

Breeding biology and reproductive success of Rock Wrens (*Salpinctes obsoletus*) in northern Colorado

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ABSTRACT—Breeding ecology plays a crucial role in avian fitness and evolution, yet basic life history is understudied for many species. Species with large distributions over a breadth of latitudes may have different strategies regarding reproduction in the northern or southern extents of their range, but those differences could be overlooked due to a sparsity of published information. Rock Wrens (*Salpinctes obsoletus*) are migratory in the northern part of their range, territorial, and monogamous songbirds with populations thought to be in decline. We collected natural history information on 21 mated pairs from a migratory population in northern Colorado to describe nesting ecology and reproductive success. We evaluated nesting life-history traits and parental care throughout the breeding season at 12 monitored nests. Results indicated that 42.9% of nests fledged at least 1 chick, with means (\pm SD) of 5.63 \pm 1 eggs per clutch, 3.44 \pm 0.53 hatchlings per nest, and 2.67 \pm 0.5 fledglings per nest. Mean duration of egg incubation was 15.10 \pm 0.32 d with 29.11 \pm 1.27 total days of eggs and chicks in the nest. Camera trapping revealed male Rock Wrens did the majority of prey delivery to chicks in the first 5 d post-hatching and fed chicks a range of prey species. The population reproductive success was mostly affected by nest predation, where predators included bullsnakes (*Pituophis catenifer*) and prairie rattlesnakes (*Crotalus viridis*). Outcomes provide the first estimates of sex-specific parental feeding behavior for this species, and document new nest predation threats. Breeding biology metrics of the studied migratory population were similar to those of sedentary populations, suggesting that knowledge gained from local studies will have relevance across the range of this widely distributed species. Received 24 July 2021. Accepted 7 March 2022.

Key words: breeding ecology, feeding rate, nesting ecology, parental care, parental effort, prey delivery.

Biologie de la reproduction et succès reproductif de *Salpinctes obsoletus* dans le nord du Colorado

RÉSUMÉ (French)—L'écologie de la reproduction joue un rôle crucial dans l'aptitude à survivre et l'évolution des oiseaux, mais l'histoire de la vie de base est sous-étudiée pour de nombreuses espèces. Les espèces ayant une large répartition sur une large gamme de latitudes peuvent avoir des stratégies différentes en ce qui concerne la reproduction dans les limites nord et sud de leur aire de répartition, mais ces différences pourraient être négligées en raison de la rareté des informations publiées. L'espèce *Salpinctes obsoletus* est un oiseau chanteur migrateur au nord de leur répartition, territorial, et monogame dont les populations seraient en déclin. Nous avons collecté des informations sur l'histoire naturelle de 21 couples accouplés d'une population du nord du Colorado pour décrire l'écologie de la nidification et le succès de reproduction. Nous avons évalué les traits d'histoire de vie de nidification et les soins parentaux tout au long de la saison de reproduction pour 12 nids surveillés. Les résultats ont indiqué que 42,9% des nids avaient au moins un poussin, avec des moyennes (\pm SD) de 5,63 \pm 1 œufs par couvée, 3,44 \pm 0,53 nouveau-nés par nid et 2,67 \pm 0,5 jeunes par nid. Les nids duraient en moyenne 15,10 \pm 0,32 jours d'incubation des œufs et 29,11 \pm 1,27 jours au total d'œufs et de poussins dans le nid. Le piégeage photographique a révélé que les troglodytes mâles livraient la majorité des proies aux poussins au cours des 5 premiers jours suivant l'éclosion et nourrissaient les poussins d'une gamme d'espèces de proies. Le succès reproductif de la population a été principalement affecté par la prédation des nids, où les prédateurs comprenaient des *Pituophis catenifer* et des *Crotalus viridis*. Les résultats fournissent les premières estimations du comportement alimentaire des parents selon le sexe pour cette espèce et documentent les nouvelles menaces des prédation des nids. Les métriques de la biologie de la reproduction de la population migratrice étudiée étaient similaires à celles des populations sédentaires, ce qui suggère que les connaissances acquises grâce aux études locales seront pertinentes dans l'ensemble de l'aire de répartition de cette espèce largement répartie.

Mots clés: écologie de la nidification, écologie de la reproduction, effort parental, livraison des proies, soins parentaux, taux d'alimentation.

Breeding biology and reproductive ecology play crucial roles in the study of avian life history and evolutionary ecology (Badyaev and Ghalambor 2001). Yet, basic life history research is still missing for a great number of species and remains one of the future challenges for avian ecologists (Martin 2004). Reports on natural history can unfold new perspectives or support current

approaches that test hypotheses of ecological and evolutionary significance (Greeney et al. 2008, Rosoni et al. 2019). Detailed data on avian nesting behavior and reproductive success are critical for conservation efforts and to help researchers understand avian population dynamics (Batary and Baldi 2004, Clark and Martin 2007, Hartway and Mills 2012).

Avian breeding biology can vary geographical-ly. Previous studies have demonstrated that birds breeding at higher elevations and latitudes increase parental investment and augment the number of feeding trips compared to those breeding at lower elevations and latitudes (Lu et al. 2009), suggest-

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ing that high rates of parental investment may be critical to offspring success in more northern populations (Badyaev 1997, Badyaev and Ghalambor 2001). On the other hand, a previous study in Sedge Wrens (*Cistothorus platensis*) showed greater male contributions to feeding nestlings in populations of South America when compared to populations in North America, indicating that trends could be different in the wren lineage (Llambías et al. 2018). Further, differences in life-history traits can be variable across latitudinal gradients of a species' range, like the smaller clutch sizes in southern populations compared to northern populations seen in House Wrens (*Troglodytes aedon*) and Sedge Wrens (Llambías et al. 2015, 2018). This suggests that different selective pressures may be experienced by breeding members of northern and southern populations of wren species.

Rock Wrens (*Salpinctes obsoletus*) are territorial songbirds that are migrants in the northern part of their range and whose populations are thought to be declining (Benedict et al. 2021). Colorado lies in the migratory–sedentary transition zone and populations in northern Colorado are predominantly migratory, marking this area as the point where conditions become too difficult for year-round territory occupation (Benedict et al. 2021). Rock Wren males arrive to northern Colorado earlier than females in the breeding season and sing in rocky areas along canyons, hogbacks (long, narrow ridges), and rocky slopes to establish breeding territories and attract females (Benedict and Warning 2017, Benedict and Najar 2019, Benedict et al. 2021). While males sing, females invest a great deal of energy in building nests tucked in tight rock crevices with walkways often paved with many small, flat stones that sometimes partially barricade the cavity entrance (Kroodsma 1975; Merola 1995; Warning and Benedict 2015b, 2016).

Although Rock Wrens are relatively common across the western United States and defended territories can be quite numerous in appropriate habitat, limited information about this species' breeding biology is available in the literature across its range, and there is very little data available about behavior at the nest or reproductive success in general (Benedict et al. 2021). Most existing information on Rock Wren breeding biology is from sedentary southern populations

that experience relatively long breeding seasons (Bailey 1904, Tramontano 1964, Merola 1995, Matiasek 1998, Benedict et al. 2021). Given the migratory divide within this species, data on the breeding success of northern, migratory populations will provide important points of comparison with more southern, sedentary populations and will help to elucidate whether northern Rock Wrens show breeding strategies that are typical of Rock Wrens in southern populations or that are more akin to other migratory species. Important differences in populations across their range may be overlooked due to the absence of information from the northern part of their distribution. Such data will also be useful in comparative studies with other wrens (Llambías et al. 2015, Barker 2017, Llambías et al. 2018).

In this study, we observed pairs of breeding Rock Wrens in northern Colorado and collected basic natural history information on breeding ecology and parental care. Previously published data from their southern distribution show that Rock Wren clutch sizes typically range 4–10 eggs with a mean of 5, incubation of 12–14 d, and nestlings are in the nest for 13–16 d, where they are provisioned by both parents with a variety of prey (Merola 1995, Matiasek 1998, Warning et al. 2014, Benedict et al. 2021). Most observed nest failures were due to predation (Hardy 1945, Benedict et al. 2021). Our study sites were at a higher latitude and elevation than most previous work on the species and represent the first detailed report of nesting life-history traits, reproductive success, and parental care from a migratory population including measures of clutch size, number of chicks hatched, number of fledglings at each nest, reproductive success for the studied population, nestling diets, and quantifying parental care through nestling feeding rates.

Methods

Study location

Study sites were located on public lands of Larimer County in northern Colorado including Lory State Park (Bellevue; 40°33'50.4"N, –105°10'30"W), Pine Ridge Natural Area (Fort Collins; 40°32'20.4"N, –105°07'55.2"W), Bobcat Ridge Natural Area (Fort Collins; 40°29'02.4"N, –105°13'48"W), and Devil's Backbone Open Space (Loveland; 40°24'43.2"N, –105°09'07.2"W). In

these sites, breeding habitat included rock talus fields with relatively steep slopes of 15–32° scattered with large boulders and cliffs with rocky outcrops and pitted with narrow crevices (Warning and Benedict 2015a).

Focal pair selection and individual identification

Previous work has shown that local Rock Wrens form a migratory population of monogamous and territorial individuals that establish breeding home ranges of $\sim 4.1 \pm 1.2$ ha (Warning and Benedict 2015a). We located 27 male Rock Wrens singing as if to defend territories during the springs of 2016 and 2017. We determined that 21 of these males had secured a female mate and we regularly monitored their behavior through the breeding seasons. Sixteen of these mated males were caught using a mist net and we affixed a unique combination of 3 colored bands in addition to a metal USFWS band to each bird's legs to allow for individual identification. Four males that remained unmated through the breeding season were captured the same way. We took multiple morphological measurements of captured wrens including weight, wing chord, tail length, culmen length, and tarsus length following established bird banding protocols for measuring and processing birds (North American Banding Council 2001). The 5 paired birds that were not successfully captured were included in measures of nest success. Conspecifics seen within home ranges that were tolerated by the resident male were counted as female mates, often confirmed by copulations, mate-feeding displays, inter-pair soft song contact calls, and presence at the same nest. We monitored all 21 pairs during 1 May–1 August 2016 and 1 May–3 August 2017 in order to locate nesting cavities, evaluate nest progress, and estimate reproductive outcomes, as well as to confirm that unmated males had still not secured a mate.

Behavioral observations and nest monitoring

Through regular behavioral observations of focal pairs during the breeding season, we determined each pair's nest location, Julian first egg date, maximum number of eggs laid in a clutch, number of chicks hatched, maximum number of chicks fledged, and Julian fledging

date. Because many of the monitored nests were in tight cracks and crevices, we could not access the eggs in order to measure or weigh them directly. We used a plumbing inspection camera (Flexible Inspection Camera, Medit Inc., Winnipeg, Manitoba, Canada) to check nest status approximately once a week early in the nesting attempt and every third day when approaching hatching and during the nestling phase for all nests. Since it was not possible to monitor all nests every day, some of the hatch or fledging dates had to be estimated based on status at a previous visit and chick size at each visit, with consideration of reported incubation and nestling phase periods available from the literature (Merola 1995). This allowed us to track the progress of nests from a full clutch of eggs through the nestling and fledgling stages. This direct nest monitoring was supplemented by indirect monitoring using motion detection field cameras for a subset of nests.

Camera monitoring

Camera trapping—When a nest was found in an accessible location (i.e., safe to access given the rocky and cliff terrain constraints) within the territory of a banded male, we installed a Hyperfire HC600 covert camera (Reconyx Inc., Holmen, Wisconsin, USA) 90–120 cm from the nest entrance. Cameras were placed about midway through the incubation period once clutches were complete to prevent nest abandonment. This allowed us to monitor nest activity without influencing bird behavior, to get estimates of prey delivery types and rates, to gather information on exact fledging count, time, and date, and to document nest predation events. Each camera was camouflaged as a rock cairn and was left to monitor nest activity continuously through to fledging (Supplemental Fig. S1). Covert cameras were placed in front of nests over 2 field seasons watching 4 nests in 2016 (mean 28 d) and 5 nests in 2017 (mean 18 d).

Photograph processing—All camera trap images were downloaded to a secure server and examined using Adobe Bridge software (Adobe Inc., San Jose, California, USA). Each independent prey delivery or nest attendance event was recorded for the male and/or female parent (determined by the presence of colored leg bands on males), and

Table 1. All prey types delivered to 9 Rock Wren nests in northern Colorado monitored with cameras.

Prey type	% of prey	Number of prey
Unknown prey	46.21%	726
Grasshopper (Order Orthoptera)	37.01%	581
Praying mantis (Order Mantodea)	3.18%	50
Grub	2.99%	47
Moth (Order Lepidoptera)	2.93%	46
Caterpillar (Order Lepidoptera)	2.61%	41
Beetle (Order Coleoptera)	2.42%	38
Spider (Order Araneae)	1.53%	24
Dragonfly (Order Odonata)	0.57%	9
Fly (Order Diptera)	0.19%	3
Butterfly (Order Lepidoptera)	0.13%	2
Snail (Order Stylommatophora)	0.13%	2
Centipede (Class Chilopoda)	0.06%	1
Total	100%	1,570

prey were identified to type (Table 1). Cameras were set to continuously photograph when motion was detected, thus prey delivery or nest attendance events were considered independent if it was clear that the parent had left and returned. We further noted if there was a prey pass-off between adults. Prey passed from one parent to another and subsequently to chicks was only counted once as a prey delivery event and was attributed to the original parent. All nest predation events were examined and predators noted. We also noted interesting behavior by the wrens not related to prey deliveries, including carrying nesting material or stones for the species' characteristic rock patio and nest cavity paving. Tagged photos were verified by a second observer for quality control and to confirm prey types.

All experimental procedures were conducted in accordance with the University of Northern Colorado Institutional Animal Care & Use Committee (Protocol No. 1506C-LB-Birds-18). All banding was performed under Federal Bird Banding Permit number 23741 and Colorado State Permit TRb2041.

Nesting ecology and parental care

We calculated means for (1) clutch size from nests where eggs could be seen using the inspection camera, (2) number of hatched chicks in the nests where chicks were observed with the inspection camera, and (3) number of fledglings for pairs that fledged at least 1 chick. As a

summary measure, we assessed overall nest success by dividing the number of nests where at least 1 fledgling was observed by the total number of pairs confirmed to have started a nest ($n = 12$) to get a percentage of successful nests. To calculate the minimum possible nest success for the population studied, we assumed that mated pairs for which we never found a nest had indeed at least attempted to breed but had failed if fledglings were never seen on the territory.

To examine feeding behavior at the nest, we calculated the proportion of each type of prey delivered (e.g., grasshopper, beetle, unknown prey) for all nests monitored using motion detection cameras ($n = 8$; one camera malfunctioned). We counted the number of prey items delivered in the first 5 d post-hatching and calculated the proportion of prey contributed in that time frame by each parent. We evaluated the amount of prey delivered by males in the first 5 d post-hatching in relation to the number of female prey deliveries. All statistics were run in JMP 9.0 (JMP, SAS Institute Inc., Cary, North Carolina, USA).

Results

Behavioral observations and nest monitoring

Of 27 males found singing as if actively defending territories, 21 were mated and all pairs were suspected to have nests, although not all nests were found or were accessible. We located nests with eggs present for 12 pairs (6 in 2016 and 6 in 2017). Of the 12 discovered nests, 9 (5 in 2016 and 4 in 2017) had at least 1 fledgling survive at least 2 weeks after emergence from the nesting cavity, meaning that 75% of discovered nests fledged at least 1 young (Table S1). One nest was abandoned after 5 eggs were laid, and 2 were depredated, one right after the first egg was laid and the other during the nestling phase.

For the remaining 9 out of 21 pairs, nests could not be found, and nest success is unknown. However, no fledglings were ever detected within the vicinity of the defended territory or in the presence of banded males in that area. It is possible that these pairs attempted to breed but failed, in which case a minimum overall estimated nest success for the population is that 42.9% of monitored pairs fledged at least 1 chick. Some of these pairs may have fledged chicks that we failed



Figure 1. Images of nest predators at Rock Wren nests in northern Colorado: (a) bullsnake (*Pituophis catenifer sayi*—lower left) that depredated part of a Rock Wren brood; (b) prairie rattlesnake (*Crotalus viridis*—lower left) preying on eggs at a nest while the male parent Rock Wren watches.

to detect, and therefore it is possible the nest success rate for this population is slightly higher than that reported here.

Complete clutch sizes in our population (in all cases we report mean \pm SD) included 4–7 eggs per nest (5.63 ± 1 eggs, $n = 8$), and nests hatched 3 or 4 chicks (3.44 ± 0.52 hatchlings, $n = 9$; Supplemental Table S1). For those nests that successfully fledged young ($n = 9$), 2.67 ± 0.5 fledglings survived at least 2 weeks. First egg lay dates were variable and estimated between 13 May and 26 June with a mean date of 2 June \pm 13.0 d (including one suspected second nest attempt; Supplemental Table S1).

Four nests out of 12 suffered predation by snakes that were either confirmed by camera trap or inferred due to the observed presence of a snake in close proximity to a depredated nest. Two of these nests were completely depredated but the other 2 nests had at least 2 fledglings old enough to escape the attack (Supplemental Table S1). Through camera trap pictures, 3 of the nest predators were identified (Fig. 1). Two of these predation events (So45 and So46) were perpetrated by bullsnakes (*Pituophis catenifer*) and one (So36) was by a prairie rattlesnake (*Crotalus viridis*; S. Mackessy, pers. comm.). One nest confirmed to have a single egg using the inspection camera had no eggs remaining when checked 3 d later (So31), but a bullsnake was seen in close proximity to the nest. This nest was not yet being monitored with a

camera trap since it could have caused abandonment to set one up so early in the nesting attempt. One nest had a woodrat (*Neotoma cinerea*) pass by on several different evenings, but it was never seen entering or exiting the cavity or tampering with the nest, although woodrats are known nest predators of Rock Wrens (Benedict et al. 2021).

Prey delivery and parental care

Our cameras monitored 9 nests and ran for a total of 183 d, with nests monitored for a mean of 22.9 ± 8.03 d (range 10–35 d). Combined, they collected over 77,000 photographs (mean $9,672.6 \pm 10,836.2$ photographs per nest; range 443–34,895 photographs). Eight nests had prey deliveries captured in the first 5 d after chicks hatched, a critical period during which the male brings food to young nestlings while the female both forages and continues incubating. Unfortunately, the camera at one nest malfunctioned a few days after the nest hatched and was excluded from prey delivery analyses looking at the 5 d post-hatching critical period.

Photographs revealed that both male and female Rock Wrens removed fecal sacs from the nests and entered the nest cavity with prey for chicks. Males would occasionally bring prey items to the incubating females, and during the nestling phase males would pass prey to the females who fed it to the chicks, but the reverse was never detected. On 2 separate occasions, once in 2016 and once in

Table 2. Number (and percentage) of prey deliveries by males and females at each of 8 Rock Wren nests from northern Colorado in the first 5 d post-hatch.

Nest ID	Male prey deliveries	Female prey deliveries	Unknown adult	Total prey deliveries
LB17	17 (89.5%)	2 (10.5%)	0 (0%)	19
So21	26 (100%)	0 (0%)	0 (0%)	26
So28	8 (50%)	6 (37.5%)	2 (12.5%)	16
So30	160 (92.5%)	13 (7.5%)	0 (0%)	173
So34	24 (66.7%)	12 (33.3%)	0 (0%)	36
So36	36 (86.1%)	4 (11.1%)	1 (2.8%)	41
So45	46 (88.5%)	4 (7.7%)	2 (3.8%)	52
So46	8 (61.5%)	2 (15.4%)	3 (23.1%)	13
Total	325 (86.25%)	43 (11.59%)	8 (2.16%)	376
Mean	40.625	5.375	1	47
SD	± 49.97	± 4.75	± 1.20	± 52.64

2017, a male was seen with a paving rock for the nest patio, a behavior that had previously only been attributed to females at our field sites (Warning and Benedict 2015b).

Images showed that prey types were variable and often times difficult to identify such that it was unknown in 46.21% of instances where a prey delivery event was certain (Table 1). Grasshoppers were the most commonly identified prey item at all nests (37.01%), and other prey types (each under 3% of deliveries) included beetles, spiders, caterpillars, butterflies, moths, dragonflies, flies, snails, centipedes, and grubs (Table 1). One wren was an expert at catching praying mantises (3.18%), delivering 50 different individuals to the nest. In the 5 d post-hatching, 376 prey delivery events were detected at the 8 monitored nests, with variable delivery rates among males and females. Overall, males were responsible for the vast majority of prey deliveries (Table 2). Males delivered 8–160 prey items in 5 d post-hatching compared to females delivering 2–13 prey items (Table 2). Overall males were responsible for 86.25% of deliveries, with males ranging from 50% to 100% of provisioning per nest, while females were responsible for 11.6% ranging from 0% to 37.5% per nest (unknown parents accounted for 2.16% overall provisioning; Table 2). The reported prey delivery numbers are the minimum amount of prey that were delivered to the nests, as it is possible that the cameras did not detect every delivery, with differences between nests potentially reflecting differences between cameras.

Discussion

We provide estimates of breeding parameters and success in a northern, migratory population of Rock Wrens. Over 2 field seasons, 12 nests were closely monitored to collect data on lay date, incubation initiation date, hatch date, fledge date, clutch size, number hatched, number fledged, days incubated, and days in the nest. We confirmed that Rock Wrens feed their chicks a range of invertebrate prey and that males are the primary provisioners when chicks are 1–5 d old. Previously published data from a southern population show that mean Rock Wren clutch sizes are typically 5.6 ± 0.8 eggs, incubation takes 12–14 d, and nestlings are in the nest for 13–16 d (Merola 1995, Benedict et al. 2021). We found mean clutch sizes of 5.6 ± 1.1 eggs ($n = 7$), which are comparable to estimates in the literature. Previous work has shown clutch sizes of 4–7 eggs in 10 nests in the Californian Sierra Nevada Mountains (Oppenheimer and Morton 2000), a mean of 5 eggs in 2 nests in New Mexico (Merola 1995), and 6 eggs found in 1 nest also in New Mexico (Bailey 1904). Birds in our population incubated for 15.1 ± 0.32 d. This is slightly higher than reported in other populations and might reflect the more northern distributions of Colorado birds nesting in colder climates. Our observed nestling period, in contrast, fell right at the center of existing estimates for the species at 14 ± 1.5 d (Benedict et al. 2021; Supplemental Table S1). Overall, the results demonstrate that Rock Wren nesting biology is fairly consistent across the range of the species.

No estimates of nestling or fledgling numbers per nest have been reported previously for Rock Wrens. We documented nests with 3 or 4 nestlings and with 2 or 3 fledglings. There are also no direct estimates of fledging success in the literature per se, though 8 of 50 nests in western Kansas suffered predation, making for a possible fledging success of 84%, which is higher than our minimum fledging success of 42.86% for the population as a whole, but similar to the success rate of 75% for our located nests (Matiasek 1998). These estimates are, by default, skewed by imperfect knowledge of nesting locations and affected by the stochastic nature of predation events, but suggest that breeding success rates are similar across the range of this species.

Camera traps provide an excellent tool to estimate parental investment at the nest and for watching natural behaviors (Swann et al. 2011). They also provide an easy way to quantify prey deliveries to nestlings, to estimate nestling diets, and to quantify parental division of labor. Previous work in northern Colorado found that food items delivered to Rock Wren nestlings included moths, crickets, grasshoppers, leafhoppers, cicadas, mantids, and robber flies (Warning et al. 2014). We found prey type delivery rates similar to Matiasek (1998) and also noted that grasshoppers were the most often-delivered identified prey items, suggesting that they make up a substantial portion of chick diets in multiple locations. The prey delivery metrics reported here do not account for quality or size of prey types delivered. Follow-up studies with more thorough investigation of prey availability on different territories in relation to nesting ecology and fledgling success would be immensely valuable (Bailey 1904; Merola 1995; Oppenheimer and Morton 2000; Warning and Benedict 2015b, 2016).

Previous work has not assessed the relative feeding contributions of male and female Rock Wren parents to the young (Wolf et al. 1985, Merola 1995, Matiasek 1998). In our study, provisioning rates were variable from nest to nest, but males consistently provisioned much more than females did when they had small chicks, providing over 86% of prey items. As chicks age and females no longer need to help them thermoregulate, it is possible that provisioning behavior becomes more evenly distributed between the parents. There is evidence, however, that

males typically continue to take the lead in feeding young fledglings for approximately 2 weeks post-fledging (Benedict et al. 2021). During this time a female might initiate a second nest if it is still early enough in the breeding season (Benedict et al. 2021). These provisioning patterns confirm that male parental effort is essential to reproductive success in this species. Mate choice preferences are therefore likely to impact nesting success, a supposition explored in other studies of this northern Colorado population of Rock Wrens (Pitt 2018).

We made multiple additional interesting natural history observations at Rock Wren nests using camera traps. We saw 2 different male Rock Wrens bring stones to the nest, which has never been recorded at our field sites (Warning and Benedict 2015b). Observations of nests in the Sierra Nevada Mountains of California have attributed rock paving to both males and females, and this is apparently also true in Colorado (Oppenheimer and Morton 2000, Benedict et al. 2021). Confirmed predators of Rock Wren nests in the United States are snake species, including western hognoses (*Heterodon nasicus*), racers (black racers [*Coluber constrictor*] and striped racers [*Masticophis taeniatus*]), and adders (unspecified) (Hardy 1945, Benedict et al. 2021). Other likely predators include woodrats, ground squirrels, and chipmunks (Hardy 1945, Benedict et al. 2021). All of our confirmed nest predators were snakes, and this study is the first to document nest predation by bullsnakes and prairie rattlesnakes. We also documented that snakes do not always depredate the entire clutch—older chicks can survive predation attempts by snakes. One hypothesis for the presence of the stone paving at the entrance of rock wren nests is that it provides an audible warning signal of an approaching predator (Warning and Benedict 2015b). A previous study (Warning and Benedict 2015b) concluded that this warning could give the incubating female time to escape before a predator enters the nest. Results of our study suggest that larger nestlings might benefit from the same warning mechanism.

Rock Wrens are widespread, but often found in inaccessible habitats occupied by few other birds and, therefore, ornithologists have a limited understanding of their life history and nesting ecology (Jones 1998, Brewer 2010). This study provides valuable information about the breeding

biology of Rock Wrens. Results include breeding metrics and natural history data and provide a baseline from which to investigate Rock Wren breeding success in the more northern, migratory part of their range. Rock Wren population numbers are thought to be relatively stable, but negative population trends have been detected in breeding bird surveys from the past 30 years and knowing more about the species' patterns of reproductive success should help to reveal drivers of these trends (Salamacha Breeding Bird Census 1992–1996, Sauer et al. 1997, Brewer 2010, Benedict et al. 2021).

High nest predation has been proposed as a factor limiting population size and our results lend support to this possibility, as snakes depredated 3 of the 9 nests watched by trail cameras (Benedict et al. 2021). Analyzing additional behavioral, ecological, and mate choice pressures that affect reproductive success would be valuable in understanding the population fluctuations of Rock Wrens and their differential fledging success across the species' range.

Acknowledgments

We thank P. (McPhail) Love and K. Strong for assistance in the field and S. Rickford, K. Nasalroad, and R. Worley for assistance with camera trap photograph tagging. Thanks for ceaseless encouragement go to Philippe Gobert. We are grateful to 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 and for access to field sites. The School of Biological Sciences at the University of Northern Colorado, the Graduate School at the University of Northern Colorado, the Office of Undergraduate Research at the University of Northern Colorado, the Colorado Field Ornithologists, and the Colorado Mountain Club Foundation supported this work.

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