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RESEARCH ARTICLE

Paving the way: Multifunctional nest architecture of the Rock Wren

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ABSTRACT

Some avian species augment nest cups by building associated architectural structures that may mitigate predation, parasitism, and/or hatching failure. Because effective nest construction is integral to reproductive success, architectural structures associated with nests are predicted to provide functional benefits. Rock Wrens (*Salpinctes obsoletus*) stereotypically augment their soft cup nests with a pavement of stones, apparently incurring considerable energy costs. We quantified Rock Wren stone use and measured how stones occlude nest cavities. We examined whether Rock Wrens adjust individual stone-carrying effort in response to nest cavity opening size and tested 3 hypotheses about the benefits of cavity occlusion: (1) stones ameliorate temperature fluctuations and improve nest thermoregulation; (2) stones improve nest microclimates by keeping them dry; and (3) stones have the potential to reduce nest predation by alerting incubating females when predators approach. We found that individual nest pavements contained up to 1.4 kg of stones, which varied in size but were relatively uniform in thickness. Stone pavements decreased nest cavity openings by a mean of 34%, with larger openings containing significantly more stones. Presence of stones did not influence temperature in unoccupied nest cavities but did significantly decrease water infiltration into the nests during simulated rainfall. Presence of stones also changed the sound of a simulated predator approach, supporting the idea that stone patios could serve as an alarm function for vulnerable incubating females. Our data indicate that Rock Wrens adjust the amount of stones used in nests according to cavity characteristics to obtain multiple benefits. Results confirm that nest site modification can be an adaptive behavior and provide evidence that birds facultatively modify nesting environments.

Keywords: Rock Wren, *Salpinctes obsoletus*, nest architecture, nesting behavior, stone carrying.

Enripiando el camino: Arquitectura multifuncional del nido de *Salpinctes obsoletus*

RESUMEN

Algunas especies de aves agrandan sus nidos en forma de tasa mediante la construcción de estructuras arquitectónicas asociadas que pueden mitigar la depredación, el parasitismo y/o el fracaso de la eclosión. Debido a que la construcción del nido es parte integral del éxito reproductivo, se predice que las estructuras arquitectónicas asociadas a los nidos brindan beneficios funcionales. La especie *Salpinctes obsoletus* agranda de modo estereotipado sus suaves nidos en forma de copa con un enripiado de piedras, aparentemente incurriendo en considerables costos de energía. Cuantificamos el uso de piedras por parte de *S. obsoletus* y medimos como las piedras obturan las cavidades del nido. Examinamos si *S. obsoletus* ajusta el esfuerzo individual de acarrear piedras en respuesta al tamaño de la abertura de la cavidad del nido y evaluamos tres hipótesis sobre los beneficios de obturar la cavidad: (1) las piedras mejoran las fluctuaciones de temperatura y la termorregulación del nido, (2) las piedras mejoran el microclima del nido manteniéndolo seco, y (3) las piedras tienen el potencial de reducir la depredación del nido al alertar a las hembras que están incubando cuando se acercan los depredadores. Encontramos que los enripiados de un nido contuvieron hasta 1.4 kg de piedras, que variaron en tamaño, pero fueron relativamente uniformes en espesor. Los enripiados de piedra disminuyeron la abertura de la cavidad del nido un 34% en promedio, con aberturas más grandes conteniendo significativamente más piedras. La presencia de piedras no influyó la temperatura de las cavidades de los nidos desocupados, pero sí disminuyó significativamente la infiltración de agua al nido durante las lluvias simuladas. La presencia de piedras también cambió el sonido del acercamiento simulado de un depredador, apoyando la idea de que los patios de piedra pueden tener una función de alarma para las hembras incubando vulnerables. Nuestros datos indican que *S. obsoletus* ajusta la cantidad de piedras usadas en los nidos de acuerdo a las características de la cavidad, de modo de obtener beneficios múltiples. Los resultados confirman que la modificación de la localización del nido puede ser un comportamiento adaptativo, y brindan evidencia importante de que las aves modifican facultativamente el ambiente del nido.

Palabras clave: acarreo de piedras, arquitectura del nido, comportamiento de anidación, *Salpinctes obsoletus*.

INTRODUCTION

Reproductive success in nesting animals depends on adaptive nesting behaviors. Major threats to nests include predation and hatching failure due to poor weather or nest microclimate (Collias and Collias 1984, Hansell 2000); therefore, many nest architectures are elaborate to combat these potential causes of nest failure, and many species have evolved complex behavioral adaptations to improve nesting success (Martin 1995, Hansell 2005). Variability in nest architecture and placement is often related to individual site characteristics including weather, predator abundance, and availability of suitable materials, but few studies have shown that birds modify sites before choosing them as nest locations (Yeh et al. 2007, Greeney 2008, Peluc et al. 2008). Comprehensive studies examining the adaptive value of nest site modification will help us understand how animals can be active architects of their environments.

For this study we examined the form and function of stone pavements built under and around nests by Rock Wrens (*Salpinctes obsoletus*; Figure 1). Extensive stone carrying is an exceptional terrestrial nest construction behavior, occurring in a few mammals, arthropods, and ~0.3% of bird species (Leader and Yom-Tov 1998, Williams et al. 2006, Ford and Johnson 2007). Carrying and placement of stones (often hundreds) is energy and time intensive, and these costs are expected to be balanced by fitness benefits such as nest protection (Moller et al. 1995, Moreno et al. 1999, Soler et al. 1999). Furthering our understanding of the arrangement and function of stone nest structures could provide insights into the evolution and diversification of nest types and the ways in which life history, environmental, and community factors interact to shape adaptive nesting behaviors (Collias 1997, Conway and Martin 2000).

Rock Wrens are the only North American birds known to make extensive use of stones in and around nest sites. They build cup nests of grasses and sticks typically located in natural cavities between boulders and rock fissures (Harrison 1979, Lowther et al. 2000). Since the first descriptions of Rock Wren nests, workers have noted that many flat stones (1) are used to line the nest cavity, (2) are placed as a foundation under the nest cup, and (3) often extend beyond the nest cavity in a nest pavement (Bailey 1904, Merola 1995, Lowther et al. 2000). Research in other species has shown that stones are used to augment avian nests for 4 primary functions: thermoregulation (hypothesized in at least 18 desert species), dryness, predator defense, and mate communication (Orr 1970, Afik et al. 1991, Moreno et al. 1994).

Early researchers hypothesized that the primary function of Rock Wren stone pavements was to decrease the effective size of the nest cavity and cavity entrance, referring to this outcome as "cavity occlusion" (Bailey 1904). We tested whether stones occlude cavity entrances and hypothesized that cavity occlusion may occur among Rock Wrens as a proximate mechanism that provides 3 benefits demonstrated in other species: (1) temperature amelioration, (2) nest dryness, and (3) predator defense. We outline our specific predictions for each of the 3 functional hypotheses below. The fourth benefit of stone carrying, mate communication, has been shown exclusively in Black Wheatears (*Oenanthe leucura*), in which females assess mate quality based on the amount of stone a male carries (Moreno et al. 1994, Moller et al. 1995). Stone use in this species is interpreted as a post-pairing, sexually selected display by males, leading to differential levels of reproductive output and parental care by females (Soler et al. 1996, 1999). Here we consider, but do not explicitly test the hypothesis that stone carrying may be a signaling display among Rock Wrens.

Pavement Function Hypotheses

Hypothesis 1: thermoregulation. The microenvironment of nests affects the daily energy requirements of the eggs, nestlings, and incubating adults, especially in harsh nesting environments (Amat and Masero 2004, Tieleman et al. 2008). Because Rock Wrens breed in exposed environments with large diurnal fluctuations in air temperature and sparse vegetative cover, regulation of nest temperature may be a strong selective pressure on nesting behaviors (Wolf et al. 1985, Nolte and Fulbright 1996). Most known stone carriers are open-nesting desert species that encircle nests with stone parapets that reflect back sunlight and buffer heat transfer from the ground, although studies have not linked stone use directly to reproductive success (Orr 1970, Afik et al. 1991). A few additional species of stone carriers, (e.g., blackstarts and wheatears), are cavity nesters (Cramp and Simmons 1988). Thus far, research has shown thermoregulatory benefits only for open-nesting stone carriers, but hypotheses suggest that cavity nesters may also derive thermoregulatory benefits (Leader and Yom-Tov 1998). Within cavities, stone foundations may raise nests into a warmer microclimate or ameliorate temperatures by insulating nests and adding to thermal mass (Orr 1970, Lyon and Montgomerie 1987, Afik et al. 1991). By reducing the effective volume of the nest cavity, stones could aid in faster warming or increased heat retention during incubation, thereby improving thermoregulation. We monitored temperature in vacant Rock Wren nest cavities with no heat inputs and therefore were only able to test for abiotic effects of stone presence. We predicted that nest cavities with stones would have smaller temperature fluctuations than control cavities containing no stones.

Hypothesis 2: nest dryness. Stones can help mechanically protect nests from moisture, especially in dry environments that experience periodic heavy rainfall

FIGURE 1. Rock Wren (*Salpinctes obsoletus*). Photo credit: D. Leatherman

events from localized, convective storm cells that could cause flooding (Sharon 1972, Collias and Collias 1984). For example, Chinstrap Penguins (*Pygoscelis antarctica*) gather stones and deposit them in piles atop shallow nest scrapes to keep melt water from infiltrating nests (Moreno et al. 1995, 1999). Previous research has supported a dryness function for stones in open-nesting species, but the same benefits may accrue to species nesting in cavities close to the ground because those sites have high suceptibility to dampness and flooding (Collias and Collias 1984). Early observers proposed that stones may help keep Rock Wren nest cavities dry (Ray 1904, Smith 1904). Stones at Rock Wren nests could promote dryness by diverting water away from the nest or by allowing water to drain or pass between stones along underlying rock or soil. We tested this hypothesis using simulated rainfall and predicted that stones would prevent water infiltration into the nest cavity.

Hypothesis 3: predator defense. Birds in cavities are vulnerable to ground-foraging predators, particularly when incubating for prolonged periods (Ghalambor and Martin 2002, Amat and Masero 2004). Some nest architectures can reduce predation on both adults and young, either by concealing nests or by thwarting predator access (Martin 1995, Weidinger 2002, Feeney et al. 2012). Rock Wren stone pavements are conspicuous to human observers and may be so for some nest predators. We therefore did not test a concealment hypothesis, instead focusing on the "early warning hypothesis" (Leader and Yom-Tov 1998) that barricades protect nests from predation by alerting adults in the nest cavity when an approaching predator gets close enough to the nest to disturb the stones. This protection would allow an incubating bird to exit the cavity before a potentially deadly predator enters as well as allow a parent to confront a nest predator before it enters the cavity (Knight and Temple 1986, Leader and Yom-Tov 1998, Ellison and Ribic 2012). We expected that nest predators, detected by motion-activated cameras, would be common on our study site. We also predicted that approaches by a simulated predator over stone pavements would be acoustically different from approaches over the underlying and surrounding substrate. Because pavements are located just outside the nest cavity entrance, this change in acoustic signature would signal an approaching predator's exact proximity to the nest.

For each of the 3 hypotheses (thermoregulation, nest dryness, and predator defense), Rock Wrens could benefit by adjusting nest pavements to suit the immediate environment surrounding the nest cavity or to effectively modify environmental conditions. Thus, we measured variables (quantity and size of stones, cavity occlusion, slope, etc.) that could indicate adaptive use and arrangement of stone structures. If stones are used to occlude nest cavities, we predicted that birds would use more stones when cavity entrances were large and that those stones would effectively decrease the size of nest cavity openings.

METHODS

Study Location

The study area encompassed $\sim$15 km^2 of (noncontiguous) semiarid montane shrublands in the northern Colorado foothills. The climate is continental, with an average rainfall of 40.3 cm. Average temperature is 9.5°C, and average summer temperature is 19.2°C (USCD 2013). Nests were typically located on rocky slopes with vegetative cover predominated by mountain mahogany (*Cercocarpus montanus*) and ponderosa pine (*Pinus ponderosa*). Elevation of nests ranged from 1605 to 1995 m.

Identification and Monitoring

Rock Wrens inhabit rocky slopes and escarpments in arid habitats from the western edge of the Great Plains to the Pacific Slope, with sedentary populations south through Mexico and migratory populations from roughly 40°N into southern Canada (Grinnell and Miller 1944, Lowther et al. 2000). Rock Wrens are small (16–18 g) songbirds that breed in socially monogamous pairs where females perform all nest incubation duties, and both parents provision offspring. We surveyed public lands in Larimer County, Colorado, near Fort Collins (40°35′N, 105°5′W) from May to June 2012–2014 using direct observation to locate active Rock Wren breeding territories. We identified 46 nests (2012, $n = 14$; 2013, $n = 23$; 2014, $n = 9$) on the territories of at least 24 pairs. We observed active nests and placed motion activated cameras (Reconyx, Holmen, WI, USA) 1 m from nests ($n = 5$) to document nesting behaviors and assess nest accessibility by predators. We captured and color-banded a subset of male Rock Wrens (11/24) with unique combinations of plastic color bands to distinguish between sexes. Wherever we report sex, it is from a pair with a banded male and an unbanded female.

Nest Attributes

To quantify stone use in pavements we processed stones post-breeding from all nests that included stones ($n = 44$); 36 of these nests (78%) were active (contained eggs or nestlings) in the year of sampling, and the remainder were inactive. At each nest we weighed stones collectively to the nearest 0.1 g using a portable electronic scale and divided the total weight by the number of stones to determine average stone weight. We did not count or remove the relatively few stones that were incorporated into nest cups to avoid damaging the nests, but all other stones were included. We individually weighed and measured the length, width, and thickness using dial calipers of at least 10 randomly selected stones from each nest (mixed up and drawn from a nylon bag) to assess stone size and shape (mean of 15.0 ± 5.8 [mean ± SD] stones per nest, $n = 690$). To measure stone availability, one researcher (N. Warning) collected stones of suitable size, thickness, and weight (determined by comparing thickness and weight to stones previously measured) within 25 m of each nest for 15 min and weighed the total amount collected.

To document cavity occlusion we used a flexible ruler to measure the height and width of the cavity entrance before and after the removal of nest stones. We used linear regression to test the predictions that birds would use more stones and achieve higher occlusion rates at nest entrances with larger pre-stone openings. All statistics were performed in JMP, v.9 (SAS Institute, Cary, NC, USA). In 2014 nests ($n = 9$) we calculated the slope of nest cavities by measuring the difference in rise (cm) with and without stones divided by the run distance from the nest cup to the plane of the cavity entrance.

These tests, and subsequent tests that required stone removal, were performed sequentially before and after stone removal on unoccupied nests that had fledged, failed, or were otherwise vacant; therefore, all experiments reflect the arrangement of stones that we encountered when the nests were discovered. After nests were manipulated, one researcher (N. Warning) returned stones as closely as possible to their original configurations.

To evaluate whether stones ameliorate cavity temperature, we logged temperature hourly for at least 48 hr in 16 randomly selected nest cavities with stone pavements (active in the year of sampling) after either the chicks fledged or the nest failed, and simultaneously in control cavities (not used as nests by Rock Wrens) of similar depth and orientation within 8 m of each focal nest. Average difference in control cavity depth and orientation was 2.3 ± 0.1 cm and 2.50 ± 1.7° (mean ± SD), respectively, and logged nests contained 620 ± 428 g of stones. We placed data buttons (ACR Systems, Surrey, BC, Canada) in plastic mounts 10 cm within nest cavities and replicated the placement distance in control cavities. In addition, we logged ambient temperature (in full shade, but not within a cavity) within 5 m of each focal nest. We used Kruskal-Wallis rank sum tests to compare temperature ranges in nests, control cavities, and shaded ambient locations.

To measure nest dryness we recorded how stones affected the water weight gain of a $5 \times 5 \times 1$ cm sponge placed inside each nest cavity directly in front of the nest cup ($n = 44$). To simulate a rainfall event we used a sprinkling can to disperse 3.8 L of water over the nest and cavity entrance from a height of 50 cm before the removal of nest stones. This method provided a sufficient amount to saturate the soil immediately surrounding the nest cavities while still being portable to remote sites. We repeated this process after experimental removal of stones, when the soil around the nest had dried for at least 24 hr. We measured sponge weight gain to the nearest 0.1 g and used a Wilcoxon matched-pairs signed-rank test to compare sponge weight gain in the 2 conditions.

To test for an antipredator alarm function of stones, we placed a Sennheiser MKH 20 microphone inside the nest cup of 18 randomly chosen unoccupied Rock Wren nest cavities (2012, $n = 9$; 2013, $n = 9$) and recorded the approach of a 35 cm rubber snake across the ground and into the cavity entrance before and after the removal of stones. We chose a rubber snake for alarm experiments because its approach was replicable and snakes are thought to be common nest predators for Rock Wrens (Lowther et al. 2000). The same researcher (N. Warning) dragged the rubber snake each time and standardized the approach as much as possible by grasping the snake's neck and pulling at an angle parallel to the slope of the ground. The microphone was not moved or adjusted between trials with and without stones at each nest. Audio recordings were made in mono at a sampling frequency of 48 kHz and a sample depth of 16 bits. Sound clips (10 s duration to standardize length and to isolate simulated snake movement) were analyzed using Raven Pro 1.3 software (Cornell Lab of Ornithology) to compare average power, which gave us a quantitative measure of the acoustic energy (related to loudness) in the entire clip. We used a one-tailed Wilcoxon signed rank test (on paired data) to test the prediction that the sound clips with stones would have more power.

Human and passerine auditory thresholds are similar, making humans good surrogates for avian acoustic perception (Okanoya and Dooling 1987). To assess qualitative differences in sound, 11 undergraduate students rated paired sets of sound clips (10 s duration) from 9 nests measured in 2013 (containing 104–602 stones, mean = 300) for discrimination of the approaching snake. Students used a 1–6 scale to rank the level of perceived stone disturbance. Trials used pairs of audio clips from the same nest with and without stones. Audio clips were presented in a blind and randomized fashion. We used paired *t*-tests to compare students' ratings for each condition.

FIGURE 2. Rock Wren nests in northern Colorado; (**A, B**) ground-based nests and (**C, D**) nests in cliff cavities. The GPS device is pictured for scale.

RESULTS

Nest Attributes

Rock Wren nests in our study area were located on slopes from 18° to 90°, either on or close to the ground ($n = 41$) or in cliff cavities ($n = 5$). Mean depth of measured nest cavities was 31.8 ± 9.6 cm (mean ± SD). Mean depth of the nest cup within cavities was 17.5 ± 5.9 cm, constructed of sticks, stems, bark, grasses, small leaves, feathers, and fur. Rock Wrens nested in a wide range of cavity sizes and types. There was no consistent pattern in cavity orientation except that cavities always faced outward, on the downsloping side of boulders and rock overhangs rather than in upsloping depressions that could collect water and debris. Two nests contained no visible stones. Notably, these nests were located in the 2 cavities with the narrowest measured openings (2.5 and 3.7 cm). When stones were present they always lined the bottom of the cavity, and in 85% (39/46) of cases they were placed outside the cavity to form a nest pavement extending 18.1 ± 11.7 cm (range 7.0–45.0, $n = 39$; Figure 2). We observed that stones often leveled the floor of the nest cavity (decreased slope by 25 ± 7%; $n = 9$) and always extended to the margins of the nest cup, anchoring it into the cavity.

Nests contained from 0 to 602 stones (mean = 222), stones collectively weighed 67–1442 g (mean = 560 g), and 15 nests (33%) contained >700 g of stones (see Appendix). Average individual stone weight across nests was 2.9 ± 1.6 g (range 0.2–12.6, $n = 690$; Figure 3). Mean stone length was 25.6 ± 7.0 mm (range 9.3–59.1), and mean stone width was 18.0 ± 4.6 mm (range 7.0–37.5; Figure 3). Stones were typically flat, and the consistent thickness of nest stones (5.1 ± 1.5 mm, range 1.6–10.6, $n = 690$) made many nests recognizable to experienced observers (Figures 2 and 3).

Stones, often scaffoleded by sticks, did occlude nest cavity entrances, decreasing average opening areas by 34 ± 20%. Cavity openings were significantly smaller ($t_{43} = 8.4$, $P < 0.001$, paired t-test) when measured with (68 ± 47 cm^2) vs. without (107 ± 68 cm^2) stones present. Greater stone mass occluded significantly larger proportions of the

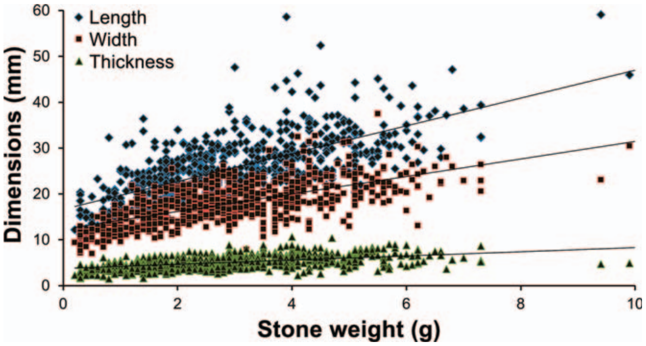

FIGURE 3. Weights of Rock Wren nest stones ($n = 690$) plotted against their lengths (diamonds), widths (squares), and thicknesses (triangles).

cavity openings ($r^2 = 0.24$, $P = 0.003$; Figure 4A), and the original (no stones) opening sizes of nest cavity entrances were positively correlated with the weight of stones used ($r^2 = 0.12$, $P = 0.009$; Figure 4B). The weight of stones in the nests was not significantly correlated with stone availability measured from collecting stones for 15 min within 25 m of focal nests ($r^2 = 0.08$, $P = 0.07$).

Nesting Behaviors

Two paired female wrens were observed carrying stones, and 2 were documented by motion cameras. We never observed a male carrying stones, although on multiple occasions the male was present while his mate was carrying stones to a nest site, and males assisted in bringing materials for the nest cup. Stones were carried in the bill, and wrens were able to fly short distances and scale cliffs while carrying stones (Figure 5). At least 2 nests were constructed entirely in a single season, and these contained 953 and 1005 g of stones, respectively. Only one nest ($n = 37$) was reused within or between years during the study period. This nest was active in 2012 and was reused by a pair with a different male in 2014. Cameras indicated that some nest cavities (4 of 5 continuously monitored) were visited by unbanded (presumably female) Rock Wrens, which on 2 occasions added stones to inactive nests.

Hypothesis 1: thermoregulation. We did not detect a significant relationship between nest stones and temperature fluctuations within nest cavities (Figure 6). Cavities that contained stones did show slightly smaller temperature variation than cavities without stones and shaded

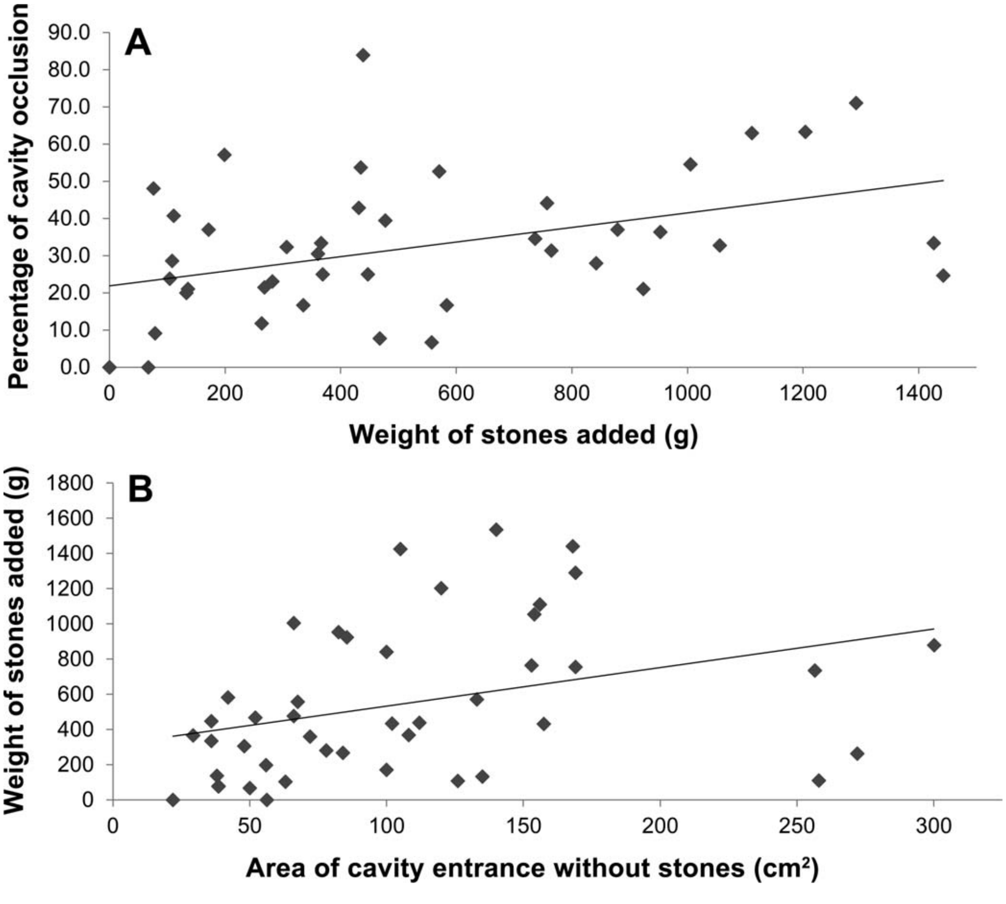

FIGURE 4. Data from 46 Rock Wren nests in northern Colorado showing the correlation between (**A**) the weight of stones used in nest construction and the percentage of the cavity entrance that was occluded, and (**B**) the size of original cavity entrances and the weight of stones used in nest construction.

FIGURE 5. Photos showing female Rock Wrens (**A**) placing stones on nest pavements and (**B**) flying short distances while carrying stones to nest sites.

ambient conditions, but the trend did not approach significance (Kruskal-Wallis test, $H_2 = 3.7$, $P = 0.16$). Standard deviation of nest temperatures was not correlated with the amount of stones in the nests ($r^2 = .09$, $P = 0.23$).

Hypothesis 2: nest dryness. If nest stones divert water or facilitate passage of water beneath Rock Wren nests, we expected an inserted sponge to gain more water weight after stones were removed. This result was observed in 57% (25/44) of nests. In 29% (13/44) of nests, there was no water gain in the sponge regardless of whether stones were present (see Appendix Table 1). Cavities with stones were drier during our experimental tests (Wilcoxon test, $z_{43} = 161$, $P < 0.001$). We also observed that stone pavements helped stabilize the soil surrounding the nest cavity; after stones were removed, the underlying soil was much more prone to erosion from water poured from the sprinkling can.

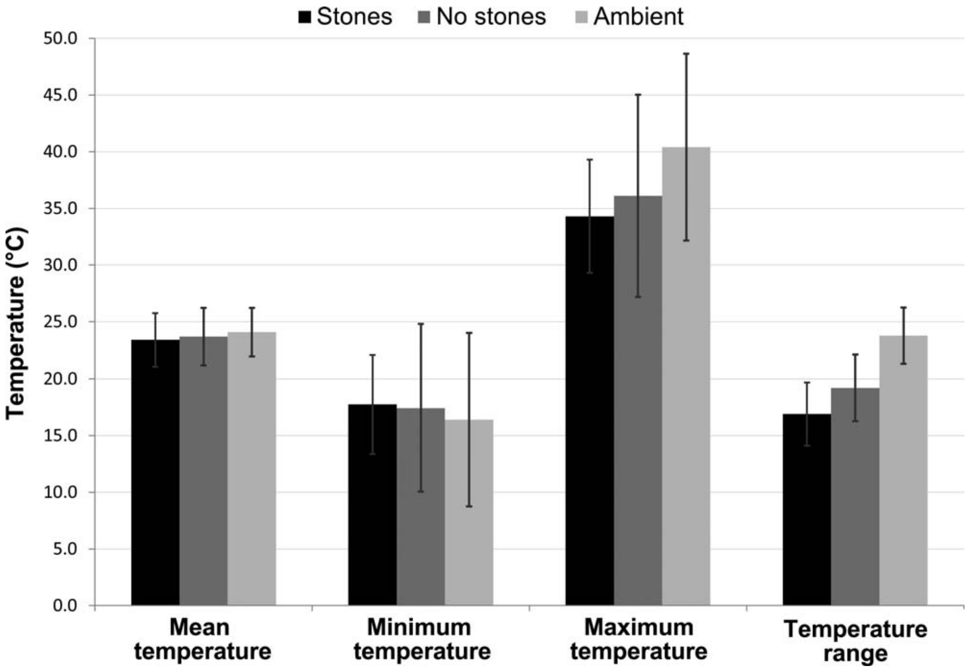

FIGURE 6. Average mean temperature, minimum temperature, maximum temperature, and temperature range for 16 Rock Wren nest cavities (black bars), control cavities without stones (dark grey bars), and ambient conditions (light grey bars). Error bars indicate SD.

Hypothesis 3: predator defense. Even with stones present, 54% (25/46) of measured nests had entrance openings of at least 50 cm^2, large enough for many small mammal predators, including rats and ground squirrels, to enter. Motion activated cameras placed at nests captured images of potential nest predators, including Mexican woodrats (*Neotoma lepida*), northern rock mice (*Peromyscus nasutus*), and golden-mantled ground squirrels (*Spermophilus lateralis*). On multiple occasions we observed male Rock Wrens attack rock squirrels (*Spermophilus variegatus*) that came near active nests. We also observed that incubating birds frequently flushed from cavities when we approached a nest.

We hypothesized that the sounds made by pavements may alert wrens to predators approaching the nest. Stones increased the average power of recordings of simulated predator approaches by 1.8 ± 4.3 dB, a significant amount (Wilcoxon test, $z_{17} = -40.5$, $P = 0.04$). Stones also changed the quality of the sound of a predator approach; human subjects were able to discriminate the noise made by stones during a simulated predator's approach (paired *t*-test, $t_{10} = -4.8$, $P = 0.001$).

DISCUSSION

Our data confirm that pavements in Rock Wren nests represent a significant energy investment and modification of the nest environment. Rock Wrens are able to not only conform nests to cavities, but also architecturally modify cavities to accommodate and protect nests. Some nests included >1 kg of stones (~62 times a Rock Wren's body weight), and birds carried individual stones that were more than half their own body weight. Results also contribute evidence to suggest that females are the primary stone-carriers in this species, although this deserves further study (Oppenheimer and Morton 2000).

Our findings suggest that nest cavity occlusion is a goal of stone carrying by Rock Wrens based on 3 lines of evidence. First, there were significant correlations between both the size of nest cavity entrances and the weight of stones placed by wrens at those entrances, and between the weight of stones at cavity entrances and the degree to which the entrances were occluded. Second, the 2 nest cavities with the smallest openings contained no visible stones. Finally, the weight of stones used was related to cavity size but not to stone availability in the immediate environment. Thus, we conclude that different rates of stone carrying are not driven by stone availability in the environment, but are directly related to nest occlusion and likely provide a benefit related to nest occlusion. Results suggest that Rock Wrens facultatively adjust stone use in response to the size of the nest cavity entrance, bringing more stones to occlude large openings and selecting stones with specific properties. Such facultative adjustments suggest advanced cognitive activity during the nest building process (Shettleworth 2009). This finding is not the only example of nest occlusion among wrens; House Wrens (*Troglodytes aedon*) build a berm of sticks between the nest cup and cavity entrance and adjust the berm height depending on the size of the cavity entrance (Alworth 1996, Stanback et al. 2013). Thus, facultative use of protective materials at nest entrances may be important to multiple species.

We found that, where there were no inputs from incubating birds, nest stones had little impact on variation in cavity temperature. Furthermore, cavity temperatures differed little from ambient shaded temperatures. All of the evidence that stones can ameliorate avian nest temperature fluctuations comes from open-cup, ground-nesting desert species, where stones can help raise or lower nest temperature by reflecting thermal energy (Orr 1970, Afik et al. 1991). In 2 other species of cavity nesting stone-carriers, there is no evidence that stones affect cavity temperatures (Moreno et al. 1994, Soler et al. 1996, Leader and Yom-Tov 1998). Our data fit this pattern, illustrating that the use of stones may be driven by different selective pressures in open-nesting desert birds than in cavity nesters. Rock Wrens do face extreme variation in temperature regimes during breeding throughout their range, and future studies could investigate whether stones play a larger role in regulating nest temperatures in desert climates. Additionally, stones may affect temperature regimes differently during active incubation, but such effects are difficult to test experimentally because stone removal from active nests would likely cause nest abandonment. Experiments measuring the thermal stability of nest cavities using an artificial heat source to mimic an incubating bird could help discern the ameliorative effects of stone pavements in active nests.

Our results indicate that stones can keep Rock Wren nests dry, which is predicted to be beneficial because dry nestlings are most likely to maintain body temperature and fledge (Story et al. 1988). We found that nests with stones remained drier during simulated rain events. With increased water from heavy rainfall and saturated soils we would expect the dryness effects to be amplified. In addition to facilitating drainage and blocking water from entering the nest cavity, stones also might stabilize the underlying soil. The stabilizing effects of stones may be an important function of stone pavements and warrants additional testing. As ground nesters on steep, rocky slopes in arid environments, Rock Wrens have apparently evolved nesting strategies to deal with periodically heavy rainfall and unstable soils using a commonly available material. This is also the case for nests built by Chinstrap Penguins in a floodplain, where nests with more rocks had increased reproductive success (Moreno et al. 1995).

Stacked stones are noisy when disturbed and could alert nesting individuals to the approach of potential predators. We confirmed that nest predators are present on our study sites. Furthermore, we observed that Rock Wrens frequently flush from nest cavities when approached by researchers, indicating that they do perform escape behaviors when a potential predator approaches the nest. Although the sounds created by a smooth rubber snake are likely different from the sounds made by an actual predator, our experiments demonstrated that consistent nest approach movements make louder and acoustically distinct sounds when they encounter stone pavements. Because nest stones touch one another, there may also be a vibrational signal that travels to the nest cup when the stones are disturbed. Overall, our experiments indicated that the noise created by stone pavements provides enough signal to function as predator detection from inside nest cavities. Early predator detection could allow female Rock Wrens to evaluate and confront a raider or to escape the nest, especially at night or during periods of sleep (Knight and Temple 1986, Ellison and Ribic 2012).

This early warning hypothesis (Leader and Yom-Tov 1998) is little tested in birds but aligns with the observations that females are the primary incubators and stone carriers in most species (Cramp and Simmons 1988, Merola 1995, Leader and Yom-Tov 1998). If predator alarm is a major function of stone pavements among Rock Wrens, then incubating females will reap the primary benefits, providing a potential explanation for why females bear the costs of stone-carrying. Notably, this mechanism is not unique to birds: turrets built by Mediterranean tarantulas (*Lycosa tarantula*) from small pebbles and sticks serve as an alarm mechanism around burrows (Shook 1978, Williams et al. 2006). Pebble mound structures built by *Pseudomys* mice around nesting burrow entrances may serve a similar function (Ford and Johnson 2007). Additional research on active Rock Wren nests could help determine whether the auditory signal produced by stones is a primary function of nest pavements or whether the noises and vibrations are incidental.

Many wrens are known to construct nests to attract prospective mates (Bent 1964, Burns 1982, Kroodsma and Verner 1997). Stone carrying in the Rock Wren has been suggested to act as a courtship display (Merola 1995, Oppenheimer and Morton 2000), as is the case in the Black Wheatear breeding in Spain (Richardson 1965, Moreno et al. 1994, Moller et al. 1995). If stones provide a display function for Rock Wrens, it is likely a female display. Post-pairing displays by female birds are rarely tested, but may benefit females if they can induce increased parental care by their mates (Palamino et al. 1998, Gill and Stutchbury 2005). More studies will be needed to determine if stone pavements themselves serve as a mating display for Rock Wrens.

As a driving component of fitness, nesting behaviors are under strong selection pressures (Schmidt and Whelan 2010, Dinkins et al. 2012). The stereotyped use of stones by Rock Wrens likely evolved as a response to selective pressures inherent to ground nests in exposed, rocky environments, including easy predator access, steep slopes, and the dynamic effects of periodically heavy rainfall. Rather than building elaborate, independent nest structures, Rock Wrens incorporate a structurally stable matrix of stones into cavities, thereby facultatively modifying their immediate nest environment. Developing the ability to modify cavities may have been an important factor in the evolution of nesting behaviors in Rock Wrens and other cavity-nesting species, leading to increased flexibility in choosing nest sites, increased nest site availability, and reduced competition for suitable nesting locations (Collias 1997). Our study is the first to experimentally test the benefits of stone carrying in a North American species, and also the first to report pavement multifunctionality. We propose that the stereotyped augmentation of nests with stones by breeding Rock Wrens improves predator avoidance and physical protection of nests. This system illustrates how ecological variables can influence the many structures built by animals and how nesting behaviors can be complex and flexible (Hansell 2000, 2005).

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Ethics statement: This study was carried out in accordance with the recommendations in the USDA Animal Welfare Act and regulations. The protocol was approved by the Animal Care and Use Committee at the University of Northern Colorado. Licenses to band birds were granted by the United States Department of the Interior (Permit # 23741) and the Colorado Department of Natural Resources (Permit TRb2041).

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APPENDIX TABLE 1. Attributes measured from 46 Rock Wren nests (from at least 24 different pairs) in northern Colorado.

Nest ID $^{pair\#}$	Location	Number of stones	Total stone weight (g)	Avg. stone weight (g)	% Occlusion by stones	Difference in sponge wt. gain (g)	Year active
Nest 01 ^{01}	Devil's Backbone	68	198	2.9	57.1	0.1	2012
Nest 02 ^{02}	Red Mountain	554	1442	2.6	24.7	4.0	2012
Nest 03 ^{03}	Devil's Backbone	260	467	1.8	7.7	0.0	2012
Nest 04 ^{04}	Shoreline Trail	439	879	2.0	37.0	5.4	2012
Nest 05 ^{05}	Pine Ridge NA	514	1292	2.5	71.0	4.5	2012
Nest 06 ^{05}	Pine Ridge NA	558	1204	2.2	63.3	0.2	2012
Nest 07 ^{06}	Blue Sky Trail	306	736	2.4	34.5	0.0	2012
Nest 08 ^{07}	Coyote Ridge	214	439	2.1	83.9	0.1	2012
Nest 09 ^{07}	Coyote Ridge	265	557	2.1	6.7	−1.1	2012
Nest 10 ^{08}	Arthur's Rock	117	306	2.6	32.3	13.9	2012
Nest 11 ^{09}	Duncan Ridge	216	477	2.2	39.4	0.0	2012
Nest 12 ^{10}	Pine Ridge NA	0	0	0.0	0.0	n/a	2012
Nest 13 ^{11}	Cherokee Park	0	0	0.0	0.0	n/a	2012
Nest 14 ^{12}	Quarry Cove	40	104	2.6	23.8	0.0	2013
Nest 15 ^{08}	Arthur's Rock	121	366	3.0	33.3	26.0	2013
Nest 16 ^{13}	Satanka Cove	32	67	2.1	0.0	0.0	2013
Nest 17 ^{13}	Satanka Cove	130	360	2.8	30.6	0.2	2013
Nest 18 ^{14}	Quarry Cove	325	764	2.4	31.4	10.4	2013
Nest 19 ^{15}	Shoreline Trail	290	757	2.4	44.1	0.6	2013
Nest 20 ^{06}	Blue Sky Trail	258	335	1.3	16.7	−0.1	2013
Nest 21 ^{16}	Shoreline Trail	154	447	2.9	25.0	1.7	2013
Nest 22 ^{17}	Pine Ridge NA	39	108	2.8	28.6	10.5	2013
Nest 23 ^{18}	Pine Ridge NA	106	282	2.7	23.1	0.1	2013
Nest 24 ^{16}	Shoreline Trail	370	953	2.6	36.4	1.9	2013
Nest 25 ^{04}	Shoreline Trail	152	435	2.9	53.7	0.4	2013
Nest 26 ^{17}	Pine Ridge NA	61	136	2.2	21.1	8.9	2013
Nest 27 ^{13}	Satanka Cove	39	79	2.0	9.1	0.0	2013
Nest 28 ^{08}	Arthur's Rock	230	583	2.5	16.7	0.0	2013
Nest 29 ^{19}	Shoreline Trail	114	263	2.3	11.8	−6.4	2014
Nest 30 ^{20}	Quarry Cove	59	133	2.3	20.0	0.0	2014
Nest 31 ^{21}	Shoreline Trail	416	1111	2.7	64.7	0.0	2014
Nest 32 ^{22}	Quarry Cove	22	76	3.5	48.1	4.0	2014

APPENDIX TABLE 1. Continued.

Nest ID $^{pair\#}$	Location	Number of stones	Total stone weight (g)	Avg. stone weight (g)	% Occlusion by stones	Difference in sponge wt. gain (g)	Year active
Nest 33 ^{16}	Shoreline Trail	500	1536	3.1	62.9	−1.7	2014
Nest 34 ^{23}	Pine Ridge NA	56	171	3.0	37.0	20.3	2014
Nest 35 ^{14}	Quarry Cove	328	1005	3.1	54.5	0.0	2014
Nest 36 ^{12}	Quarry Cove	196	570	2.9	60.0	0.1	2014
Nest 37 ^{24}	Dun. Ridge	371	1140	3.1	56.7	32.3	2014
Nest 38	Quarry Cove	196	570	2.9	52.6	38.3	unkn*
Nest 39	Quarry Cove	307	924	3.0	21.1	−8.1	unkn
Nest 40	Pine Ridge NA	104	268	2.6	21.4	0.2	unkn
Nest 41	Quarry Cove	422	1056	2.5	32.8	0.2	unkn
Nest 42	Quarry Cove	135	369	2.3	25.0	0.0	unkn
Nest 43	Quarry Cove	602	1426	2.4	33.3	13.7	unkn
Nest 44	Quarry Cove	310	842	2.7	45.8	0.0	unkn
Nest 45	Quarry Cove	156	431	2.8	42.9	0.0	unkn
Nest 46	Pine Ridge NA	42	111	2.7	40.7	−3.6	unkn

*unkn = likely constructed before 2012