Am. Midl. Nat. (2015) 174:150–160

Canyon Wren Territory Occupancy and Site Attributes in Northern Colorado

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Abstract.—In this study we examined patterns of habitat occupancy by canyon wrens (*Catherpes mexicanus*), an insectivorous, cliff-obligate bird species, in Northern Colorado. Canyon wren territories are generally large and widely spaced, and it is currently unclear if their densities are limited by the availability of cliff habitats that have particular biotic and/or abiotic attributes. We used playback of conspecific song to survey 138 cliff sites and found 23 occupied territories, confirming the species occurs in low densities. Using a model-fitting approach, we assessed the importance of seven factors hypothesized to be important to canyon wren territory settlement and found occupied territories had cliffs that were more likely to be overhung, rather than vertical. Habitat occupancy of canyon wrens was also associated with the presence of cliff swallows (*Petrochelidon pyrrhonota*) and their nests, with canyon wrens observed nesting and foraging within cliff swallow nests throughout the year. As no abiotic factors predicted both the presence of canyon wrens and cliff swallows, we suggest the biotic resources provided by cliff swallows might be important in driving patterns of canyon wren territory occupation. If canyon wren settlement patterns are affected by the presence of cliff swallows, this system could represent a rare case of heterospecific attraction, where a migratory species (cliff swallow) drives patterns of habitat occupation by a non-migratory species (canyon wren).

Introduction

Cliff ecosystems are relatively understudied but can harbor important patterns of biodiversity (Graham and Knight, 2004). In particular cliff habitats increase local avian diversity by housing unique avian species that are closely associated with steep rock formations (Rossi and Knight, 2006; Camp and Knight, 2007). We examined habitat occupancy by a cliff obligate bird species, the canyon wren (*Catherpes mexicanus*), in order to determine what features drive patterns of territory settlement. The canyon wren inhabits arid, rocky areas containing cliffs, canyons, and rock faces (Bent, 1948; Mirsky, 1976; Jones and Dieni, 1995). Across most of their range in Western North America, canyon wren populations are declining, but estimated rates of decline are uncertain because the species typically occurs in low densities is generally is not well surveyed (Jones and Dieni, 1995). A better understanding of canyon wren habitat requirements and density throughout the species' range will improve conservation monitoring techniques by helping researchers to identify suitable habitat. This, in turn, will provide insight into the abiotic and biotic factors that govern avian habitat use in cliff ecosystems and will help us to understand how cliff-obligate species might contribute to larger patterns of biodiversity.

Canyon wrens are year-round residents of permanent (Type A) territories within which they conduct all of their foraging and breeding activities (Nice, 1941; Jones and Dieni, 1995). Canyon wrens often occur in low densities, with large (>1 ha in size; Bock, 1987; Johnston and Ratti, 2002; Jones *et al.*, 2002), widely spaced territories (>600 m apart in contiguous habitat; Jones *et al.*, 2002). It is unknown, however, if these large territories and wide spacing are due to a lack of abundant suitable habitat in parts of their range, or if they

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are due to other factors, such as particular habitat requirements. Canyon wrens are probing insectivores, making them entirely dependent on the terrestrial resources that they obtain on and around the surface of the cliffs where they reside (Bent, 1948). Therefore, individual fitness in canyon wrens is likely to depend strongly on successful habitat selection at suitable cliff sites (Greene and Stamps, 2001; Stamps, 2001). Cliff obligate bird species can evaluate a number of different habitat features when making territory settlement decisions. For example, although they differ greatly in ecology, both cliff swallows (*Petrochelidon pyrrhonota*) and peregrine falcons (*Falco peregrinus*) nest exclusively in cliff habitats and show patterns of habitat occupancy that correlate with abiotic factors related to cliff structure and with biotic factors related to foraging opportunities and the presence of conspecifics or heterospecifics (Brown and Brown, 1996; Brown *et al.,* 2000; Gainzarain *et al.,* 2000; Brown *et al.*, 2002; Brambilla *et al.,* 2006).

Previous work on canyon wrens has shown evidence of preference for large cliffs with sparse vegetation (Johnston and Ratti, 2002; Jones *et al.*, 2002; Rossi and Knight, 2006), but no studies have identified particular attributes of large cliffs that may affect canyon wren usage patterns. For this study we assessed the availability of cliff habitats in Northern Colorado and examined the following seven abiotic and biotic attributes of potentially suitable cliff habitats which were hypothesized to drive patterns of territory occupation: (1) cliff height, (2) cliff length, (3) cliff orientation, (4) cliff maximum slope (overhang), (5) distance from the cliff to water, (6) cliff crevice density, and (7) presence of cliff swallows. We predicted that occupied cliffs would be: (1) taller and (2) longer than unoccupied cliffs assuming territory density is limited by a lack of large cliffs, (3) oriented to achieve thermoregulatory benefits (Brambilla *et al.,* 2006), (4) overhung to provide protection from precipitation, (5) close to water because water sources may provide opportunities for hydration and prey capture (Jones and Dieni, 1995; Johnson and Ratti, 2002), (6) characterized by high crevice density in which canyon wrens forage for insect prey (Mirsky, 1976; Jones and Dieni, 1995), and (7) in close proximity to cliff swallow nest colonies. This last prediction was based on previous observations of canyon wrens and cliff swallows inhabiting and nesting on the same vertical cliff sites, leading us to hypothesize that heterospecific attraction may cause canyon wrens to nest near cliff swallow colonies (Mönkkönen and Forsman, 2002). Cliff swallows use mud to build durable, protective, domed nests, which are known to harbor insect ectoparasites (Hopla and Loye, 1983; Brown and Brown, 1986; Brown and Brown, 1995). Cliff swallows migrate away from our study sites between August and May, but their nests remain and could provide a valuable source of food and shelter for canyon wrens throughout the year. In sum the specific objectives for this study were to: (1) develop predictive models of canyon wren occupation using the above abiotic and biotic variables, (2) use natural history observations to verify models and provide additional information on canyon wren behavior in relation to the above variables, and (3) describe territory persistence by canyon wrens within and across years.

METHODS

OCCUPANCY SURVEYS

We surveyed potential canyon wren habitat in May–August 2011 by visiting public lands housing large cliffs in Larimer County, Colorado from N40 28.915 to N40 35.706 and W105 10.844 to W105 13.472 and from 1631 m to 1673 m in elevation. Private land adjacent to or between public areas was not surveyed; therefore, results do not cover all potentially viable habitats in the county. Occupancy surveys were conducted at all sites that were judged to be available canyon wren habitat because they included vertical or near vertical cliffs over 10 m

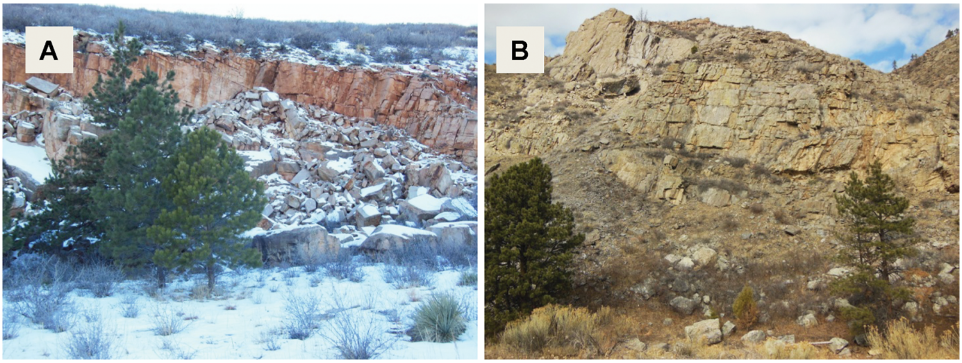

FIG. 1.—Two cliffs occupied by canyon wrens in Larimer County, Colorado, 2011–2012: **(A)** shows a 15 m tall northwest facing cliff **(B)** shows a 75 m tall south facing cliff. Photos by N. Warning

in height (Rossi and Knight, 2006). Sites were scattered across semi-arid montane shrublands characteristic of the Colorado foothills region, with rocky, coarse textured soils and high runoff (Mutel and Emerick, 1992). Most survey sites included both rocky outcrops and sedimentary cliffs with fissures and crevices that provide protected microhabitat suitable for canyon wrens (Fig. 1). The slopes approaching the cliffs were typically steep (15–32°), contained talus fields, boulders, and rock ledges, and were dominated by mountain mahogany (*Cercocarpus montanus*), three-leaf sumac (*Rhus triolbata*), and wax currant (*Ribes cereum*).

Researchers conducting surveys spent 3–5 min in a fixed location (survey site) at the base of a cliff looking and listening for evidence of canyon wrens. If no canyon wrens were visible or audible within the first minute then the researcher played a recording of a local canyon wren vocalization at a volume similar to the natural volume of song in this species (as judged by ear). Territory-holding canyon wrens are highly aggressive to perceived intruders and typically respond to playback by approaching the speaker and singing (Benedict *et al.,* 2012). We considered a survey site to be occupied if we either saw or heard a canyon wren there. In order to avoid counting a single territory multiple times, we only considered neighboring survey sites to both be occupied if we heard males singing simultaneously from both sites, or we visually confirmed the presence of pairs of adult birds at the two sites simultaneously.

Survey sites were variably spaced following habitat availability. Average distance between subsequent survey sites was 4693.1 m (SD = 9904.5 m). When suitable cliffs were less than 300 m in length and widely spaced, researchers conducted a single survey at the center of each cliff. In areas with cliffs that were continuous for distances over 300 m, we walked along the base of the cliff and stopped to conduct a survey approximately every 300 m. This protocol ensured complete coverage of appropriate habitat, such that our playback would be heard by an individual bird, regardless of what portion of his territory he was on. Given that canyon wren territories are typically spaced 600 m apart, this sampling scheme means that we might have surveyed multiple times within a single potential territory. We surveyed a total of 201 sites, but because 93 were less than 600m from the previous site we removed them from the data set. Therefore, our occupancy surveys covered 138 sites that were potentially unique canyon wren territories (Jones and Dieni, 1995).

Individual birds were not observed for extensive periods during initial surveys, but we monitored 17 canyon wren territories with follow-up site visits through 2011 and 2012. Three sites were visited only once in 2012 and 14 were monitored with multiple site visits.

These follow-up visits allowed us to estimate territory persistence over the course of a year. In 2012 we did not systematically monitor sites that were unoccupied in 2011. We visited most of these sites only once, making it impossible for us to formally estimate detection rates for the purposes of this study.

CLIFF ATTRIBUTES

In August 2011 we measured cliff habitat features at all occupied sites and at a randomly chosen sample of unoccupied sites equal to the number of occupied sites. Unoccupied control sites were chosen from our sampling sites using the RAND function in Microsoft Excel and cumulatively excluding sites within 600 m of each other to ensure statistical independence. During these second visits, we confirmed canyon wrens were either present or absent as expected and we measured the following site attributes: (1) cliff height, (2) cliff length, (3) cliff orientation, (4) cliff maximum slope (overhang), (5) distance from the cliff to water, (6) cliff crevice density, and (7) presence of cliff swallows (Tapia *et al.,* 2007). We measured cliff height in meters either directly using a range finder (Bushnell, Overland Park, KS) or indirectly using a range finder and clinometer (Suunto, Vantaa, Finland) and the cosine rule ($a^2 = b^2 + c^2 - (2 * b * c * \text{Cos } A)$. We measured cliff length and distance to water in meters using aerial imagery and the measure tool in Garmin Basecamp (Garmin, Olathe, Kansas). We measured cliff orientation from the survey site in degrees (of 360, 0 = North) using a compass (Suunto, Vantaa, Finland). We determined cliff maximum slope by sighting the cliff from below using a clinometer (Suunto, Vantaa, Finland) and determining the maximum upslope angle, which was always either 90 degrees (vertical) or 95 degrees (overhung). To measure crevice density we digitally photographed (Nikon, Tokyo, Japan) each survey site 50 m from the base of the cliff at a 300 DPI resolution and analyzed the photographs using a modified dot-grid technique (Avery, 1975). We overlaid photos with a transparent grid (64 × 48 squares) in Microsoft PowerPoint and counted crevices that were intersected by grid lines. We divided number of crevices intersected by the total number of grid squares that contained suitable habitat in each photo to determine relative crevice density. We determined cliff swallow presence through observation of swallows or evidence of swallow nests at each site during habitat measurement.

STATISTICAL ANALYSES

We used a model-fitting approach to test the following six independent variables for significant effects on territory occupancy by canyon wrens: cliff height, cliff length, distance to water, crevice density, maximum slope (overhang), and presence of cliff swallows. Because all maximum slope values were either 90 degrees (vertical) or 95 degrees (slightly overhung), we treated these values as categorical variables in our analyses. Cliff swallow presence or absence was also fitted as a categorical variable and all others were continuous. We fit all univariate factors independently using logistic regression from which we calculated Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 1998). We then constructed multivariate models that included all combinations of univariate factors which reduced the AIC_c relative to the intercept-only null model. This provided one additional candidate model, for a total of seven candidate models. In order to assess whether cliff swallow presence was driven by the same factors as canyon wren presence we ran the model-fitting procedure described above but with cliff swallow presence as the dependent variable and canyon wren presence as one of the independent variables. This analysis was done post-hoc and provides information on the abiotic factors that relate to cliff swallow presence at survey sites but should be interpreted with the knowledge that our sampling scheme was designed relative to canyon wrens and not to cliff swallows.

TABLE 1.—Means and standard errors for five cliff attributes measured at 23 occupied canyon wren sites and 23 unoccupied control sites in Northern Colorado, 2011–2012

Site attribute	Occupied site mean (SE)	Unoccupied site mean (SE)
Cliff height (m)	33.2 (4.84)	30.9 (3.90)
Cliff length (m)	230.4 (30.1)	210.4 (26.9)
Crevice density	0.30 (0.03)	0.33 (0.03)
Distance to water (m)	146.7 (33.9)	133.7 (29.8)
Cliff orientation (°)	187.9 (20.3)	269.5 (16.8)

To compare cliff orientation between occupied and unoccupied sites we did a separate analysis using the Mardia-Watson-Wheeler test for circular data. The Mardia-Watson-Wheeler test was run in ORIANA, version 4 (Kovach computing services), and all other statistics were run in JMP, version 9.0 (SAS institute).

RESULTS

OCCUPANCY SURVEYS

We conducted occupancy surveys at 138 sites which we judged to be available territories for canyon wrens, and we located only 23 occupied sites in 2011. We visited 17 of these sites in 2012 and found 14 remained occupied. We surveyed one of the three unoccupied sites only once, but the other two were surveyed multiple times during which we found no evidence of canyon wren presence.

CLIFF ATTRIBUTES

In general cliff attributes were quite variable across survey sites, but averages were similar between cliffs occupied by canyon wrens and unoccupied control sites (Table 1). Cliff orientation did not vary among occupied and unoccupied sites (Mardia-Watson-Wheeler: $W_{44} = 5.89$, $P = 0.053$), although there was a trend towards occupied sites facing South. Two variables: (1) the presence of cliff swallows and (2) the cliff maximum slope, improved model fit relative to the intercept-only model. Our strongly-supported ($w_i = 0.96$) best fit model describing site occupancy by canyon wrens included both of these parameters (Table 2). Based on the parameter estimates, we found that canyon wren occupancy was

TABLE 2.—Model selection metrics for logistic regression models of six site attributes predicting habitat occupancy by canyon wrens in Northern Colorado, 2011–2012

	K^a	AIC_c	$\Delta AIC_c{}^b$	$w_i{}^c$
Cliff swallows + Maximum slope	3	54.89	0.00	0.96
Cliff swallows	2	62.25	7.36	0.02
Maximum slope	2	63.71	8.82	0.01
Intercept-only	1	65.86	10.97	0.00
Distance to water (m)	2	67.96	13.07	0.00
Crevice density	2	70.78	15.89	0.00
Cliff length (m)	2	71.17	16.28	0.00
Cliff height (m)	2	71.28	16.39	0.00

[a] Number of parameters.

[b] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[c] AIC_c relative weight attributed to model.

TABLE 3.—Parameter estimates, standard errors, and 95% confidence intervals for the top-ranked logistic regression model predicting canyon wren site occupancy in Northern Colorado, 2011–2012

Parameter	Estimate	Standard error	Confidence interval
Intercept	−0.705	0.464	−1.757 – 0.128
Cliff swallows	0.950	0.361	0.273 – 1.708
Max slope	1.039	0.459	0.214 – 2.080

positively related to the presence of cliff swallows (β = 0.950; CI = 0.273–1.708) and overhung cliffs (β= 1.039; CI = 0.214–2.080; Table 3). Ten sites that housed canyon wrens were overhung (max slope = 95°), while only two sites without canyon wrens were overhung (max slope = 95°). Fifteen of the 23 sites that housed canyon wrens also housed cliff swallows, while only five of the control sites without canyon wrens housed cliff swallows.

Among our multivariate logistic regression models testing factors potentially driving cliff swallow site occupancy we again found two variables that improved model fit relative to the intercept-only model: (1) presence of canyon wrens and (2) distance to water (Table 4). A model including these two variables explained cliff swallow presence better than any univariate model ($w_i = 0.73$). Based on the parameter estimates, we found that cliff swallow occupancy was positively related to the presence of canyon wrens (β = 1.072; CI = 0.404–1.831) and distance to water (β = 0.005; CI = 0.0004–0.013; Table 5).

OBSERVATIONS

Our observations confirmed that canyon wrens forage and nest on cliff faces and confine most of their behaviors to cliff locations. We frequently observed canyon wrens foraging in rock crevices (Fig. 2A) on cliff surfaces and among boulders and rubble near cliffs. Through 2011 and 2012, we never observed canyon wrens accessing or interacting with water sources. They sometimes foraged in areas next to flowing or still water, but they did not drink or bathe. At multiple sites we observed canyon wrens interacting with cliff swallow nests. On the only territory that we monitored through the winter (1 January through 31 March 2012) we consistently observed a canyon wren pair foraging inside unoccupied cliff swallow nests (Rose and Phan, 2013). This behavior continued into June 2012. From 15 April through 5 August 2012 canyon wren pairs in three other locations exhibited similar foraging

TABLE 4.—Model selection metrics for logistic regression models of six site attributes predicting habitat occupancy by cliff swallows in Northern Colorado, 2011–2012

	K[a]	AIC_c	ΔAIC_c[b]	w_i[c]
Canyon wrens + Distance to water (m)	3	55.88	0.00	0.73
Canyon wrens	2	58.08	2.21	0.24
Distance to water (m)	2	63.96	8.09	0.01
Intercept-only	1	65.08	9.20	0.01
Maximum slope	2	65.81	9.94	0.01
Crevice density	2	67.17	11.30	0.00
Cliff length (m)	2	67.22	11.34	0.00
Cliff height (m)	2	67.25	11.37	0.00

[a] Number of parameters.

[b] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[c] AIC_c relative weight attributed to model.

TABLE 5.—Parameter estimates, standard errors, and 95% confidence intervals for the top-ranked logistic regression model predicting cliff swallow site occupancy in Northern Colorado, 2011–2012

Parameter	Estimate	Standard error	Confidence interval
Intercept	−0.378	0.494	−1.412 – 0.568
Canyon wrens	1.072	0.360	0.404 – 1.831
Distance to water (m)	0.005	0.003	0.0004 – 0.012

behaviors. While foraging at cliff swallow nests, canyon wrens moved from nest to nest, spending approximately 5–15 sec within each nest and also probing with their bills along the outsides of cliff swallow nests and in crevices between the nests. As cliff swallows arrived at nest colonies in May they usually repelled foraging canyon wrens from the entrances of occupied swallow nests.

We also observed canyon wrens nesting on and inside cliff swallow nests both before the arrival of cliff swallows and during the period of active swallow breeding in May–August 2012. On 24 May 2012, a canyon wren pair was seen nest-building within a cliff cavity, using the top of a cliff swallow nest as the base for their own nest. At least four chicks fledged from the nest on 2 July. This east-facing nest was located 4 m up a 7 m high cliff, 8 m from the nearest occupied cliff swallow nests. On 21 May 2012, a different canyon wren pair was observed entering and exiting a cliff swallow nest, bringing food to begging chicks inside (Fig. 2B). Observations made 23 May and 25 May confirmed this nesting location. On 1 June the adults were observed feeding at least two fledged chicks on rock ledges below the nest site. The pair was actively feeding a second brood of chicks inside the same nest on 25 June (Fig. 2B), and four chicks successfully fledged on the morning of 2 July. This south-facing nest was located 8 m up a 12 m high cliff, 12 m from an active cliff swallow nesting colony. Both cliff swallow associated nesting sites were protected by overhanging cliff outcrops.

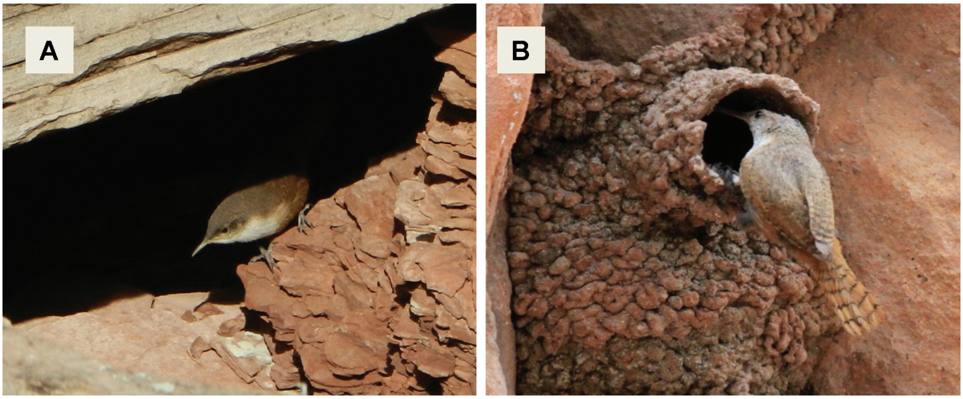

FIG. 2.—Two photos showing canyon wren habitat use in Larimer County, Colorado, 2011–2012. Foraging canyon wrens captured prey in rock crevices (A) and on and around cliff swallow nests. Canyon wrens successfully nested above and within (B) cliff swallow nests. Photos by N. Warning (A), and A. Meyer (B).

DISCUSSION

Our study confirmed canyon wrens do not occupy all potentially suitable available habitat in Northern Colorado. Canyon wrens were detected at only 23 of 138 survey sites with appropriate abiotic habitat characteristics. Future studies accurately estimating detection probability for this species would be valuable. If canyon wren detectability is low, then more than 23 of these sites may have been occupied, but previous research indicates that male canyon wrens are highly responsive to playback on their territories (Benedict *et al.,* 2012). Therefore, it is likely our playback survey technique accurately detected the presence of most birds, and even with errors in detection, the data suggest that the occupancy rate of this species at large cliffs in Northern Colorado is low.

There are, of course, many potential habitat features that birds evaluate when making settlement decisions and we did not measure all of those. We did, however, measure features predicted to have relevance to canyon wren ecology, and most of them did not appear to drive habitat occupancy. The similarity in cliff height, cliff length, and cliff orientation between occupied and unoccupied sites suggests that these abiotic factors do not drive or limit canyon wren settlement decisions. We found no evidence that canyon wrens preferentially settle close to water or interact with water sources. Canyon wrens might be associated with water because water creates canyon habitats, but there is very little evidence that canyon wrens rely directly on water (Jones and Dieni, 1995). Because canyon wrens are specialist cliff crevice foragers, we expected that crevice density would drive patterns of settlement, but we found no evidence to support this. Unoccupied cliffs had crevice densities as high as occupied cliffs. Therefore, Northern Colorado contains many cliffs with suitable size, orientation, and foraging potential for canyon wrens.

Resurveys one year after our initial surveys indicated that 82% of occupied territories remained occupied, but three sites occupied in 2011 were not occupied in 2012. Canyon wrens are year-round residents and pairs typically remain on the same territory through the winter. Site occupancy from year to year is likely due to persistence of a single pair through time, although this requires more study (Jones and Dieni, 1995). Our study and others have observed that sites which were active in one year were empty in subsequent years, indicating that when territory vacancies arise, they are not immediately filled (Jones *et al.,* 2002). This adds to the evidence some unoccupied sites are potentially viable canyon wren territories. Taken together, our results suggest not all appropriate habitat is saturated, which likely indicates that canyon wren population sizes in Northern Colorado are governed by factors other than habitat limitation (Newton, 1998).

Our study identified two cliff site attributes that did correlate with canyon wren occupancy: cliff maximum slope and the presence of cliff swallows. Both of these variables were not diagnostic, as evidenced by multiple canyon wren territories that were not overhung and lacked cliff swallows. They did, however, significantly predict canyon wren presence. Cliffs with a maximum slope greater than 90° can be beneficial because they protect foraging and nesting birds from rain and prevent snow from settling in foraging sites (Larson *et al.,* 2005). Cliff overhangs also provide suitable habitat for cliff swallows, but we did not find evidence that cliff maximum slope affects cliff swallow presence. Instead, the only abiotic factor that predicted cliff swallow presence was the distance to water—a variable that was unrelated to canyon wren site occupancy patterns. Therefore, results suggest canyon wrens do not co-occur with cliff swallows because the two species prefer cliffs with similar attributes. We interpret cliff maximum slope and presence of cliff swallows as separate drivers of canyon wren presence and as two important sources of information to canyon wrens making territory settlement decisions (Brown and Brown, 1996; Szymkowiak, 2013).

Combined evidence from multiple territories in Larimer County indicates that cliff swallow nests provide benefits to canyon wrens. Canyon wrens near our study area have been known to use cliff swallow nests as night roosts (Sooter *et al.,* 1954), but previous studies have not reported that cliff swallow nests act as nesting sites for canyon wrens. Many species of birds (including cliff swallows) reuse nests created by conspecifics or heterospecifics, and such reuse may reduce the energetic costs associated with nest-building (Gauthier & Thomas, 1993; Hansell, 2000). Since canyon wrens typically nest in existing cavities we expect that their use of cliff swallow nests does not decrease nest-building costs (Jones and Dieni, 1995). Instead, it is likely that cliff swallow nests provide nesting canyon wrens with thermoregulatory benefits and shelter from weather, as they do for cliff swallows (Brown and Brown, 1995).

Natural history observations suggest that canyon wrens derive foraging benefits from cliff swallow nests. Although we were not able to identify individual prey items captured within swallow nests, it is probable that the nests contained swallow bugs, cimicid bugs, ticks, fleas, beetles, lice, mites, nematodes, trematodes, and protozoans (Brown and Brown, 1986; 1995), many of which have been documented in Colorado cliff swallow colonies (Sooter *et al.*, 1954; Stabler and Kitzmiller, 1972; Kayton and Schmidt, 1975). Several of these species are known to persist in swallow nests for over a year and could serve as an important year-round food resource for canyon wrens (Sooter *et al.,* 1954; Hopla and Loye, 1983; Loye, 1985; Brown and Brown, 1995). Other authors have suggested that canyon wren population sizes are limited by overwinter survival (Jones *at al.*, 2002). By choosing to settle on territories that include cliff swallow nests, canyon wrens might provide themselves with an important winter food source. This hypothesis deserves further study, as this system could represent a rare example of heterospecific attraction where a nonmigratory species (canyon wren) makes territory settlement decisions based on the distribution of a migratory species (cliff swallow) (Mönkkönen and Forsman, 2002). It is also possible that this system represents a heterospecific attraction mechanism whereby cliff swallows choose to settle near canyon wrens, but our preliminary observations do not support this interpretation; we found no evidence that cliff swallows benefit from canyon wren presence and instead observed that cliff swallows are aggressive towards and regularly defend cliff areas from canyon wrens.

Habitat selection decisions can have significant impacts on individual fitness (Cody, 1985; Leonard and Picman, 1987). Though the canyon wren remains one of the least-studied North American birds, our knowledge of its habitat use, breeding biology and behavior is increasing (Jones and Dieni, 1995; Jones, 1998; Jones *et al.,* 2002; Johnston and Ratti, 2002; Benedict *et al.,* 2013). Our study confirms that canyon wrens occur in low densities and do not saturate all available habitat in Northern Colorado. Cliff maximum slope and cliff swallow presence correlate with canyon wren habitat occupancy, potentially indicating the importance of maintaining food resources and protection from the elements throughout the year in harsh cliff environments. The co-occurrence of canyon wrens and cliff swallows at many sites indicates that protection efforts towards one species are likely to help the other, and also suggests interesting avenues for future research on heterospecific interactions.

Acknowledgments.—We thank the City of Fort Collins Natural Areas Program, the Larimer County Department of Natural Resources, the Colorado Division of Parks and Wildlife, and The Nature Conservancy for access to study sites. This manuscript was improved by comments from D. Leatherman and four anonymous reviewers. Thank you to A. Meyer for field assistance and photography. Thank you to D. Lashaway for assistance with data collection. Research was funded by a grant from The Colorado Field Ornithologists and by The University of Northern Colorado's College of Natural and Health Sciences.

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SUBMITTED 14 MAY 2014 ACCEPTED 21 MARCH 2015