The Audubon Society of Greater Denver - Lois Webster Fund

Final Report

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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 alpine habitats 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* (Sumichrast's) wrens, but also group separately as a sister taxon ancestral to all other wrens based on DNA comparisons (Barker et al. 2004; Lowther et al. 2000; 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territory size in Kansas is 1.8 ha (Lowther et al. 2000), and mean home range size in northern Colorado is 3.6 ha (NW unpublished data), within which rock wrens nest, forage, and raise young. Rock wren migratory movements are not known (Lowther et al 2000), and 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 breed exclusively in these areas. Though their home ranges sometimes contain water, rock wrens are not known to drink free water, and obtain water both metabolically and from invertebrate 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; NW pers obs.).

Nest 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 behavior 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). These stone nest foundations often, but not always, 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 1). 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). The cup nests 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; N.W. pers. obs.) Materials are gathered by both sexes (Merola 1995; Oppenheimer 1995; Oppenheimer and Morton 2000), and nest cups are usually set back from the cavity entrance (Matiasek 1998; Oppenheimer and Morton 2000; N.W. pers. obs.).

Figure 1. Rock wren (*Salpinctes obsoletus*) nest "pavement" with typical small, flat stones interspersed with sticks and vegetation to form a stable matrix at the cavity entrance. Nests in Larimer County, CO contained a mean of 234 stones (range 32–602, n=34), averaging 568 g (range 67–1442 g). Nest composition depended on the availability of materials near the nest site.

It was Bailey's publication (1904) of rock wren nests in New Mexico that was first widely read, and this spurred a flurry of nest 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

In birds, competition for high quality nest sites has led to increased complexity in nest architecture (Gill 2007). The quality of nest cavities depends on many factors, including the effectiveness of eluding and keeping out predators (Nilsson 1986), and the cavity depth, height, and microenvironment (Collias and Collias 1984; Oppenheimer and Morton 2000; Yeh et al. 2007). Rock wrens are atypical cavity nesters in that their nests are placed amongst rock; 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), all sites without leaf or vegetative cover (Wolf et al. 1985). These unique environments on steep slopes are subject to mechanical forces, temperature regimes, and potential predators 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; N. W. pers. obs.), and erosion from heavy rains and runoff. While cavities naturally ameliorate fluctuations in temperature (McComb and Noble 1981), rock wren nests can shift below ambient temperature overnight and above ambient temperature during the day (Wolf et al. 1985). Ground nests are most susceptible to predators (Gill 2007). Nest predators in rupicoline habitats could include snakes; racer (*Coluber constrictor* and *Masticophis taeniatus*), western hognose (*Heterodon nasicus*), bull (*Pituophis catenifer*), and rattlesnake (*Crotalus viridis*), and mammals; rock squirrel (*Spermophilus variegatus*), golden-mantled ground squirrel (*Spermophilus lateralis*), Mexican woodrat (*Neotoma lepida*), and northern rock mouse (*Peromyscus nasutus*) (Peabody 1907; Hardy 1945; Lowther et al. 2000; NW pers obs; Figure 2). 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), rock wren nesting behaviors may have been selected for in response to the complex interactions in their environments, the effects of which vary throughout their range.

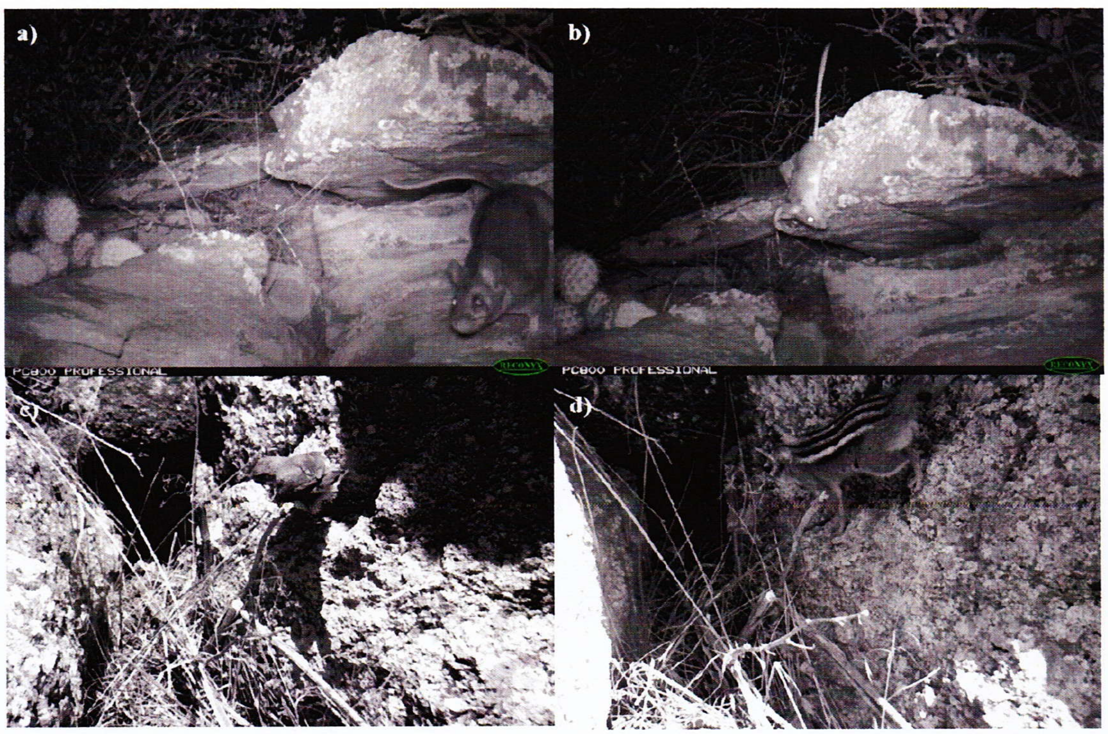

Figure 2. **a)** Mexican woodrat (*Neotoma lepida*) exiting a rock wren (*Salpinctes obsoletus*) nest. **b)** Northern rock mouse (*Peromyscus nasutus*) investigating a rock wren nest. **c)** Rock wren entering a nest cavity and **d)** Golden-mantled ground squirrel (*Spermophilus lateralis*) following 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 our study area in northern Colorado.

Direct Benefits of Stones

For over a century workers have postulated the function and significance of the stone foundations placed in rock wren nest cavities. Theories from early workers can be grouped into three general categories; nest marking, cavity occlusion, and nest dryness. All focus on the direct benefits that placing stones in nests might provide considering the costs to rock wrens in time and energy use.

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 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 minimize predation risks, and 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. We tested the nest marking hypothesis indirectly by moving the stones from 2012 nests into relocated nest cavities nearby. We predicted that rock wrens would not be induced to use different nest cavities, even if they contained stones.

Many more 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; NW unpublished data), 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 stones when they are unavailable. Stone barricades could also keep nests level, and keep nestlings from falling out of the nest (Ray 1904; Smith 1904). Smith (1904) asked "could not this walk have been built to keep the young birds from falling into crevices or getting their feet caught in the same?" Rock cavities are rarely uniform, and often do contain cracks and crevices that could trap nestlings. We predicted that the opening area of active nest cavities would be reduced by the presence of stones, and that the percent occlusion would correlate to the number of stones that were used. We also predicted 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 and Smith (1904) remarked that cliff nests were situated in comparatively dry locations, and contained fewer stones, also noting that cliff cavities had no place to hold stones at their entrances (Figure 3). Both workers predicted a relationship between nest dryness and the amount of stones that a nest contained. Stones could aid in keeping nests dry by diverting water away from the nest, or by allowing water to pass beneath and between stones along the underlying surface, whether it is rock or soil. We also predicted a correlation between the amount of water that is able to infiltrate a nest cavity and the number and configuration of stones present.

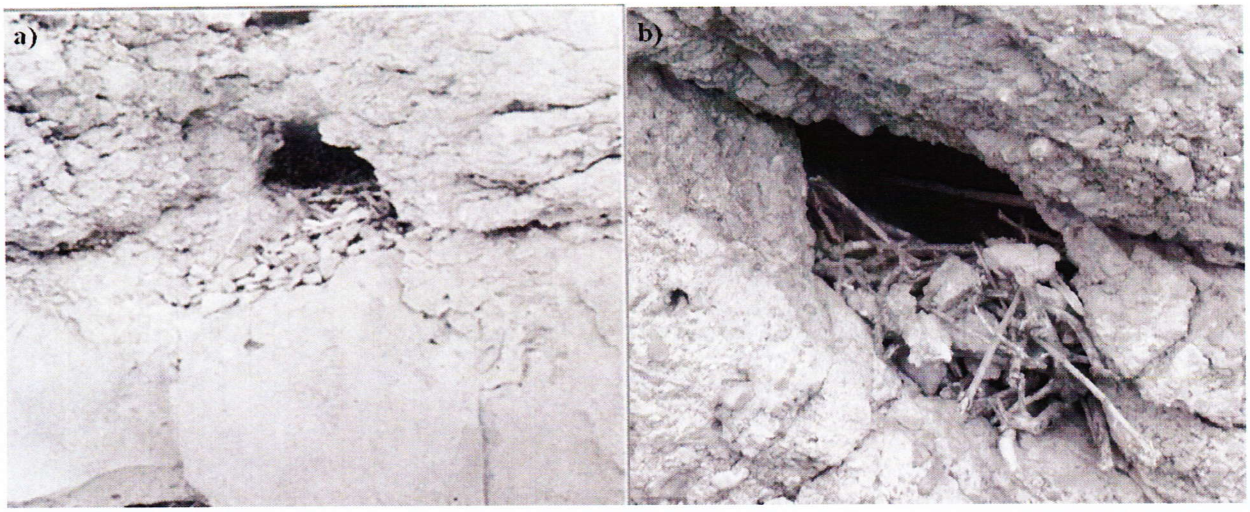

Figure 3. Rock wren (*Salpinctes obsoletus*) nests in cliff cavities. **a)** Cliff nest photographed and described by Florence Bailey in New Mexico in 1902 with a "stone walk" (Condor 6(3):68-70). **b)** Nest within a cliff cavity in Larimer County, CO, with no surface for a stone walkway. Cliff nests were described by early researchers as being dryer, and holding fewer stones than nests that were built on the ground. This was taken as evidence that stones provided a dryness function.

The microenvironment of the nest effects the daily energy requirements of the eggs, nestlings, and adults (Gill 2007). Because rock wrens breed in exposed environments, regulation of nest temperature may strongly 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 night (Wolf et al. 1985; Oppenheimer and Morton 2000). Nest stones should add to the ameliorating effects of the rock cavity by increasing the thermal mass (Figure 3). Stones that extend outside the cavity entrance could radiate heat into or out of the nest cavity depending on the temperature gradient. 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, nest in cliff crevices (Jones et al. 2001), and can receive many hours of sunlight depending on nest placement and the overlying strata (Figure 4). 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.; Figure 4). We predicted that nests with stones would have lower standard deviations of temperature fluctuations than surrogate cavities containing no stones. We also predicted that nests that had accumulations of stones outside the cavity would have higher daytime temperatures from solar heat gain (Figure 3).

Figure 4. Nests of two wren species in similar habitat. **a)** Canyon wren (*Catherpes mexicanus*) nest located in a cliff crevice, exposed to full sunlight. 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.

Indirect Benefits of Stones

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 (*Oenanthe leucura*) 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 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; NW pers obs.), and males only 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, and nest-building gives opportunities for females to advertise their quality, but post-pairing displays by female birds have never been documented (Palamino et al. 1998; Gill and Stutchbury 2005).

MATERIALS AND METHODS

Study Location

All nests were located on public lands in Larimer County, CO. Sites were in semi-arid montaine 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 typically 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

We surveyed public lands in Larimer County May-June 2012-2013 using direct observation to locate active rock wren breeding territories. We monitored 21 rock wren territories over two breeding seasons, and identified 34 nests from 18 pairs (12 nests in 2012, and 22 nests in 2013). We color-banded a subset of male rock wrens (8/21) that we monitored with unique combinations of plastic color bands (Gey, Norristown, PA) to help distinguish between sexes. Wrens were captured in mist nets (Avinet, Dryden, NY) under which conspecific audio playbacks were broadcast. We observed active nests and placed motion cameras (Reconyx, Holmen, WI) at nests to document nesting behaviors. We logged temperature data in vacant nests, after either the chicks fledged or the nest failed, and in surrogate cavities of similar depth and orientation within five meters of the focal nest cavity. We 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 this placement distance in surrogate cavities without stones.

Nest Attributes

We weighed nest stones to the nearest 0.1 gram using a portable electronic scale (Ohaus, Pine Brook, NJ) and measured length, width, and thickness of at least 20 randomly selected stones from each nest using dial calipers (Avinet, Dryden, NY). We weighed and measured a total of 497 stones from 34 nests. We used Arc GIS (ESRI 2010) to measure nest spacing between and within rock wren pairs. To measure stone availability in the area one of us (NW) collected stones within 25 m of each nest that were appropriately sized and shaped from our observations of local rock wren nests, and weighed the total amount collected. To document cavity occlusion we measured the height and width of the cavity entrance before and after the removal of nest stones and related accoutrements. To measure nest dryness we recorded the water weight gain of a 5cm x 5cm sponge placed inside the nest cavity directly in front of the nest cup (Figure 5). We 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, during dry conditions. We measured sponge weight gain to the nearest 0.1 g with a portable electronic scale (Ohaus, Pine Brook, NJ). We returned all stones to nests in their original formations except to nests that were manipulated. All statistics were performed in JMP, v.9 (SAS Institute Inc., Cary, NC).

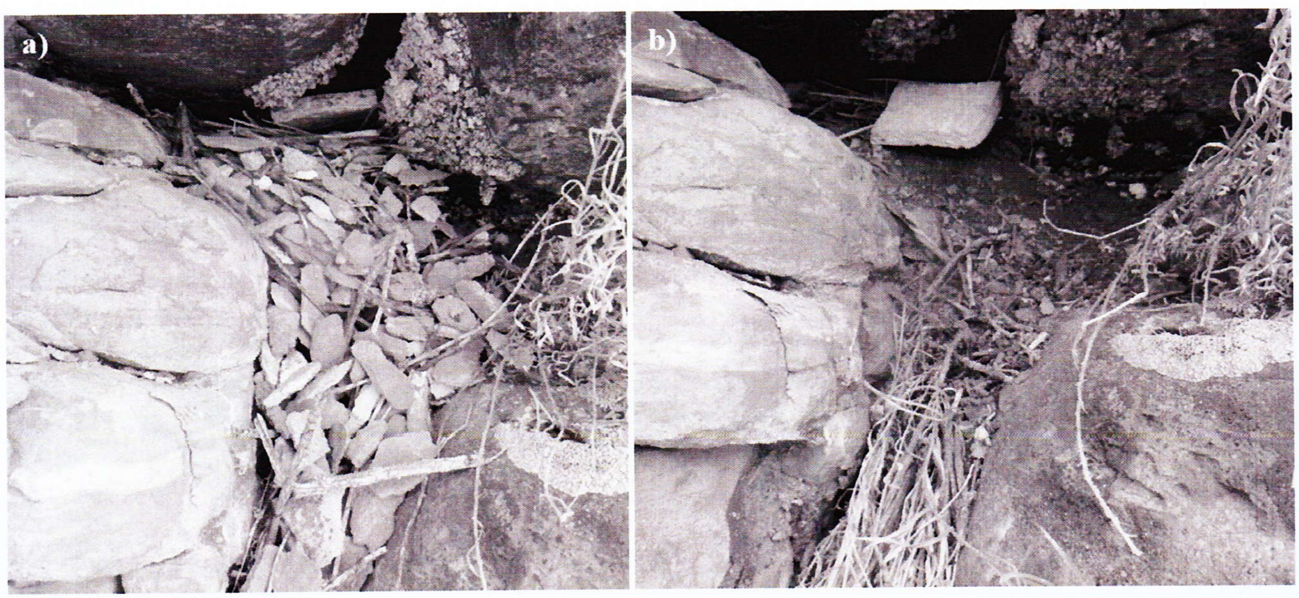

Figure 5. A rock wren (*Salpinctes obsoletus*) nest during a nest dryness experiment. **a)** Sponge (5 cm x 5 cm) inserted into the nest cavity with stones present. **b)** Sponge in the nest cavity after the removal of stones. In both pictures the sponge is not fully inserted so that it shows up in the picture. This nest was constructed midway through the breeding season, and contained 370 stones weighing 950 grams, all placed within a 10 day period.

RESULTS

Nest Attributes

Mean spacing of active rock wren nests in neighboring pairs was 158.3 ± 88.4 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 and maintained nests from 5 May-17 Aug in 2013, visiting and maintaining nests well into October (Figure 7).

Figure 7. Rock wrens (*Salpinctes obsoletus*) visited and maintained old and recently active nest sites even after the breeding season. **a)** Rock wren female adding a stone to one of the previous year's nests on 17 Aug 2013. **b)** Rock wren adding a stick to a newly constructed nest on 19 Sept 2013.

Seventy percent (24/34) of measured nests were active in either the 2012 or 2013 breeding seasons while 30% (10/34) were inactive at the time of discovery. None of the 12 active nests discovered in 2012 were reused in 2013, though they were visited frequently by the wrens (Figure 7). 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. Both sexes delivered nest materials, but only females were observed carrying stones. Nests contained from 32-602 stones (mean= 234, n=34) and 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 that were inaccessible, and these were not measured. 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 very 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 7). Nest stones always lined the bottom of the cavity, and often (28/34) were placed outside the cavity in a nest pavement (Appendix 3). At least two nests were constructed entirely in 2013, and these contained 950 g (Figure 5) and 686 g of stones respectively.

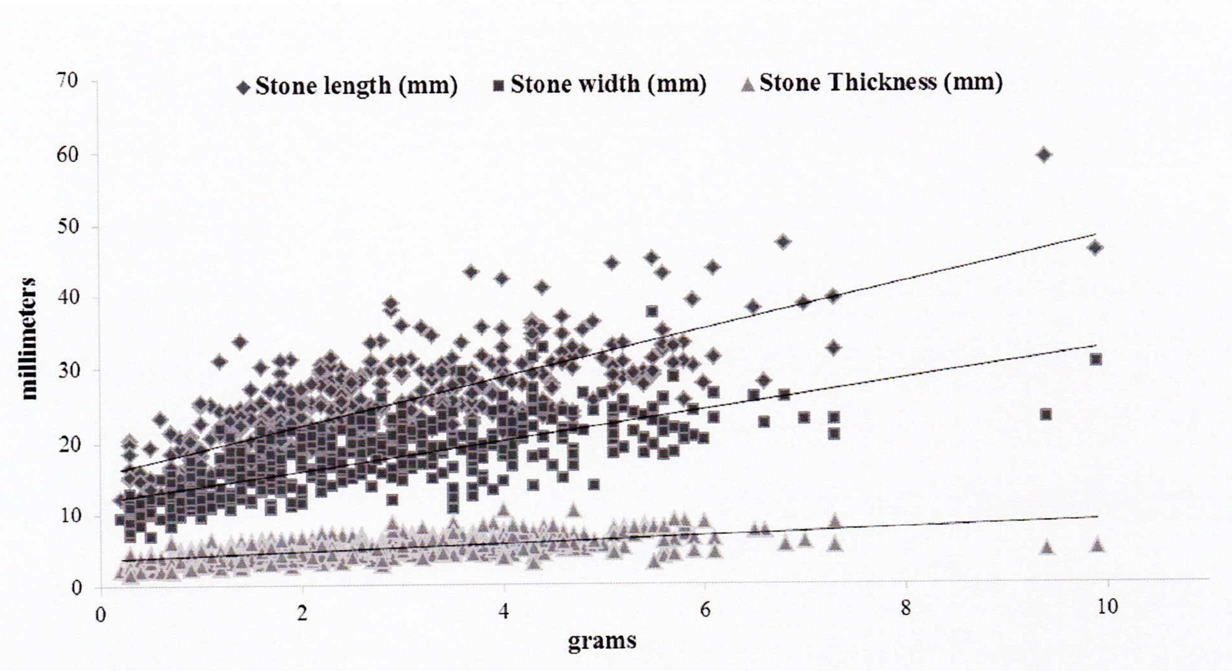

Figure 8. The weights of rock wren (*Salpinctes obsoletus*) nest stones from Larimer County, CO plotted against their length, width, and thickness. Stones were most consistent in thickness, making nest entrances highly recognizable. Stones must be thin enough to be carried in the bill, and are probably selected to be stackable at the nest entrance.

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 and wind (Figure 1). Mean area of the cavity entrance was 67.5 ± 41.3 cm^2 SD with nest stones present, and 106.1 ± 67.1 cm^2 SD with nest stones removed. Nest stones significantly occluded the cavity entrance ($t_{33} = 6.48$, $p < .0001$), and also acted to stabilize the nest cup by leveling the floor of the cavity (Smith 1904), and bracing and anchoring the base of the cup, usually made of sticks (Collias and Collias 1984, Figure 9). The hypothesis that larger cavities would contain more stones was supported ($F = 5.79$, $p = .0221$). relationship between the area of the nest cavity opening (without stones) and the total weight of stones in the nest (Figure 10), suggesting an optimal or target opening size.

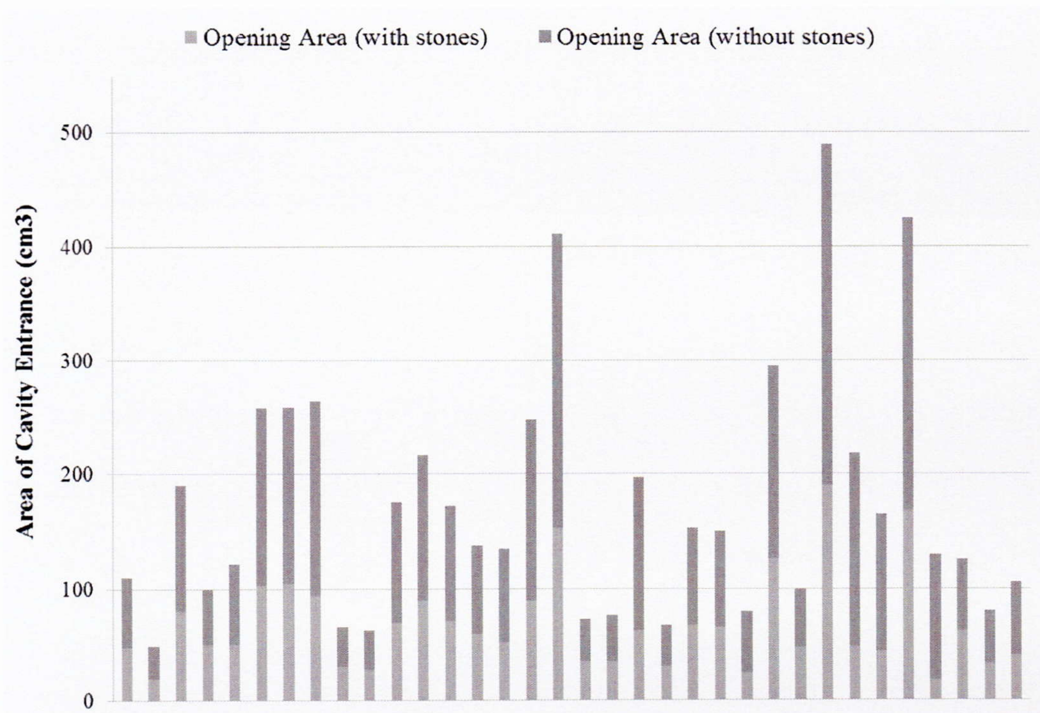

Figure 9. Areas of the cavity entrances of 34 rock wren (*Salpinctes obsoletus*) nests from Larimer County, CO with nest stones (light gray bars) and without nest stones (dark gray bars). Stones significantly decreased the area of nest cavity openings.

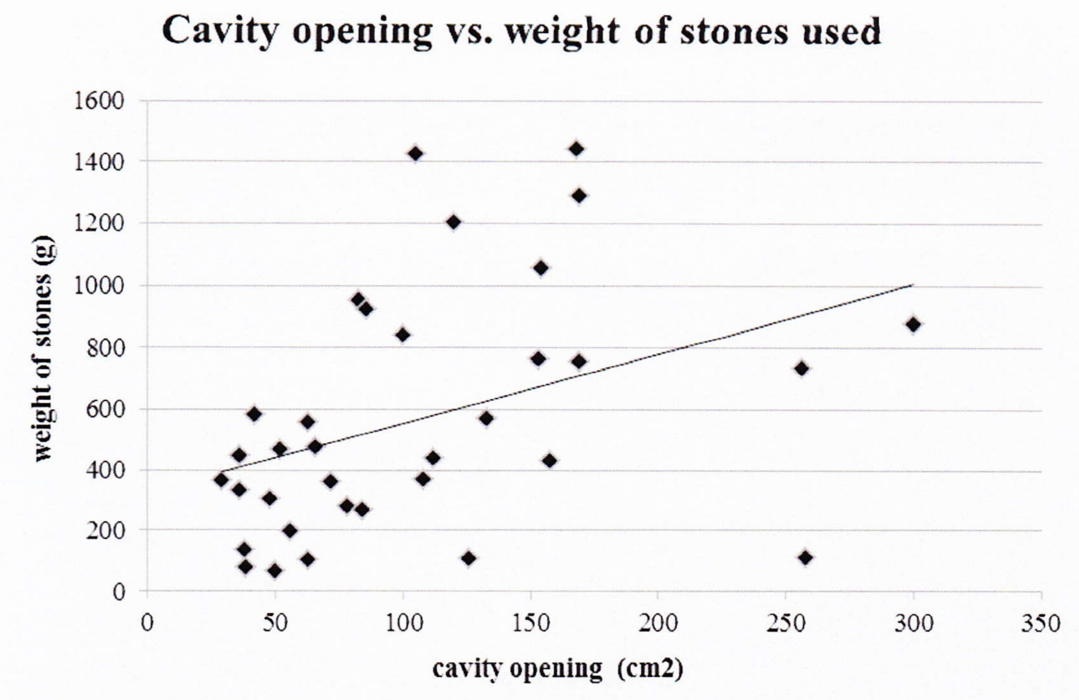

Figure 10. Area of the nest cavity opening (cm^2) vs. collective weight of stones used in 34 nests from 18 rock wren (*Salpinctes obsoletus*) pairs in Larimer County, CO. Nests with larger cavities contained more stones, suggesting an optimal or target opening size ($F = 5.79$, $p = .0221$).

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 is little soil to absorb water as it flows downslope. If nest stones divert water, or facilitate passage of sheet flows beneath the nests, we expect an inserted sponge to gain more water weight after stones are removed from the nest cavity. This was the case in 59% (20/34) of nests. In 20% (7/34) of nests there was absolutely no water gain in the sponge, whether or not stones were present (Appendix 2). These nests were located in cavities beneath large, sheltering rock overhangs protected from direct rainfall. Four nests gained less water after we removed nest stones. Despite variability in the results, we did observe that stones significantly increase nest dryness ($t_{33} = 2.52$, $p = .0165$, matched pairs) in the majority of rock wren nests.

We did not detect a significant relationship between nest stones and temperature or temperature fluctuations within nest cavities (Figure 11). Cavities that contained stones did exhibit slightly less variation in nest temperatures, but not at a significant level ($t_{24} = -1.17$, $p = .2533$). Temperatures were monitored in unoccupied cavities, and occupied nests would likely show more stable temperature patterns (Wolf et al. 1985; Oppenheimer and Morton 2000).

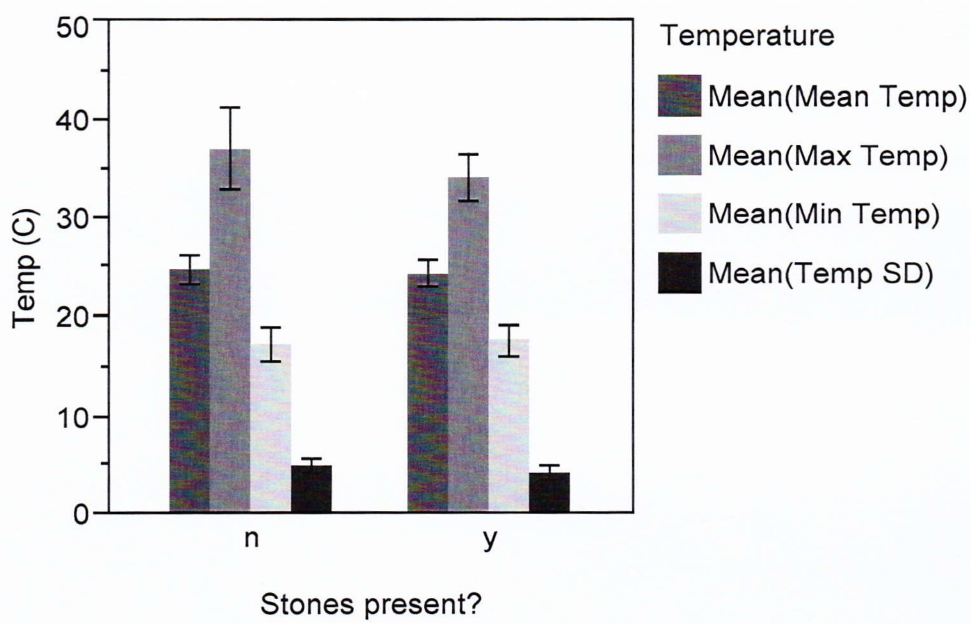

Figure 11. Mean, mean minimum, and mean maximum cavity temperatures and temperature standard deviations (SDs) from 12 rock wren (*Salpinctes obsoletus*) nest cavities (with stones), and 12 surrogate cavities (without stones) in Larimer County, CO. Error bars show 2 SDs from the mean. Cavities that contained stones did not significantly affect cavity temperatures.

Nest Manipulations

We 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 known to include 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 seemed at least possible. Rock wrens investigated at least 41% (5/12) of relocated nests, and 100% (5/5) nests that were monitored by cameras (Figure 6). Rock wrens added stones to 25% (3/12) of relocated nests, adding from 6 - 89 stones (collectively 21.6 – 291 g), but only nested and reared chicks in one relocated nest (Figure 11). The cavity 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 we are 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 we typically observed both sexes caring for young, one exception gives further evidence for overlapping broods. We 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 (Figure 12). The female wren was still seen occasionally on the territory, and may have been incubating at another nest, though we were unable to locate it. Overlapping broods could occur if nest failures disrupt the timing of sequential broods. In this case the male rock wren completely provisioned the 4 young in the nest for 11 days before they fledged.

Figure 12. 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

Nest Temperature and Dryness

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. Our 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. In environments where rock is prevalent, and there are no heat imputs from incubating birds, nest stones have little impact on cavity temperature. Even in a nest that contained 1.5 kg of nest stones (Figure 13), a single rock comprising the nest entrance weighed 5 kg, shadowing the thermal effects of nest stones. 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).

Stones 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). We saw stones increase dryness in the majority of nests experimenting with a single gallon of water. With increased water via heavy rainfall and saturated soils we would expect these effects to amplify. Besides facilitating drainage, the stabilizing effects of stone pavements were illustrated by the dryness experiments. After the removal of the stones (and sticks), the underlying soil was much more prone to erosion from water poured from the sprinkling can. During a rainfall event the stability of the soil around a nesting cavity could keep the cavity from being undercut by water (Figure 13). The stabilizing effects of stones that cover the soil surrounding nest cavities may be a critical function of the pavements that extend outside the entrances. This function 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 the most commonly available material.

Figure 13. Rock wren (*Salpinctes obsoletus*) nest in Larimer County, CO containing over 600 stones weighing 1.5 kg. This slope 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. If not for the amplifying effects of the fire, the nest stones may have been enough to stabilize the cavity.

Cavity Occlusion

Workers have long recognized that nest stones decrease the size of the cavity entrance. But in the 12 nests described by Bailey (1904), she comments "in special cases where the entrance to the nest is partially closed by the stones, the purpose can be easily understood." Bent (1964) wrote that stones "in *some* cases are piled up so high at the entrance that only the flattened body of the wren can enter." Both authors, along with Smith (1904) and Ray (1904) did not believe that cavity occlusion could explain the stones in the majority of nests. Not all rock wren nests contain stones, (Smith 1904; Oppenheimer and Morton 2000; N.W. 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. But this could be only coincidental with opening size. In our nest research it was often difficult to visualize how much area the pavements were occupying until we removed stones and took measurements. Indeed, even with stones decreasing the entrance areas, 58% (20/34) of nests still had entrace openings >50 cm^2, enough space for many predators to enter. Some occlusion is better than no occlusion, but it seems unlikely that the configurations that we see in rock wren nests today developed only from predator deterrence. It is unknown whether stone barricades deter nest predators, a question we hope to answer through long-term deployment of motion-activated cameras.

Nest Manipulations

We predicted that rock wrens would not be induced to use cavities with relocated stones. The relatively large home ranges in our study area (mean = 3.6 ha; NW unpublished data) seem to offer abundant cavities suitable for nesting. We observed rock wrens space 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. The use of one relocated nest cavitiy, along with the re-use of older nests suggests that high quality nesting cavities may be limiting for rock wrens, or that nest stones are indicators of high quality nest sites. 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, we 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, we located 14 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.

Nest Attributes

As a basal, and possibly ancestral wren lineage (Barker et al. 2004; Mann et al. 2006) rock wrens have probably retained at least some root characteristics and behaviors, including nesting behaviors which are under strong genetic control (Gill 2007). Since rock wren nests were first described over a century ago ornithologists have puzzled over the "pavements" or collections of flat stones that characterize nesting cavities. Though we don't know what promoted the behavioral specialization of stone manipulation in rock wrens, it may have had far-reaching implications. Speciation is driven by reproductive specialization (Rundle and Boughman 2010). If stone use in rock wrens preceded their distinct use of rock environments, then this behavior may have helped to precipitate the shift into rock. If stone use followed specialization of rock environments, then this behavior could have reinforced breeding amoung rocks. The proximate factors (physiological, genetic, or developmental) under which stone carrying has evolved in rock wrens likely came about as a response to selective pressures inherent in rocky environments. These include; physical cavity dynamics, predation, and water flow. 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, lending creedance to the idea that stones are used to provide direct benefits. It is important to document these direct benefits to rock wren nests before we can evaluate potential indirect benefits that have developed in the species.

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 is an unlearned behavior requiring an investment in time and energy that must have developed under strong selective pressures. We examined direct benefits of nest stones, and found that stones significantly occlude cavity openings, increase nest dryness and stability, and may mark potential nest cavities. These benefits vary from nest to nest, suggesting that stones are multi-functional depending on the nest microenvironment.

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Appendix 2. Summary of quantitative stone attributes of rock wren (*Salpinctes obsoletus*) nests from the few published nest studies. Use of stones by rock wrens is apparently widespread, but may vary regionally or with stone availability. Our nest stone data is shown in bold.

Location	Mean # stones	Range	Mean stone mass	Range	n	# with pavement	Citation
New Mexico	778	n/a	2.85	0.7 – 6.1	1	8/9	Merola 1995
S.California	n/a	101 - 558	n/a	n/a	11	n/a	Oppenheimer 1995
Kansas	n/a	n/a	3.5	1.7 – 6.8	20	n/a	Matiasek 1998
Arizona	142	n/a	n/a	n/a	1	1/1	Harrison 1979
California (Sierras)	329	150 - 558	n/a	n/a	9	13/14	Oppenheimer and Morton 1999
California (Farralon Island)	492	n/a	n/a	n/a	1	1/1	Ray 1904
Texas	½ pint	n/a	n/a	n/a	13	7/13	Smith 1904
New Mexico	131	50+ - 260	n/a	n/a	3	12/12	Bailey 1904
Colorado	**234**	**32 - 602**	**2.45**	**0.2 – 9.9**	**34**	**34/39**	**Uplshd. data**

CONSERVATION AND MANAGEMENT IMPLICATIONS

Rock Climbing:

The Colorado Front Range from Colorado Springs to Fort Collins is quickly growing in population, and in recreational use of public lands (Graham and Knight 2004; Rossi and Knight 2006). Rock climbing continues to grow in popularity (Pyke 1997; Krajick 1999), and the Front Range canyons and cliffs are premier climbing and bouldering areas (Graham and Knight 2004). Increasingly, climbing trails are traversing the rocky bluffs, and crevices are sought out as routes for both climbing and bouldering (Krajick 1999). Rock climbing adversely affects plant communities, with climbed cliffs containing smaller plants and lower plant density and diversity (Camp and Knight 1998). The same areas that attract climbers are the same discontinuous rock and cliff habitats favored by canyon and rock wrens.

It is not known whether adverse effects on plant communities, as well as direct disturbances from rock climbers are negatively impacting canyon and rock wren populations in Colorado. Canyon and rock wrens are highly territorial, defending established territories and mates (Merola 1995; Jones et al. 2002). On the Colorado Front Range canyon wrens occur at low densities, with pairs defending and holding large, widely-spaced territories (Benedict et al. 2012). Because canyon and rock wrens rely on their territories for foraging, nesting, and rearing young they may be more susceptible to human disturbances on all or portions of their territory, particularly during critical breeding periods. Under pressure from recreational users, it is important to document the specific habitat requirements of rock wrens and canyon wrens to better understand the impacts of rock climbing on these specialized bird species. Land management agencies are seeking input regarding the specific habitat utilization of wildlife on public lands, and our home range data will provide valuable guidance for management decisions, particularly regarding rock climbing policies. In Jefferson County, at least one canyon wren nest failure was attributed to dislodgement by rock climbers (Jones et al. 2002). Measuring home ranges for both canyon and rock wrens will help to determine whether breeding birds have sufficient space in which to retreat during periods of active bouldering and rock climbing. Our GIS analysis shows that although canyon wrens use large home ranges, they focus their activities in core areas along cliffs. Rock wren core areas are focused on slopes below cliffs, where bouldering and staging areas are commonly located. Recommendations can be made to land managers regarding restrictions on any new or existing climbing routes.

Rock and Canyon Wren Declines

There is some evidence that the spatial distribution of rock wrens may be changing. Increasingly rock wrens are remaining as residents in more northern portions of their range including in Washington (Leake and Johnson 1974), Idaho (Burleigh 1972), Oregon (Gilligan et al. 1994), and British Columbia (Campbell et al. 1997). Rock wrens have been observed as far north as Mackenzie, BC, Fort Chipewyan, Alberta, and Last Mountain Lake, Saskatchewan (Renaud 1979; Godfrey 1986), and there are multiple records of breeding near Churchill, Manitoba (Crosby and Beckett 1957; Seutin and Chartier 1989). Eastward sighting records include Iowa (Bennett 1925), Indiana (Carter 1978), Missouri (Easterla and Ball 1973), Arkansas (James and Neal 1986), Minnesota, (Janssen 1987), Michigan (McPeek 1994), Kentucky (Kemper and Loetscher 1968), Virginia (Hughes and Harris 1993), New Jersey (Sibley 1997), Ontario (Burger and Brownstein 1967). Rock wrens have the ability to colonize new areas, as they have on barren islands including Farallon island (Ray 1904; Small 1994), Guadalupe Island (Mirsky 1976; Howell and Webb 1995), San Benito (Brewer 2001), and San Benedicto Island before the 1952-3 volcanic eruption which caused the extinction of endemic rock wrens there (Swarth 1914;

Brattstrom et al. 1956). These records could indicate natural excursions outside the range or human facilitated habitat alteration including additions of rock for reservoir dams (Mcnicholl 1981), and forest clearcuts (Marshall and Horn 1973). Indeed, some of the largest increases in rock wren populations from 2000-2010 were detected in Alberta and the Prairie Potholes regions (Sauer et al. 2011). Despite their potential range expansion, rock wren population sizes are declining in many areas (Jones 1998; Lowther et al. 2000; Sauer et al. 2011). Breeding bird survey data show declines on average of 1.4 % per year from 1966-1997, with the highest declines in the Great Plains (2.5% per year; Sauer et al. 1997; Lowther et al. 2000). The reasons for declines are unknown, but could include collisions with cell-phone and radio towers during migration (Easterla and Ball 1973), brood parasitism by brown-headed cowbirds (Mataisek 1998), increased predation, or increased development and loss of breeding or wintering habitat (Brattstrom 1995). More recent data (2000-2011) indicates stabilizing rock wren populations overall, with continued declines on the Great Plains (Sauer et al. 2011). In Colorado, surveys indicate population declines of 2.6% from 2000-2011 (Sauer et al. 2011).

Canyon wren populations are not adequately sampled in most areas (Jones and Dieni 1995), and breeding bird survey indicates stable population trends in most regions, but population declines in Colorado of 2.7% from 2000-2011 (Sauer et al. 2011).

Our study is the first to document rock and canyon wren home ranges, and the data can be used to estimate or compare space use in other portions of the range, and to correlate declines with habitat changes within home ranges. Our foraging microhabitat data could be used to predict new areas where rock wrens might be expected to reach, and predict the limits to range expansion.

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