.5 (7.0–37.5)	5.13 ± 1.5 (1.2–10.6)

¹Includes 20 nest stones from nest B32790 collected by Florence Bailey in 1903, and catalogued at the Smithsonian Institution (Bailey, 1904).

Values are means ± SD (range).

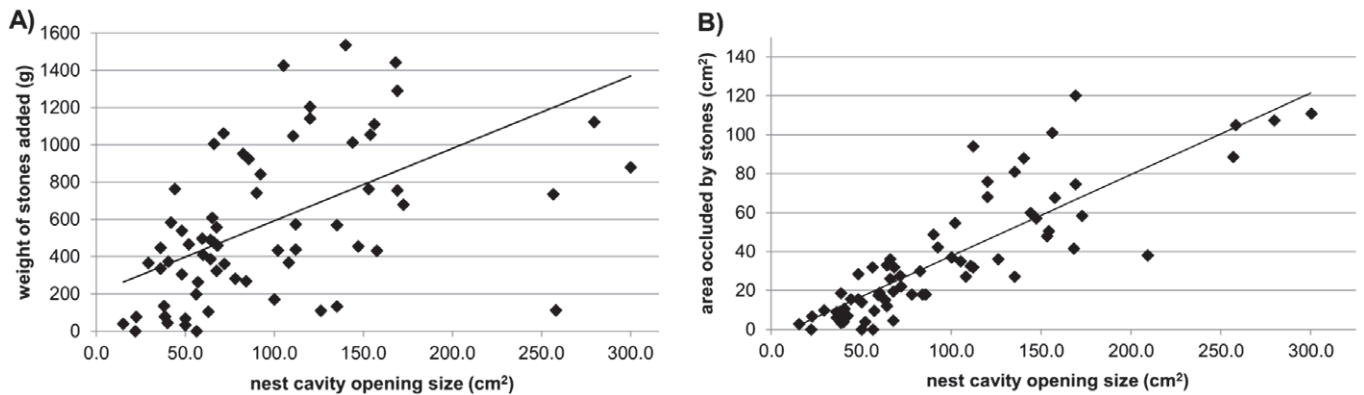


Figure 3 Relationships between the size of Rock Wren nest cavity entrances (without stones) and (A) the total weight of stones added, and (B) the area of the cavity entrance occluded by stones.

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 cm² 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 \pm SD [range], 61.2 ± 40.1 [12.2–189] cm²; 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 of a bird species achieving an outcome “via a secondary

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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APPENDIX 1 Locations, entrance dimensions, stone quantities, and occlusion rates of 68 Rock Wren nests

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
027	Lory State Park	Larimer, CO	48	63	15	40	104
028	Lory State Park	Larimer, CO	50	92.3	42.3	310	842
029	Lory State Park	Larimer, CO	103	154	51	422	1056
030	Lory State Park	Larimer, CO	81	108	27	135	369
031	Lory State Park	Larimer, CO	67.5	85.5	18	307	924
032	Lory State Park	Larimer, CO	90	157	67	156	431
033	Lory State Park	Larimer, CO	70	105	35	602	1426
034	Lory State Park	Larimer, CO	105	153	48	325	764
035	Lory State Park	Larimer, CO	41.3	90	48.7	215	742
036	Horsetooth Reservoir	Larimer, CO	27	36	9	154	447
037	Horsetooth Reservoir	Larimer, CO	52.5	82.5	30	370	953
038	Pine Ridge NA	Larimer, CO	30	38	8	61	136
039	Devil's Backbone OS	Larimer, CO	24	56	32	68	198
040	Devil's Backbone OS	Larimer, CO	48	52	4	260	467
041	Bobcat Ridge NA	Larimer, CO	90	147	57	211	454
042	Pawnee Buttes	Weld, CO	15.8	22.5	6.7	37	77.2
043	Pawnee Buttes	Weld, CO	114	172	58	349	678
044	Horsetooth Reservoir	Larimer, CO	19.5	48	28.5	223	538
045	Pine Ridge NA	Larimer, CO	90	126	36	39	108
046	Pawnee Buttes	Weld, CO	52	64	12	142	490
047	Lory State Park	Larimer, CO	55	156	101	416	1111
048	Lory State Park	Larimer, CO	47.5	57	9.5	114	263
049	Lory State Park	Larimer, CO	108	135	27	59	133

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	Pine Ridge NA	Larimer, CO	36	50	14	10	33.2
051	Lory State Park	Larimer, CO	52	140	88	500	1536
052	Pine Ridge NA	Larimer, CO	63	100	37	56	171
053	Reservoir Ridge NA	Larimer, CO	42	59.5	17.5	242	497
054	Red Mountain OS	Larimer, CO	36	68	32	158	459
055	Lory State Park	Larimer, CO	20	38.5	18.5	22	76
056	Lory State Park	Larimer, CO	80	112	32	297	575
057	Lory State Park	Larimer, CO	54	135	81	196	570
058	Lory State Park	Larimer, CO	30	66	36	328	1005
059	Lory State Park	Larimer, CO	84	144	60	295	1012
060	Slaughter Canyon	Eddy, NM	41.3	60	18.7	120	410
061	Santa Rosa SP	Guadalupe, NM	171	209	38	1256	2819
062	Santa Rosa SP	Guadalupe, NM	172	280	108	412	1121
063	Lory State Park	Larimer, CO	78	111	33	325	1048
064	Lory State Park	Larimer, CO	29.8	40.5	10.7	124	373
065	Coyote Ridge NA	Larimer, CO	31	64	33	165	386
066	Lake McConahuy	Keith, NE	12.2	15.1	2.9	15	40
067	Coyote Ridge NA	Larimer, CO	48	67.5	19.5	94	324
068	Lory State Park	Larimer, CO	44	71.5	27.5	468	1062
B32790	Santa Rosa	Guadalupe, NM	?	?	26	260	522

^aCO, Colorado; NM, New Mexico; NE, Nebraska.