Rock Wren Nest Attributes – Nat Warning- University of Northern Colorado

ROCK WREN NEST ATTRIBUTES

INTRODUCTION

The rock wren inhabits open, arid, rocky slopes, and barren rock outcrops, often residing in habitats occupied by few other bird species (Brewer 2001). In western North America rock wrens are found from the western edge of the Great Plains to the Pacific Slope, south through Mexico, and north into southern Canada (Ray 1904; Bent 1964; Lowther et al. 2000). Rock wrens breed from below sea level in Death Valley (Wauer 1964) to above timberline (3500m) (Grinnel and Miller 1944; Wolf et al. 1985; Oppenheimer and Morton 2000), as long as there is sufficient rock-strewn habitat. In 1902 Florence Bailey, an ornithological pioneer, wrote one of the earliest descriptions of the rock wren; "To the worker in the arid regions of the west...on the wind-blown rock stretches where you seem in a bleak world of granite with only rock, rock, everywhere, suddenly, there on a stone before you, stands this jolly little wren, looking up at you with a bob and a shy, friendly glance." Though familiar and well-noted, rock wrens are little studied in most portions of their range, and many of their behaviors remain enigmatic.

Rock wrens are basal members of the wren family (Troglodytidae), which includes over 80 species of relatively small, vocal passerines in 17 genera (Mann et al. 2006). Rock wrens are most closely related to *Microcerculus* (nightingale), *Catherpes* (canyon), and *Hylorchilus* (slender-billed) wrens, but also group separately as a sister taxon ancestral to all other wrens based on DNA comparisons (Lowther et al. 2000; Barker et al. 2004; Mann et al. 2006). Rock wrens are highly territorial, and males establish and defend territories using large song repertoires (Kroodsma 1975; Lowther et al. 2000), singing from exposed rock, boulders, or vegetation. Mean territory size in Kansas is 1.8 ha (Lowther et al. 2000), and mean home range size in northern Colorado is 3.6 ha (NW Chapter II), within which rock wrens nest, forage, and raise young. Rock wren migratory movements are not well known (Lowther et al 2000). Most northern populations are migrants or partial migrants, arriving in breeding areas between 10 April and 8 May, and departing in September-October (Burleigh 1972; Renaud 1979; Skaar et al. 1985; Thompson and Ely 1992; Gilligan et al. 1994; Campbell et al. 1997).

Rock wrens are distinguished by their habitats, which contain cliffs, canyons and arroyos, cut banks, boulders, and rock outcrops (Gentry 1882; Bent 1964; Oppenheimer and Morton 2000; Brewer 2001), and they breed exclusively in these areas. Rock wrens are not known to drink free water, and obtain water both metabolically and from prey (Smyth and Bartholomew 1966; Lowther et al. 2000). This allows rock wrens to inhabit arid regions where few other bird species are found (Bent 1964; Tramantano 1964; Brewer 2001), and connects rock wrens inexorably to their invertebrate prey which includes grasshoppers and crickets, leaf-hoppers, beetles, bugs, caterpillars, and other insects (Knowlton and Harmston 1942; Tramantano 1964).

Nesting Habits

Rock wren nests are typically located on the ground, in natural cavities beneath boulders and overhanging rocks, in cliff cavities, or in earthen banks (Linton 1911; Bent 1964; Harrison 1979; Merola 1995; Lowther et al. 2000). Rock wren nest construction is unique in that small, flat stones are used to line the base of the nesting cavity (Gentry 1882; Bailey 1904; Ray 1904; Smith 1904; Linton 1911; Bent 1948; Merola 1995; Oppenheimer 1995; Lowther et al. 2000). Stone foundations often extend beyond the nest cavity creating a nest "pavement" (Ray 1904; Bent 1964; Oppenheimer 1995), and are often mixed with sticks and vegetation to form a stable matrix (Figure 10). Stones are reported to vary in length from 12mm to 50mm (Bent 1964; Merola 1995), and in weight from 0.7 g to 6.8 g (Merola 1995; Matiasek 1998), and are placed as a foundation before the construction of the cup nest (Ray 1904; Peabody 1907; Merola 1995; Oppenheimer 1995; Matiasek 1998; Oppenheimer and Morton 2000). Nest cups are typically made of sticks, grasses, and stems, and lined with fine grasses, hair, and feathers (Bent 1964; Harrison 1979), and may incorporate pavement stones on the outer margins (Bailey 1904; NW pers. obs.) Materials are gathered by both sexes (Merola 1995; Oppenheimer 1995; Oppenheimer and Morton 2000), and nest cups are typically set back from the cavity entrance (Matiasek 1998; Oppenheimer and Morton 2000).

Figure 10. Rock wren nest "pavement" with typical small, flat stones mixed with sticks and vegetation to form a stable matrix at the cavity entrance.

Bailey's 1904 publication on rock wren nests in New Mexico was the first to be widely read, and spurred a flurry of observations in other locations, including Texas (Smith 1904), the Farallon islands off the coast of San Francisco (Ray 1904), the Bighorn mountains of Wyoming (Peabody 1907), and the channel islands of southern California (Linton 1911). At the end of her short article Bailey wrote "it is impossible to imagine that such accumulations of stones could be the result of accident…how general is the Salpinctian use of stones, and what proportion of nests have the walks leading away from them?" The response suggested that stone use was widespread, but it wasn't until Bent's publication of wren life histories in 1948 that the subject was taken up again, paving the way for further research.

Stone Pavements

The quality of nest cavities depends foremost on protection against predators which cause most nest failures (Ricklefs 1969; Nilsson 1986; Martin 1995). The susceptibility of ground nests to predators depends on the environment in which they are placed (Martin 1988; 1993), and mammals and snakes are the most likely nest predators of rock wren nests (Peabody 1907; Hardy 1945; Lowther et al. 2000). Adaptive responses to predation are balanced with the need for proper microenvironments for embryonic development, especially in extreme environments (Amat and Masero 2004; Tieleman et al. 2008). Rock wrens are atypical cavity nesters in that their nests are placed amongst rock at sites without leaf or vegetative cover (Wolf et al. 1985); under and between boulders and rock fissures (Bailey 1904; Oppenheimer and Morton 2000), beneath firmly embedded rock overhangs (Ray 1904; Harrison 1979), or in cliff cavities (Smith 1904; Matiasek 1998). These unique environments on steep slopes are subject to environmental factors that may differ from other cavity nesting birds (Wolf et al. 1985; Oppenheimer and Morton 2000). Mechanically, nest cavities are subject to collapses by shifting rocks and landslides (Cameron 1908), and erosion from heavy rains and runoff (NW pers. obs.). Cavities naturally ameliorate fluctuations in temperature (McComb and Noble 1981), and rock wren nests in continental climates fall below ambient temperature during the day and climb above ambient temperature throughout the night due to the alternate cooling and heating of the surrounding rock (Wolf et al. 1985).

As one of the driving components of fitness, nesting behaviors are under strong selection pressure (Schmidt and Whelan 2010). Because nest structure and nest function are interlinked with nest architecture (Gill 2007), the use of stones in rock wren nests likely reflects selection pressures. Though rare, stones are used in the nests of other bird species for multiple functions. Chinstrap penguins (*Pygoscelis antarctica*) gather stones and deposit them in piles atop shallow nest scrapes to enhance nest protection (Williams 1995; Moreno et al. 1999). Desert larks (*Ammomanes deserti*) enclose nests with a semi-circle of small stones as protection from sun and wind (Orr 1970), and black wheatears (*Oenanthe* *leucura*) carry stones to nest sites as a post-pairing display (Moreno et al. 1994; Soler et al. 1996). For over a century workers have postulated the function and significance of stone pavements built by rock wrens. Theories from early workers point to cavity occlusion, nest dryness, and nest marking as possible functions. All focus on the direct benefits that placing stones in nests might provide considering the costs to rock wrens in time and energy use. My aim was to document the use of nest stones locally, and to isolate the function of stone pavements by measuring nest attributes with and without stones present. I predicted that by decreasing the size of the cavity opening, stones would affect the structure, temperature, and dryness of rock wren nests. I also examined evidence pertaining to the hypothesis that rock wrens carry stones as part of a mating display.

Researchers have noted that stones act to partially occlude the entrances to rock wren nest cavities, excluding predators (Gentry 1882; Bailey 1904; Ray 1904; Linton 1911; Bent 1964; Oppenheimer and Morton 2000). Stacked stones can reach heights of at least 6 cm at cavity entrances (Harrison 1979; Matiasek 1998), creating a structural and visual barrier to the nest, while blocking direct sunlight and wind. Sticks are also incorporated in many barriers (Bryant 1887; Bent 1964; Lowther et al. 2000; Oppenheimer and Morton 2000), and may substitute for or accompany stones. Stone barricades could keep nests level, and keep nestlings from falling out of the nest (Ray 1904; Smith 1904). Rock cavities are rarely uniform, and often contain fissures and crevices that could trap nestlings. I predicted that stones would reduce the areas of nest cavity entrances and that larger cavity entrances would contain more stones.

Nest dryness theories propose that stones help to keep nests dry, noting that "those nests with earthen floors, of varying moistness, have more pretentious stone walks", and importantly that "stones were equally deep below completed nests, and nests in the first stages of construction had the stone-ways already finished" (Ray 1904). Both Ray (1904) and Smith (1904) remarked that cliff nests were situated in comparatively dry locations, and contained fewer stones, and that cliff cavities had no place to hold stones at their entrances (Figure 11). In contrast, nests on rocky slopes were more likely to have many stones. In any location, stones could aid in dryness by diverting water away from the nest, or in drainage by allowing water to pass beneath and between stones along underlying rock or soil. In chinstrap penguins, rocks help to keep melt water from infiltrating nests (Moreno et al. 1995). I predicted a correlation between the amount of water infiltrating a nest cavity (when stones were removed) and the amount of stones present.

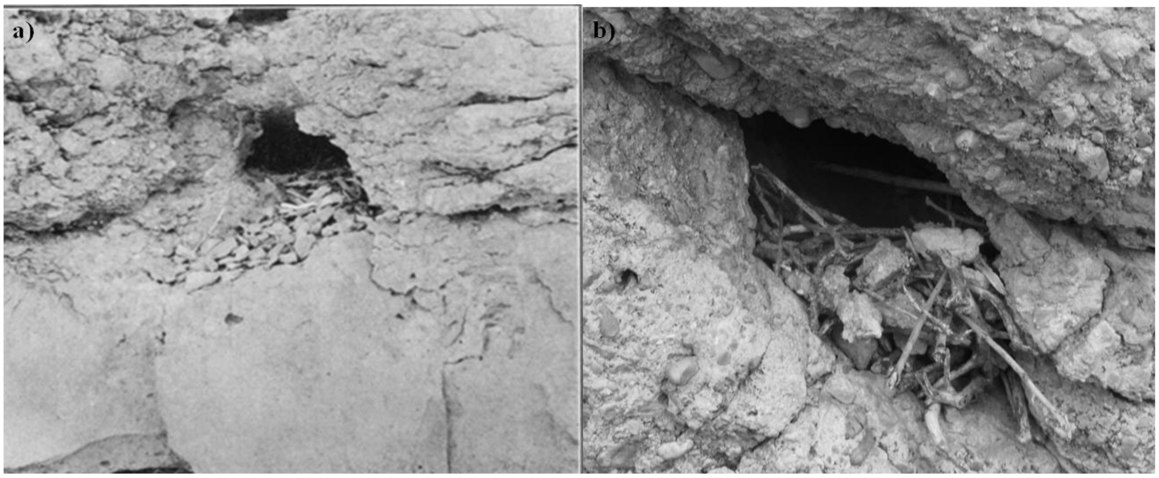

Figure 11. Rock wren nests in cliff cavities. **a)** Cliff nest photographed and described by Florence Bailey in New Mexico in 1902 with a "stone walk" (Condor 6(3):70). **b)** Nest within a cliff cavity in Larimer County, CO, with no surface for a stone walkway. Cliff nests were described by early researchers as being dryer, and holding fewer stones than nests that were built on the ground. This has been interpreted as evidence that stones provided a dryness function.

The microenvironment of the nest affects the daily energy requirements of the eggs, nestlings, and adults (Gill 2007). Because rock wrens breed in exposed environments, regulation of nest temperature may influence nesting behaviors. During periods of sun, rock surfaces heat quickly, but there is a time lag before this heat penetrates into rock wren nest cavities (Wolf et al. 1985). At night, as ambient temperatures drop, rocks retain heat gained during the day, sometimes throughout the entire night (Wolf et al. 1985; Oppenheimer and Morton 2000). Nest stones should add to the ameliorating effects of rock cavities by increasing the thermal mass. Stones that extend outside the cavity entrance could radiate heat into or out of the nest cavity depending on the temperature gradient. Hoopoe (*Alaemon alaudipes*) and desert (*Ammomanes deserti*) larks position nests to catch morning sun when females are foraging away from the nests (Orr 1970; Tieleman et al. 2008). Cactus wrens (*Campylorhynchus brunneicapillus*) build nests that are exposed to sunlight early in the season, relying on solar radiation to help maintain the nest temperature (Proudfoot et al. 2000). Canyon wrens (*Catherpes mexicanus*), which co-occur with rock wrens in our study area, nest in cliff crevices (Jones et al. 2001), and can receive many hours of sunlight depending on nest placement and the overlying strata (Figure 12). Rock wren nest cavity entrances are typically exposed to full sunlight; while the nests, usually at least 12 cm deep, are almost always shaded (NW pers. obs.). I predicted that nests with stones would have smaller temperature fluctuations than surrogate cavities containing no stones, and that nests with accumulations of stones outside the cavity would have higher daytime temperatures.

Figure 12. Nests of two wren species in similar habitat. **a)** Canyon wren (*Catherpes mexicanus*) nest located in a cliff crevice, exposed to full sunlight for part of the day. **b)** Rock wren (*Salpinctes obsoletus*) nest located 12 cm inside a cavity, perpetually in shadow. Regulation of nest temperature may influence rock wren nest building and incubation behaviors.

Nest marking theories point to the abundance of suitable nest cavities in many rock wren environments, noting that rock wrens may require stone pavements in order to mark and help birds relocate nesting sites (Bailey 1904; Ray 1904; Bent 1964; Oppenheimer and Morton 2000). Subsequent research has shown that memory, which underlies many behaviors, is plastic in response to changing ecological situations (Healy and Andrew 2004), and that birds, including non-food storing species, are able to return to a particular location after a single experience there (Clayton and Krebs 1994). Cryptic nest sites are expected to minimize predation risks. Nest marking would compete with demands for keeping nests well hidden from predators, but could advertise nest sites to mates, other conspecifics, heterospecifics, or descendants. I tested the indicator function of stones indirectly by moving the stones from twelve 2012 nests into similar nest cavities nearby. If rock wrens returning in 2013 could be induced to nest in relocated cavities with stones, this would lend support to an indicator function for stones. If pairs ignored the relocated nests, or moved new stones into the original cavities, this would counter the nest marker function. An indicator function of stones is difficult to separate from other benefits of stones, which could also induce wrens to nest in cavities with stones already present, and I interpret results of this experiment cautiously.

Many wrens are known to construct nests to attract prospective mates (Bent 1964; Burns 1982; Kroodsma and Verner 1997). It has been suggested that stone carrying in the rock wren might 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). Male wheatears carry small, flat stones to a nest site, while females assess mate quality by the amount of stones carried (Moreno et al. 1994; Soler et al. 1996). The stones do not contribute to nest stability, temperature regulation, or predator deterrence (Moreno et al. 1994), and their use is interpreted as a post-pairing, sexually selected display leading to differential levels of reproductive output and parental care by females (Soler et al. 1996; Soler et al. 1999). In rock wrens, females are the primary stone carriers (Merola 1995; Oppenheimer 1995; Mataisek 1998, Oppenheimer and Morton 2000), and males deliver stones to the nests only occasionally (Oppenheimer 1995; Oppenheimer and Morton 2000). Males are also expected to benefit from assessing the fitness of their mates, though post-pairing displays by female birds are rarely tested (Palamino et al. 1998; Gill and Stutchbury 2005). I wanted to further document gender differences in rock wren stone carrying behavior, and predicted that I would see evidence for stereotyped stone carrying as a display. Placement of stones in non-breeding nests, or delivering stones to a mate would suggest, but not verify a display function. A more intensive study will be needed to determine if nests themselves serve as a display.

MATERIALS AND METHODS

Study Location

All nests were located on public lands in Larimer County, CO. Sites were in semi-arid montane shrublands characteristic of the northern Colorado foothills region, with rocky, coarse textured soils and high runoff (Mutel and Emerick 1992). The climate is continental, with average rainfall of 40.3 cm, with 70% of rain falling in April–September (USCD; Price and Amen 1983). Average temperature is 9.5°C, and average summer temperature is 19.2°C (USCD). The slopes approaching cliffs are steep (15-32˚), and are dominated by mountain mahogany (*Cercocarpus montanus*), wax currant (*Ribes cereum*), three leaf sumac (*Rhus triolbata*), rabbitbrush (*Chrysothamnus nauseosus*), and Rocky Mountain juniper (*Sabina scopulorum*), and contain cliffs, talus, large boulders, escarpments, and rocky outcrops. Elevation of nest sites ranged from 1600-2000 m.

Identification and monitoring

I surveyed public lands in Larimer County May-June 2012-2013 using direct observation to locate active rock wren breeding territories. I monitored 22 rock wren territories over two breeding seasons, and identified 34 nests from 18 pairs (12 nests in 2012, and 22 nests in 2013). Colleagues color-banded a subset of male rock wrens (8/21) with unique combinations of plastic color bands (Gey, Norristown, PA) to distinguish between sexes. Wrens were captured in mist nets (Avinet, Dryden, NY) under which conspecific audio playbacks were broadcast. I observed active nests and placed motion cameras (Reconyx, Holmen, WI or Cuddeback, De Pere, WI) at nests (n = 1 in 2012; n = 7 in 2013) to document nesting behaviors. I used Arc GIS (ESRI 2010) to map the locations of active nests within and between pairs, and used the measure tool to calculate distances between nests.

Nest Attributes

To test the microclimates in cavities with and without stone pavements I logged temperature data in vacant nests, after either the chicks fledged or the nest failed, and simultaneously in surrogate cavities of similar depth and orientation within five meters of the focal nest. I collected hourly temperature data in 13 nest cavities using data logger buttons (ACR Systems, Surrey, BC) in plastic mounts placed directly in front of the cup nests within cavities, and duplicated the placement distance in surrogate cavities without stones. I used a paired t-Test to compare mean, maximum, and minimum temperatures and temperature fluctuations in nests vs. surrogate cavities. All statistics were performed in JMP, v.9 (SAS Institute Inc., Cary, NC).

I processed stones during non-breeding periods from 34 nests, 11 of which were active in 2012 and 12 in 2013. Eleven nests tested were inactive in 2013, but may have been active in 2012. At each nest I weighed stones collectively to the nearest 0.1 gram using a portable electronic scale (Ohaus, Pine Brook, NJ) to gauge total stone weight, and divided by the number of stones to determine average stone weight. I did not count or remove stones that were incorporated into the nest cup. I weighed and measured length, width, and thickness of at least 20 randomly selected stones from each nest using dial calipers (Avinet, Dryden, NY) to assess stone size and shape. To measure stone availability in the area I collected stones of appropriate size and thickness within 25 m of each nest for 15 minutes and weighed the total amount collected.

To document cavity occlusion I measured the height and width of the cavity entrance before and after the removal of nest stones using a flexible 15 cm ruler. I compared the area of the cavity opening (without stones) to the total weight of stones in the nest using linear regression. To measure nest dryness I recorded how patio presence affected the water weight gain of a 5cm x 5cm sponge placed inside the nest cavity directly in front of the nest cup (Figure 13). I sprinkled one gallon of water over the nest and cavity entrance from a height of 50 cm before and after the removal of nest stones, and measured sponge weight gain to the nearest 0.1 g with a portable electronic scale (Ohaus, Pine Brook, NJ). I returned all stones to nests in their original formations except in nests that were manipulated. I used a paired t-Test to compare differences in weight gain.

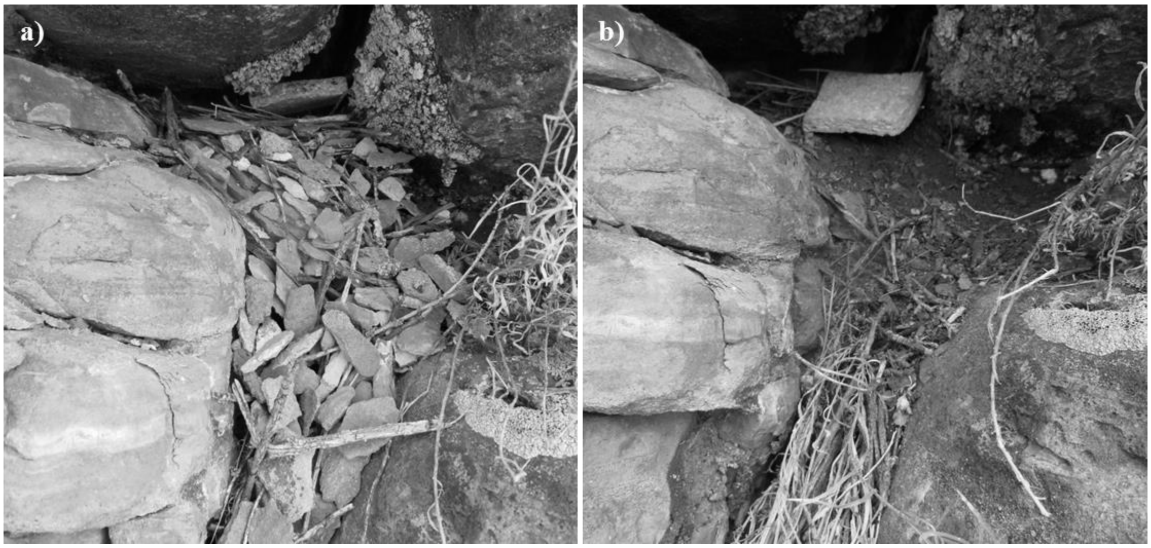

Figure 13. Rock wren nest during a dryness experiment. **a)** Sponge (5 cm x 5 cm) inserted into the nest cavity with stones present. **b)** Sponge in the nest cavity after the removal of stones. In both pictures the sponge was not fully inserted so that it could be seen.

Nest Manipulations

To test the nest marking or indicator function of stones, I removed and marked (with a small dot of paint) the stones from 12 nests representing 9 rock wren pairs, and replicated the stone arrangement in nearby cavities that appeared to be suitable for nesting. Relocated nest cavities were located from 1 – 40 (mean = 12.8) m from focal nests, and had similar characteristics. Relocated nests were in natural cavities, but I bolstered their entrances with large rocks to protect cavities from rain. Nest cups, if still present, were left in place and not relocated with the stones. I manipulated nests in Nov-Dec 2012, when rock wrens were absent from territories (Figure 14), and monitored nests via observation and motion activated cameras beginning in April 2013. By marking stones I was able to tell if new stones were added to relocated sites. Cameras detected bird visits by taking a photo or burst of photos with each motion trigger, with a 5 sec delay between triggers.

Figure 14. Rock wren nest manipulation experiments. **a)** A relocated nest site that we chose pictured before stones were moved. **b)** The same cavity with stones (439) marked and relocated from a nearby nest. **c)** Close up of the cavity entrance for a relocated nest site. **d)** Rock wren perched at the entrance to a relocated nest site.

Figure 15. **a)** Rock wren female moving a nest stone on 17 Aug 2013. **b)** Rock wren placing a stick in a nest cavity 19 Sept 2013. Rock wrens visited nest sites well after the breeding season in 2013.

RESULTS

Nest Attributes

Mean spacing of active rock wren nests in neighboring pairs was 158 ± 88 m SD (range 73–344 m, n=10) and for multiple nests within pairs was 79 ± 83 m SD (range 5-380 m, n=17). Rock wrens built nests from May-Aug 2013, and visited and maintained nests well into October 2013 (Figure 15). No cameras were deployed on nests in Fall 2012.

Nests were located either on or close to the ground (n=31) or in cliff cavities (n=3). At least four additonal cliff nests were observed (2 in each season) that were inaccessible, and these were not measured. None of the 12 active nests discovered in 2012 were reused in 2013, though some were visited frequently by rock wrens. One bird took shelter in an old nest during a spring snowstorm on 1 May 2013. Nests contained a mixture of stones, sticks, and plant material.

Two paired female wrens were observed carrying stones, and a third was documented on camera. I never observed a male carrying stones, although on multiple occasions the male was present while his mate was carrying stones to a nest site. Stones were carried in the bill, and wrens were able to fly short distances and scale cliffs while carrying stones.

Nests contained from 32-602 stones (mean = 234, n = 34) weighing 67-1442 g (mean = 568). Average stone weight across nests was 2.45 ± 0.37 g (range 1.3 – 3.0, n = 496). At least two nests were constructed entirely in 2013, and these contained 950 g (Figure 13) and 686 g of stones respectively.

Mean stone length was 24.7 ± 6.8 mm SD (range 9.3 - 59.1 mm), and mean stone width was 17.7 ± 4.7 mm SD (range 7.0 - 37.5 mm). Nest stones were generally consistent in thickness (mean ± SD, 5.2 ± 1.5 mm, range 1.6 – 10.6 mm) and in weight (mean ± SD, 2.75 ± 1.6 g, range 0.2 – 9.9 g (Figure 16). Nest stones always lined the bottom of the cavity, and in 82% (28/34) of cases were placed outside the cavity forming a nest pavement (Appendix C). The weight of stones in the nests was not significantly correlated with stone availability measured from collecting stones within 25 m of nests ($r^2 = .02$, $p = 0.42$).

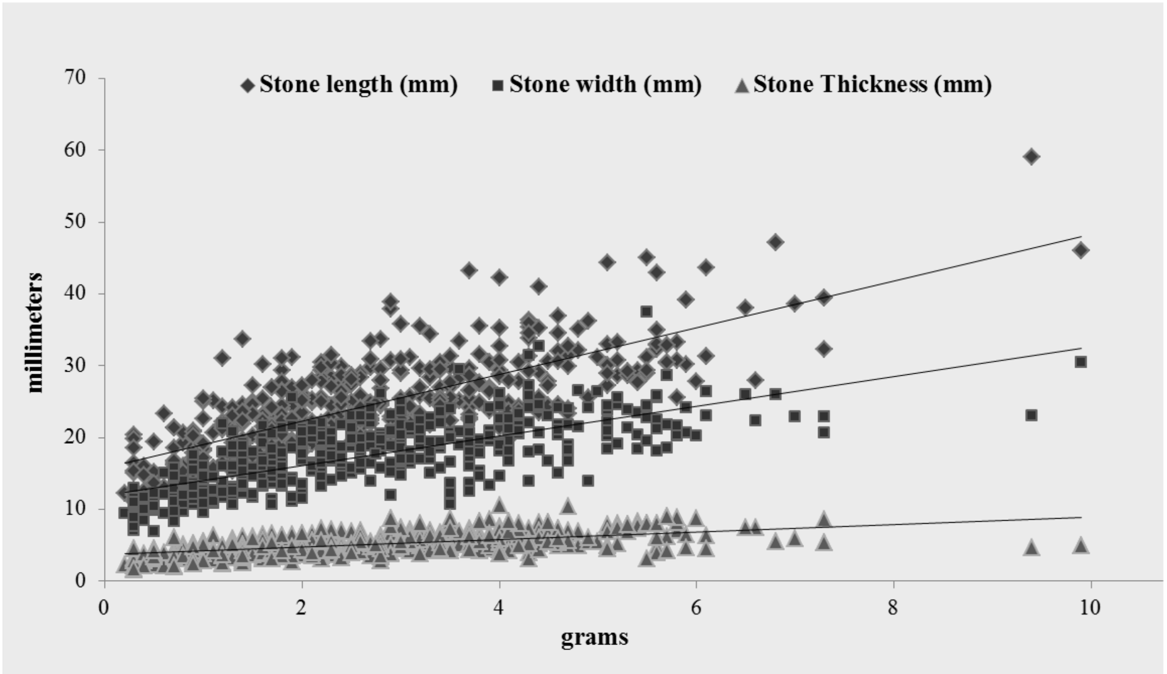

Figure 16. The weights of rock wren nest stones plotted against their length (diamonds), width (squares), and thickness (triangles). Stones were consistent in thickness, making nest entrances highly recognizable.

Cavity Occlusion

Rock wrens nested in a wide range of cavity sizes and shapes. 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. Stones, combined with sticks, formed matrices that barricaded nest cavity entrances and shielded nests from direct sunlight. Cavity opeinings were significantly larger when measured without stones ($t_{33} = 6.48$, $p < .0001$). Mean area of the cavity entrance was 67.5 ± 41.9 cm^2 SD with nest stones present, and 106 ± 68.2 cm^2 SD with nest stones removed (Figure 17). I observed that stones often leveled the floor of the nest cavity and anchored the nest cup. The size of the cavity entrance area correlated negatively with the cumulative weight of stones ($r^2 = 0.15$, $p = .022$) (Figure 18). Matiasek (1998) found a similar correlation between cavity size and the dimensions of stone pavements in Kansas rock wren nests.

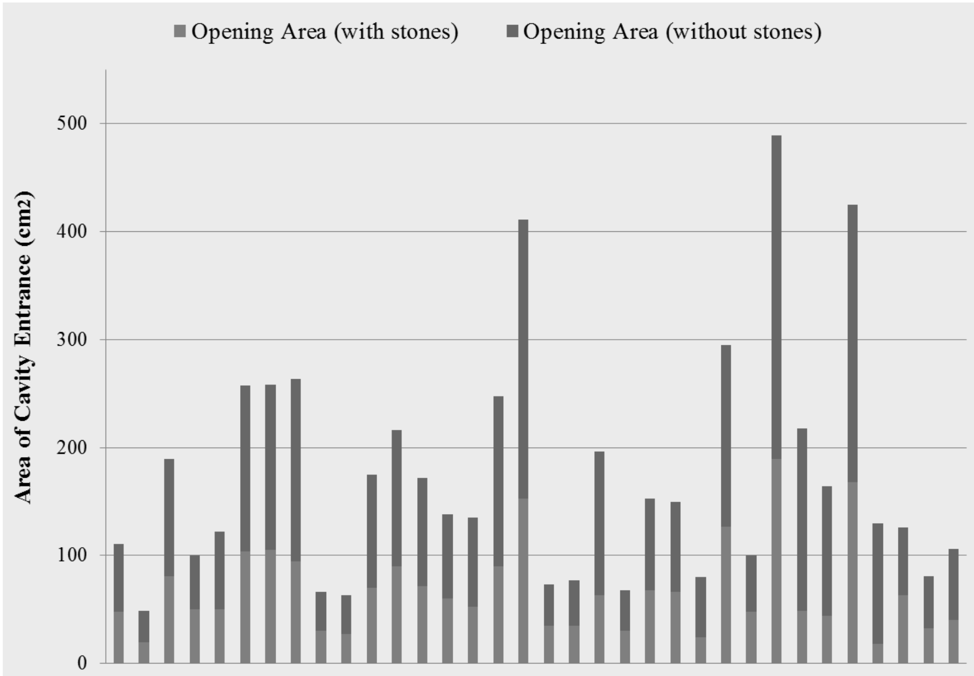

Figure 17. Areas of the cavity entrances of 34 rock wren nests from Larimer County, CO with nest stones (light gray bars) and without nest stones (dark gray bars). Stones significantly decreased the area of nest cavity openings.

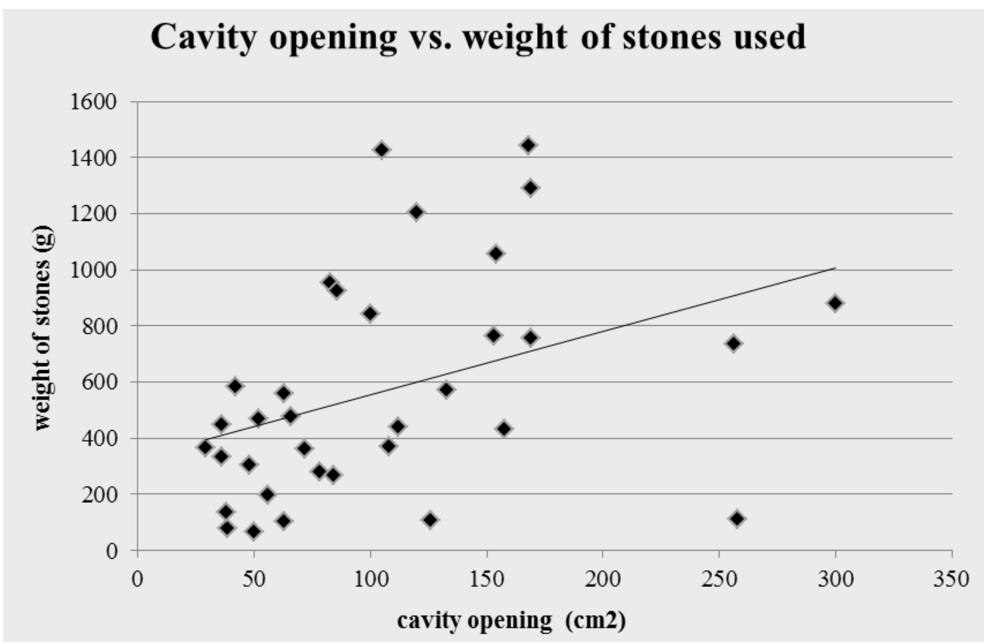

Figure 18. Area of the nest cavity opening (cm^2) vs. collective weight of stones used in 34 nests from 18 rock wren pairs in Larimer County, CO with linear regression line ($r^2 = 0.15$, p = .022).

I did not disturb active nests to check eggs or chicks, and was unable to document specific nest predation. Motion activated cameras at 5 different nest cavities captured images of potential mammalian predators, including Mexican woodrats (*Neotoma lepida*), northern rock mice (*Peromyscus nasutus*), and golden-mantled ground squirrels (*Spermophilus lateralis*) (Figure 19). Motion cameras are triggered by heat differences, and reptilian predators may not have been detected by cameras. On 13 June 2013 I observed a male rock wren attack a rock squirrel (*Spermophilus variegatus*) that came near to an active nest located on a rock dam.

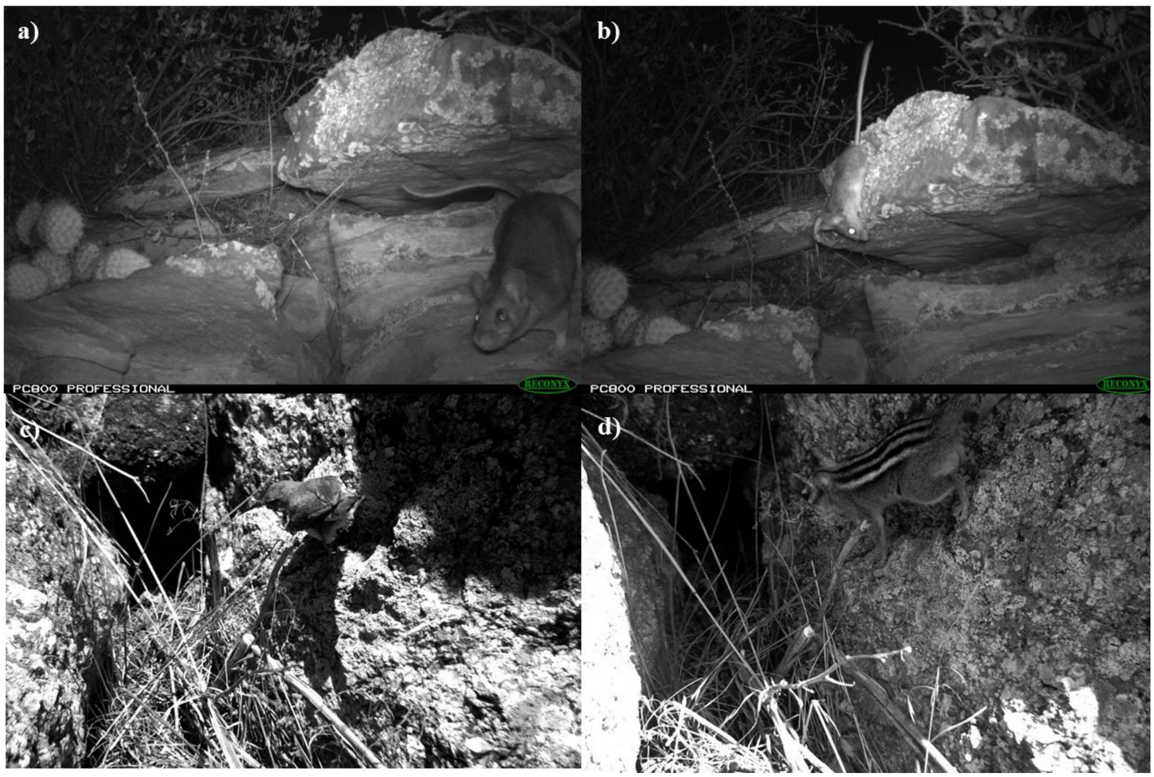

Figure 19. **a)** Mexican woodrat (*Neotoma lepida*) exiting a rock wren nest. **b)** Northern rock mouse (*Peromyscus nasutus*) investigating a rock wren nest. **c)** Rock wren entering a nest cavity and **d)** Golden-mantled ground squirrel (*Spermophilus lateralis*) following a rock wren to a nest cavity. Rats, mice, and ground squirrels were the most common mammals to visit nests with camera traps from May-September in my study area in northern Colorado.

Nest Dryness and Temperature

Though nests situated in cavities close to the ground have increased insulation (Weathers and Sullivan 1989; Oppenheimer and Morton 2000), they are also subject to dampness and flooding. Rock wren nests in our study area were always situated on slopes from 18˚- 90˚ in areas where coarse soils are underlaid by impervious rock (Mutel and Emerick 1992), and there was little soil to absorb water as it flowed downslope. If nest stones divert water, or facilitate passage of sheet flows beneath the nests, I expected an inserted sponge to gain more water weight after stones were removed. This was the case in 59% (20/34) of nests. In 20% (7/34) of nests there was no water gain in the sponge regardless of whether stones were present (Appendix B). These nests were located in cavities beneath sheltering rock overhangs protected from direct rainfall. Four nests gained less water after we removed nest stones. Overall, these results indicate that stones significantly increased nest dryness ($t_{33} = 2.52$, $p = .0165$, matched pairs) in rock wren nests. I also observed that stones helped to stabilize the soil surrounding the nest cavity during the dryness experiments. After stone pavements were removed, the underlying soil was much more prone to erosion from the water poured from the sprinkling can.

I did not detect a significant relationship between nest stones and temperature or temperature fluctuations within nest cavities (Figure 20). Cavities that contained stones did exhibit slightly less variation in nest temperatures, but not at a significant level ($t_{24} = -1.17$, $p = .2533$).

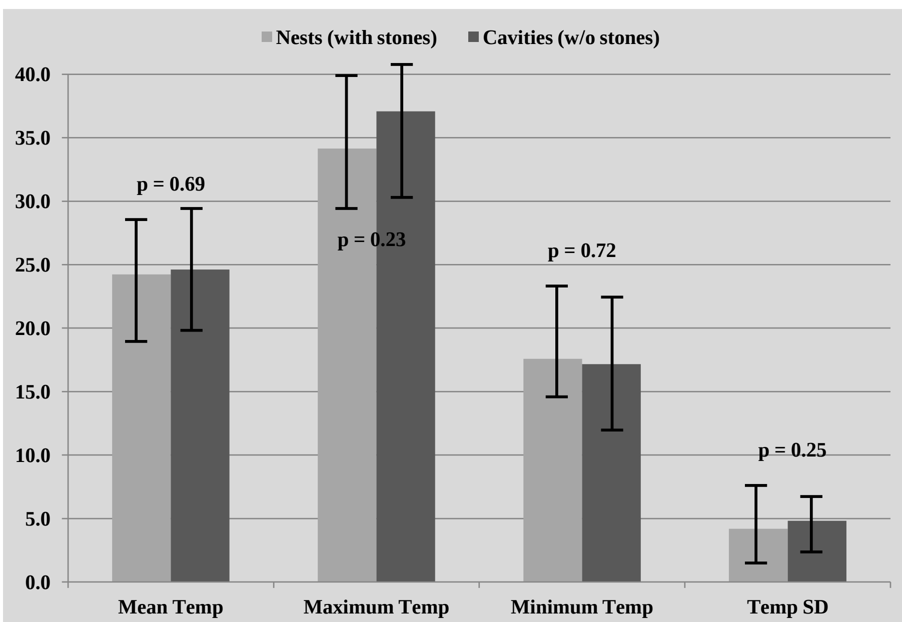

Figure 20. Comparison of mean, mean maximum, and mean minimum cavity temperatures and temperature standard deviations (SDs) from 12 rock wren nest cavities (with stones; light gray bars), and 12 surrogate cavities (without stones; dark gray bars). Error bars show data ranges.

Nest Manipulations

I relocated nest stones to neighboring cavity sites to see if rock wrens could be induced to use a new cavity based on the presence of pavement stones. Rock wrens sometimes reuse nests from year to year (Merola 1995), but rarely use the same nest for successive broods (Tramantano 1964; Lowther et al. 2000). This may be in response to predation risks (Collias and Collias 1984; Weathers and Sullivan 1989), and to body parasites including botflies and feather lice (Peabody 1907; Rockwell and Wetmore 1914; Price 1977). Rock wrens have been observed using nest cavities that were occupied by different (banded) birds in previous years (Merola 1995), so the use of cavities with stones already in place was plausible. Rock wrens investigated at least 41% (5/12) of relocated nests, and 100% (5/5) of nests that were monitored by cameras. Rock wrens added stones to 25% (3/12) of relocated nests, adding from 6 - 89 stones (collectively 21.6 – 291 g), but only nested in one relocated nest which contained 395 stones weighing 727 g, to which the female added 89 stones weighing 291 g. This nest cavity was 40 m from a nest used in 2012, though I am unsure if it was the same wrens that used the nests in sequential years.

Brood Overlap

Rock wrens have been observed to have overlapping broods (Walsh and Bock 1997). Though I typically observed both sexes caring for young, one exception gives further evidence for overlapping broods. I monitored one pair that nested and began to feed chicks in mid July, but from 27 July to fledging on 8 Aug only the male provisioned the nestlings. The female wren was still seen occasionally on the territory, and may have been incubating at another nest, though I was unable to locate it. This pair had a nest earlier in the season that failed. In this case the male rock wren completely provisioned the 4 young in the nest for 11 days before they fledged (Figure 21).

Figure 21. A rock wren nesting sequence for one pair in Larimer County, CO. **a)** Female carrying a stone into the nest area 7 July 2013. **b)** Male feeding the female just outside the nest cavity 14 July 2013. **c)** Male delivering food to nestlings 6 August 2013. **d)** Fledgling emerging from the nest cavity 8 August 2013. After 27 July 2013 only the banded male provisioned the nestlings, successfully fledging 4 chicks. The female wren may have been incubating on a second nest, leaving the male to care for the first brood.

DISCUSSION

Cavity Occlusion as a Proximate Cause

Workers have long recognized that nest stones decrease the size of rock wren cavity entrances, but most did not believe that cavity occlusion alone could explain the stones in every nest that they observed (Bailey 1904; Ray 1904; Smith 1904; Bent 1964). Not all rock wren nests contain stones, (Smith 1904; Oppenheimer and Morton 2000; NW uplshd. data). Though rare, these nests are located in cavities or crevices with the smallest sized openings, suggesting that stones are not required in all situations (Oppenheimer and Morton 2000). It follows that cavity occlusion should be viewed as a situation-specific proximate cause for stone use, serving multiple functions. Smaller cavities and cavity openings could deter predators, increase nest dryness, and protect the nest from exposure and temperature fluctuations. This multi-functionality could help explain selection for stone carrying behavior in rock wrens living in varying environments, and synthesize disparate observations.

Benefits of Cavity Occlusion

Nest predation rates depend on the types of predators and the coexisting species present (Martin 1988). Predation can lead to both specialization of nests within species and stereotyped nest placement (Martin 1993a). In measuring nests it was often difficult to visualize how much area the pavements were occupying until I removed stones. Even with stones decreasing the entrance size, 58% (20/34) of nests still had entrance openings > 50 cm^2 (max of 9.5 cm on a single axis), enough for many small mammal predators, including woodrats and ground squrirrels, to enter. This suggests that stone barricades are built to obscure nests rather than to block predator access. Nest placement should reduce visual and olfactory predator cues (Martin 1993b), while allowing rapid escape from nests (Davis 2005). Data from motion cameras suggest that small mammals may be important predators of rock wren nests. In mixed forests of Arizona, red squirells can account for 80% of nest predation events, taking both eggs and chicks (Martin 1988). My data show that long term deployment of motion-activated cameras could help determine whether stone barricades deter nest predators. Stones are noisy, and another idea is that stone pavements act as an alarm system, alerting incubating females to potential predators at the nest entrance. I am currently testing this hypothesis.

Two studies, Wolf et al. (1985) and Oppenheimer and Morton (2000), document rock wren nest temperatures and incubation behavior. They show that rock wrens have long incubation bouts and long inattentive bouts compared to other passerines (Oppenheimer and Morton 2000), but that nest temperature is more constant than ambient temperature (Wolf et al. 1985). Johnston and Ratti (2002) found a similar pattern comparing active canyon wren (*Catherpes mexicanus*) nest cavities to surrogate cavities, constancy that they attribute to large diameter rock. My goal in monitoring rock wren nest cavity temperatures was only to isolate the temperature effects of nest stones, which theoretically could ammeiliorate temperature fluctuations by adding to the thermal mass, or alter the way that heat or cold transfers from the ground or cavity base. Cold air can collect in the depressions of ground nests, creating harsh conditions (Lyon and Montgomerie 1987), and stone foundations could raise nests into a warmer microclimate. In environments where rock is prevalent, and there are no heat imputs from incubating birds, nest stones apparently have little impact on cavity temperature. Even so, stones could play a larger role in controlling nest temperature in areas with little underlying rock or in cases where rock wrens nest in dirt burrows (Bent 1948; Tramantano 1964). I monitored temperature in unoccupied cavities, and occupied nests have shown more stable temperature patterns (Wolf et al. 1985; Oppenheimer and Morton 2000). Additionally, occluded nests are protected from direct wind, which my temperature data may not reflect. Objects, including rocks, tuft grasses, and cow dung have been shown to reduce nest exposure to sun and wind in grassland nests (Nelson and Martin 1999; Hartman and Oring 2003).

My results indicate that stones can play a larger role in keeping rock wren nests dry, and dry nests are most likely to maintain temperature and succeed (Story et al. 1988). I recorded stones increasing dryness in the majority of nests experimenting with a single gallon of water. With increased water via heavy rainfall and saturated soils I would expect the dryness effects of stones to be amplified. Besides facilitating drainage, stones also apparently stabilize the underlying soil. During a rainfall event the stability of the soil around a nesting cavity could keep the cavity from being undercut by water (Figure 22). The stabilizing effects of stones may be a critical function of the pavements that extend outside the entrances, and warrants additional testing. In arid environments that are nonetheless shaped by water, it is logical that rock wrens could have evolved nesting strategies to deal with periodically heavy rainfall and sheeting water using a commonly available material.

Figure 22. Rock wren nest containing over 600 stones weighing 1.5 kg. The area burned in the spring of 2013, and subsequent heavy rains and runoff destabilized and undercut the nest cavity, washing most of the nest stones downslope.

Nest Manipulations

Because stone functions are interlinked, it was difficult to predict whether rock wrens would be induced to use cavities with relocated stones. The relatively large home ranges in our study area (mean = 3.6 ha; NW Chapter II) seem to offer abundant cavities suitable for nesting. Wrens spaced their nests an average of 80 m apart (n = 17) between broods, so locating surrogate cavities near to existing nests did not inherently make them candidates for nesting. That wrens nested in one relocated cavitiy and added stones to two others can be interpreted in multiple ways; 1) that high quality nesting cavities may be limiting for rock wrens, 2) that nest stones are indicators of high quality nest sites, or 3) that previously placed stones can save rock wrens from expending uneccesary energy. Unless stones are removed by the birds, this also means that stones can accumulate in nests from year to year, explaining the large accumulations (> 2 kg) of stones in some nests. While it is known that rock wrens use pre-existing nests that they did not initiate (Merola 1995), the criteria for choosing nest sites is not known. If cavities are chosen based only on the presence of nest stones, I likely would have seen a greater percentage of relocated cavities utilized. Additions of stones to relocated cavities suggests that wrens were at least considering them for potential nesting sites, or engaging in display behavior. It is also possible that rock wrens build non-breeding nests typical of other wren species (Metz 1991; Lowther et al. 2000; Brewer 2001) for detering predators or displaying to mates and conspecifics. In a three year study in western Kansas, no identified nest sites were reused (Lowther et al. 2000). If high quality habitat is occupied year after year, we can expect these sites to accumulate nests, and for nests to eventually be recycled. In a single valley of our most densely populated study site, I located 15 old and active nests in a 1 km^2 area. Long term studies are needed to determine the patterns of nest occupancy for rock wrens, and the frequency at which nests are reused. Juncos (*Junco hyemalis*) re-use more productive off- ground nests at a higher rate than ground nests (Yeh et al. 2007), and rock wrens may show similar patterns.

Nest placement of the (allopatric) Northern Wheatear (*Oenanthe oenanthe*) is strikingly similar to that of rock wrens. Females choose a nest site beneath boulders, in piles of stone, or in stone crevices on or above the ground, and build a large foundation beneath the nest of plant stems and feathers (Sutton and Parmelee 1954; Kren and Zoerb 1997). Males accompany females while the materials are collected (Conder 1989). The (sympatric) Brown-capped Rosy Finch (*Leucosticte australis*) nests are constructed in rock slides, fissures, and cliff ledges by females, with a base of mosses, plant stems, and mud chips (Bailey and Niedrach 1965).

Only female rock wrens were observed building pavements. If stones provide a display function, it is likely a female display. Males provide extensive, sometimes exclusive parental care and defend territories, but carry stones infrequently. Overall, evidence supporting a display function are inconclusive, and dryness benefits seem like a simpler explanation.

Future Directions for Research

Even though half of all avian orders nest in cavities or holes (Gill 2007), few species modify their nesting cavities as much as rock wrens. This modification takes place prior to nest building, and is integral to most rock wren nests that have been studied. Stone use requires an investment in time and energy that must have developed under strong selective pressures. Many bird species are known to occasionally use stones or like materials in their nests. Horned Larks (*Eremophila alpestris*) sometimes place flat, sun-baked mud chips at a nest site before constructing the grass cup (Dubois 1935). American Kestrels are secondary cavity or scrape nesters, and have been observed arranging large (2.5 cm) wood chips around nest scrapes (Richards 1970).

Stereotyped use of stones may have evolved as a response to selective pressures inherent in rocky environments including physical dynamics of rock cavities, water flow, and predation. It is possible that similar selection pressures led to stone carrying in the black wheatear, which makes use of similar habitats, and now uses stone carrying as a male display (Moreno et al. 1994; Soler et al. 1996). All evidence indicates that female rock wrens, who are considered less likely to display (but see Gill and Stutchbury 2005), are the primary stone carriers, and future research should focus on the possible display functions of stone carrying in rock wrens.

I examined several possible benefits of nest stones, and found that stones significantly occlude nest cavity openings, increasing nest dryness and stability. By reducing cavity opening size, rock wrens protect nests in multiple ways, and cavity occlusion can be viewed as a proximate mechanism that underpins rock wren nesting behavior.

FUNDING

This work was supported by Department of Natural Sciences at University of Northern Colorado, Colorado Field Ornithologists, **Audubon Society of Greater Denver (Lois Webster Fund)**, and Larimer County Department of Natural Resources.

Acknowledgments

I thank N. Covy, L. Gaechter, D. Leatherman, A. Meyer, N. Najar, A. Rose, P. Watson, and M. Webb for assistance in the field. I acknowledge the City of Fort Collins Natural Areas Program, Larimer County Department of Natural Resources, and Colorado Division of Parks and Wildlife for enabling this work.

REFERENCES

Amat JA, Masero JA. 2004. Predation risk on incubating adults contrains the choice of thermally favourable nest sites in a plover. Anim Behav. 67:293-300.

Bailey FM. 1904. Twelve Rock Wren Nests in New Mexico. Condor. 6(3):68-70.

Barker FK., Cibois A, Schikler P, Feinstein J, Cracraft J. 2004. Phylogeny and diversification of the largest avian radiation. *Proc Natl Acad Sci U.S.A.* 101(30):11040-11045.

Bent AC. 1964. Life histories of North American nuthatches, wrens, thrashers, and their allies. New York (NY): Dover Publications Inc.

Brewer D. 2001. Wrens, dippers, and thrashers. New Haven (CT): Yale University Press.

Bryant WE. 1887. Additions to the ornithology of Guadalupe Island. Bull Calif Acad Sci. 2:269-318.

Burleigh TD. 1972. Birds of Idaho. Caldwell (ID): Caxton Printing, Ltd.

Burns JT. 1982. Nests, territories, and reproduction of Sedge Wrens (*Cistothorus platensis*). Wilson Bull. 94:338-349.

Cameron ES. 1908. The birds of Custer and Dawson Counties, Montana. Auk. 25:39-56.

Campbell RW, Dawe NK, McTaggart-Cowan I, Cooper JM, and Kaiser GW. 1997. The birds of British Columbia, Vol. 3. Passerines: flycatchers through vireos. Vancouver (BC): Univ. of British Columbia Press.

Clayton NS, Krebs JR. 1994. Memory for spatial and object-specific cues in food-storing and nonstoring birds. J Comp Phys A. 174:371-379.

Collias NE, Collias EC. 1984. Nest building and bird behavior. Princeton (NJ): Princeton University Press.

ESRI. 2010. Arc GIS for Windows. Version 10.0. Redlands (CA): Environmental Systems Research Institute Inc.

Gentry TG. 1882. Nests and eggs of birds of the United States. Philadelphia (PA): JA Wagenseller.

Gill SA, Stutchbury BJM. 2005. Nest building is an indicator of parental quality in the monogamous neotropical buff-breasted wren (*Thryothorus leucotis*). Auk. 122(4):1169-1181.

Gill F B. 2007. Ornithology. New York (NY): W. H. Freeman and Company.

Gilligan J, Rogers D, Smith M, Contreras A. 1994. Birds of Oregon: status and distribution. McMinnville (OR): Cinclus Publ.

Grinnell J, Miller AH. 1944. The distribution of the birds of California. Berkeley (CA): Cooper Ornithological Club.

Hardy R. 1945. Breeding birds of pigmy conifers in the book cliff region of eastern Utah. Auk. 62:523-542.

Harrison HH. 1979. A field guide to western birds' nests of 520 species found breeding in the United States west of the Mississippi River. Boston (MA): Houghton Mifflin Co.

Healy SD, Andrew HT. 2004. Spatial Learning and Memory in Birds. *Brain Behav Evol.* 63(4):211-220.

Hensley MM. 1954. Ecological relations of the breeding bird population of the desert biome in Arizona. Ecol Monogr. 234:185-207.

Johnston HL, Ratti JT. 2002. Distribution and habitat selection of canyon wrens, Lower Salmon River, Idaho. J Wildlife Mgmt. 66(4):1104-111.

Knowlton GF, Harmston FC. 1942. Insect food of the Rock Wren. Great Basin Nat. 3:22

Kroodsma DE. 1975. Song patterning in the rock wren. Condor. 77(3):294-303.

Kroodsma DE, Verner J. 1997. Marsh Wren (*Cistothorus palustris*). In: Poole A, editor. The Birds of North America Online. Ithaca (NY): Cornell Lab of Ornithology.

Linton CB. 1911. Nests of the San Nicolas Rock Wren. Auk. 28(4):489.

Lowther PE, Kroodsma DE, Farley GH. 2000. Rock Wren (*Salpinctes obsoletus*). In: Poole A, editor. The Birds of North America Online. Ithaca (NY): Cornell Lab of Ornithology.

Mann NI, Barker FK, Graves JA, Dingess-Mann KA, Slater P. 2006. Molecular data delineate four genera of *Thryothorus* wrens. Mol Phylogenet Evol. 40(3):750-759.

Martin TE. 1988. On the advantage of being different-nest predation and the coexistence of bird species. Proc R Soc Lond B. 271:S317-S320.

Martin TE. 1993. Nest predation among vegetation layers and habitat types-revising the dogmas. Am Nat. 141:897-913.

Martin TE. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. Ecol Monogr. 65:101-127.

Matiasek JJ. 1998. Nest-site selection and breeding behavior of the migratory Rock Wren (*Salpinctes obsoletus*) in western Kansas. [Master's Thesis]. Hays (KS): Fort Hays State Univ.

McComb WC, Noble RE. 1981. Microclimates of nest boxes and natural cavities in bottomland hardwoods. J Wildlife Mgmt. 45:284-289.

Merola M. 1995. Observations on the nesting and breeding behavior of the rock wren. Condor. 97:585-587.

Moreno J, Soler M, Moller AP, Linden M. 1994. The function of stone carrying in the black wheatear, *Oenanthe leucura*. *Anim Behav*. 47:1297-1309.

Moreno J, Bustamente J, Vinuela J. 1995. Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis Antarctica*). I. Sex roles and effects on fitness. Polar Biol. 15:533-540.

Moreno E, Moreno J, de Leon A. 1999. The effect of nest size on stone gathering behaviour in the chinstrap penguin. Polar Biol. 22:90-92.

Medin DE. 1987. Breeding birds of an alpine habitat in the southern Snake Range, Nevada. Western Birds. 18(3): 163-169.

Mutel CF, Emerick JC. 1992. From Grassland to Glacier: the Natural History of Colorado and the Surrounding Region. Boulder (CO): Johnson Books.

Nilsson SG. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk. 103:432-435.

Oppenheimer S. 1995. Natural history, breeding biology, and incubation rhythm of the Rock Wren (*Salpinctes obsoletus*). [Master's Thesis]. Los Angeles (CA): Occidental College.

Oppenheimer SD, Morton ML. 2000. Nesting habits and incubation behavior of the Rock Wren. J Field Ornith. 71(4):650-657.

Orr J. 1970. Temperature measurements at the nest of the Desert Lark (Ammomanes deserti). Condor 72(4):476-478.

Palamino JJ, Martin-Vivaldi M, Soler M, Soler JJ. 1998. Functional significance of nest size variation in the Rufous Bush Robin *Cercotrichas galactotes*. Ardea. 86:177-185.

Peabody PB. 1907. Rock Wren the cliff dweller. Warbler. 3:7-14.

Price RD. 1977. The *Menacanthus* (Mallophaga: Menoponidae) of the Passeriformes (Aves). J Med Entomol. 14:207-220.

Price AB, Amen AE. 1983. Soil survey of Golden Area, Colorado: parts of Denver, Douglas, Jefferson, and Park Counties. Washington (DC): U.S. Dept Ag Soil Cons Service.

Ray MS. 1904. A fortnight on the Farallones. Auk 21:425-442.

Renaud WE. 1979. The Rock Wren in Saskatchewan: status and distribution. Blue Jay. 37:138-148.

Richardson F. 1965. Breeding and feeding habits of the black wheatear in southern Spain. Ibis. 107:1-16.

Ricklefs RE. 1969. An analysis of nestling mortality in birds. Smithsonian Contrib. Zool. 9: 1-48.

Rockwell RB, Wetmore A. 1914. A list of birds from the vicinity of Golden, Colorado. Auk. 31:309-333.

Rumble MA. 1987. Avian use of scoria rock outcrops. Gr Basin Nat. 47(4): 625-630.

Rundle HD, Boughman JW. 2010. Behavioral ecology and speciation. In: Westneat DF, Fox CW, editors. Evolutionary Behavioral Ecology. New York (NY): Oxford University Press. p. 471–487.

Schmidt KA, Whelan CJ. 2010. Nesting in an uncertain world: information and sampling the future. Oikos. 119(2):245-253.

Skaar D, Flath D, Thompson LS. 1985. P. D. Skaar's Montana bird distribution. Montana Acad Sci Monogr. no. 3.

Smith PW. 1904. Nesting habits of the Rock Wren. Condor. 6:109-110.

Smyth M, Bartholomew GA. 1966. The water economy of the black-throated sparrow and the rock wren. Condor. 68:447-458.

Soler M., Soler JJ, Moller AP, Moreno J, Linden M. 1996. The functional significance of a sexual display: stone carrying in the black wheatear. *Anim Behav*. 51:247-254.

Soler JJ, Moller AP, Soler M. 1998. Nest building, sexual selection and parental investment. *Evol Ecol.* 12(4):427-441.

Soler MM. Martin-Vivaldi M, Martin JM, Moller AP. 1999. Weight lifting and health status in the black wheatear. *Behav Ecol.* 10(3):281-286.

Story AE, Montevecchi WA, Andrews HF, Sims N. 1988. Constraints on nest site selection: A comparison of predator and flood avoidance in four species of marsh-nesting birds (Genera: Catoptrophorus, Larus, Rallus, and Sterna). J Comp Psych. 102(1):14-20.

Szaro RC. 1986. Guild management: An evaluation of avian guilds as a predictive tool.
Env Mgmt. 10(5): 681-688.

Thompson MC, Ely C. 1992. Birds in Kansas. Univ. Kans. Mus. Nat. Hist., Publ. Ed. Ser. no. 12.

Tieleman BI, VanNoordwijk HJ, Williams JB. 2008. Nest site selection in a hot desert: trade-off between microclimate and predation risk? Condor. 110(1):116-124.

Tramontano JP. 1964. Comparative studies of the rock wren and the canyon wren. [Master's Thesis]. Tucson (AZ): University of Arizona.

United States Climate Data (USCD). Accessed from http://www.usclimatedata.com/climate on October 8, 2013.

Walcheck KC. 1970. Nesting bird ecology of four plant communities in the Missouri River Breaks, Montana. Wilson Bull. 82:370-382.

Walsh JJ, Bock CE. 1997. Likely occurrence of overlapping broods in the Rock Wren. Western Birds. 28(4): 223-224.

Wauer RH. 1964. Ecological Distribution of the Birds of the Panamint Mountains, California.
Condor. 66(4): 287-301.

Weathers WW, Sullivan KA. 1989. Nest attentiveness of incubating female Tree Sparrows (*Spizella arborea*) at a northern latitude. Auk. 83:368-388.

Wolf L, Lejnieks RM, Brown CR, Yarchin J. 1985. Temperature fluctuations and nesting behavior of Rock Wrens in a high-altitude environment. Wilson Bull. 97:385-387.

Yeh PJ, Hauber ME, Trevor D. 2007. Alternative nesting behaviours following colonisation of a novel environment by a Passerine bird. Oikos. 116(9):1473-1480.