

OVERLAPPING HOME RANGES AND MICROHABITAT PARTITIONING AMONG CANYON WRENS (*CATHERPES MEXICANUS*) AND ROCK WRENS (*SALPINCTES OBSOLETUS*)

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ABSTRACT.—Patterns of animal space use may vary according to species identity, presence of conspecifics, presence of heterospecifics, and resource availability. We evaluated joint space use by Canyon Wrens (*Catherpes mexicanus*) and Rock Wrens (*Salpinctes obsoletus*) by comparing home range sizes, home range overlap, and foraging behavior. Canyon and Rock wrens are ecologically similar species which frequently co-occur along rocky cliffs where members of both species feed on terrestrial invertebrates. Interactions between Canyon and Rock wrens provide information about avian space use and foraging strategies in understudied cliff habitats. We estimated home range for each species using ArcGIS, and quantified foraging microhabitat use. Canyon Wren home ranges were widely spaced, did not overlap conspecifics, and were significantly larger than those of Rock Wrens. Rock Wrens occurred at higher densities and home ranges overlapped conspecifics in 33% of cases by an average of 19%. Canyon and Rock wren home ranges overlapped in 68% of cases by an average of 28%, but overlapping pairs rarely shared core use areas. The two species differed significantly in foraging microhabitat use. Results suggest that heterospecific territory defense between Canyon and Rock wrens is low, and that these species have adopted different methods for using shared resources in escarpment and cliff habitats. Received 25 November 2014. Accepted 27 February 2015.

Key words: Canyon Wren, *Catherpes mexicanus*, home ranges, interspecific interactions, joint-space use, Rock Wren, *Salpinctes obsoletus*.

Population and community ecologists have described distinctive and varied ways in which organisms use space and resources (MacArthur 1972, Schoener 1974, Virzi et al. 2012). Many birds defend territories and occupy delineated home ranges which may differ widely in size depending on resource needs and resource availability (Adams 2001, Moorcroft and Lewis 2006). Furthermore, intraspecific and interspecific interactions among individuals of different species can impact population densities and the extent and spatial patterning of territories or home ranges (Law and Watkinson 1989, Adams 2001, Farwell and Marzluff 2013). Here we provide quantitative estimates of home-range size, along with the first information on home range overlap and foraging behavior among two closely related avian species known to use similar resources.

Canyon Wrens (*Catherpes mexicanus*) and Rock Wrens (*Salpinctes obsoletus*) both feed on terrestrial invertebrates, overlap broadly in distribution, and co-occur in exposed rock habitats containing cliffs and escarpments (Jones and Dieni 1995, Lowther et al. 2000). Rock and Canyon wrens are grouped basally in the wren phylogeny, and in western North America are each other's closest

relatives (Barker et al. 2004). While it is known that Rock Wrens sometimes nest within Canyon Wren territories (Jones and Dieni 1995), there is little information on the degree to which interspecific home ranges overlap and GIS-based estimates of home range size and overlap are lacking for both species. Canyon Wren home ranges are predicted to be large according to ecological and life history traits including small song repertoires and year-round residency (Jones and Dieni 1995, Benedict et al. 2013). Existing studies suggest that Canyon Wren home ranges are widely spaced and highly variable in size (Miller and Stebbins 1964, Mirsky 1976, Jones and Dieni 1995). Migratory Rock Wren home ranges are reported to be closely spaced (0.25–0.40 birds/ha) in areas with appropriate rock-strewn habitat (Hensley 1954, Lowther et al. 2000, Rossi and Knight 2006) or more widely spaced (0.1–0.2 birds/ha) in areas containing less rock (Walcheck 1970, Medin 1987, Rumble 1987). In our study area Canyon Wrens are permanent residents, while Rock Wrens are migrants, so interspecific territory overlap could occur if Rock Wrens settle on Canyon Wren home ranges during the breeding season.

Studying similarities and differences between co-occurring Canyon and Rock wren home ranges, proximity to conspecifics and heterospecifics, and habitat use for foraging will help us to

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assess how these wrens interact, and will provide information about space use and foraging strategies in exposed rock and cliff habitats. Cliff habitats are relatively understudied, and therefore we lack good estimates of avian space use within these ecosystems (Berry and Bock 1998, Larson et al. 2000, Rossi and Knight 2006). Furthermore, cliff habitats are relatively structurally simple and typically house unique but sparse vegetation, providing limited foraging microhabitats (Cooper 1997, Matheson and Larson 1998). Distinct foraging preferences may allow similar species to avoid competing even on overlapping home ranges, but such resource partitioning may be difficult in structurally simple habitats (Gorton 1977, Navarro et al. 2009).

Our objectives in this study were 1) to estimate home range sizes for Canyon and Rock wrens, 2) to assess the degree to which their home ranges overlap within and between species, and 3) to assess fine-scale resource use within rocky cliff habitats by measuring foraging microhabitat locations for each species.

METHODS

We monitored 13 Canyon Wren and 21 Rock Wren pairs between April and September in 2012 ($n = 12$ Canyon Wren pairs, 15 Rock Wren pairs) and 2013 ($n = 1$ Canyon Wren pair, 6 Rock Wren pairs). The study area encompassed 14 km² of montane shrublands on public lands in Larimer County, CO near Fort Collins (40° 31.56' N, 105° 09.29' W) containing cliffs, escarpments, and rocky slopes with vegetative cover dominated by mountain mahogany (*Cercocarpus montanus*), three-leaf sumac (*Rhus trilobata*), and Rocky Mountain juniper (*Juniperus scopulorum*). We selected focal Canyon and Rock wren pairs based on initial surveys in April 2012 in which we identified singing males. The identities of territorial pairs were assessed through repeated site visits and simultaneous observations of adjacent territories. In addition, we color-banded 4 of 13 male Canyon Wrens and 8 of 21 male Rock Wrens for which we mapped home ranges. We used our observations of color banded individuals to confirm that members of both species stayed within well-defined local areas, and to support the use of site-based identification of unbanded pair identities.

We recorded GPS locations (UTM, NAD 1983, zone 13N) of wren pairs from 5 Apr to 30 Sept in 2012 and from 4 Apr to 2 Sept in 2013 using

handheld GPS units (Garmin International Inc., Olathe, KS, USA) accurate to within 3 m. We monitored both banded and unbanded pairs using burst sampling (regularly spaced, rapid sampling over a specified time period), and recorded locations at least 5 mins and 5 m apart during 1-hr focal observation periods throughout the entire study period (Swihart and Slade 1997, Barg et al. 2005, Frietas and Rodrigues 2012). Locations were recorded by waiting until the focal bird had moved away from a location point, and then approaching that point to collect a GPS point, always taking care not to interrupt the bird's natural movements. This method produced 12 ± 4 locations per visit, over at least seven site visits throughout the study period. When a wren location could not be reached (i.e., on an inaccessible cliff), we recorded the closest accessible GPS point and used a range-finder (Bushnell Outdoor Products, Overland Park, KS, USA) to determine the distance to the bird, and a compass (Suunto, Vantaa, Finland) to take the bearing, and estimated the location using the measure tool in Garmin BaseCamp (Garmin International Inc., Olathe, KS, USA). Ninety percent of data points represent bird locations, while 10 % are estimated.

We calculated home ranges in ArcGIS Version 10.0 (Esri 2010) using fixed kernel density estimators (Worton 1989). Kernel density interpolation is commonly used to display patterns of home range use (Barg et al. 2005, Laver and Kelly 2008), and allowed us to delineate core use areas and estimate the overlap between Canyon and Rock wren utilization distributions (UDs).

We used a bivariate normal density fixed kernel to construct the UD for each wren pair using the kernel density tool. We chose a single value bandwidth (smoothing parameter) for each species equal to the average distance traveled between contiguous sampling intervals based on our entire dataset (Laver 2005). We divided kernels into twenty regions of use, and considered the area inside the 95% isopleth (regions 1–19) as the home range boundary and the region within the 50% isopleth (regions 1–10) as the core area (Seaman and Powell 1996, Howell and Chapman 1997, Barg et al. 2005). We measured the two dimensional (area-based) intersection of fixed kernels by overlaying UD in ArcGIS as polygons, and calculating the area of overlap (Silverman 1986). To quantify overlap of kernel volumes we used the Volume of Intersection Index (VI; Seidel 1992, Millspaugh

TABLE 1. Canyon Wren ($n = 13$) and Rock Wren ($n = 21$) pair home range area estimates. Values are means \pm SD (with ranges in parentheses), and t and P show results of a Student's t -test comparing mean home range estimates between species.

Estimator	Canyon Wren (ha)	Rock Wren (ha)	t	P
95% fixed kernel ^a	5.6 \pm 2.0; (2.5–9.1)	4.1 \pm 1.2; (2.7–6.9)	$t_{33} = -2.6$	$P = 0.012^*$
50% fixed kernel ^a (ha)	0.65 \pm 0.41; (0.26–1.6)	0.53 \pm 0.21; (0.25–1.1)	$t_{33} = -1.1$	$P = 0.272$

^a The bandwidths for fixed kernels were based on the average distance between contiguous sampling locations for each species (Canyon Wrens = 49 m, Rock Wrens = 42 m).

et al. 2000) yielding overlap index values from 0–1. We used Student's t -tests to compare home range area estimates by species. In order to test for sampling bias we used standard linear regression to compare number of sampling points with area output, and we tested for an effect of year on home range size in Rock Wrens using a Student's t -test. We ensured that our data met statistical assumptions by checking for homogeneity of variances using a two-tailed F -test, and for normality using a Shapiro-Wilk test.

We determined the geographic center of each home range kernel and measured distances between centroids for which we mapped neighboring home ranges in a single year to determine the distance to nearest neighbor (Hayne 1949, Krebs 1999). We strove in each sampling year to map contiguous territories that accurately estimated territory spacing. All home range overlap measurements are from neighboring territories.

To examine microhabitat use by each species we assigned each of the burst sampling locations from 2012 in which a focal bird was foraging ($n = 2,700$ locations) into one of six categories: (1) boulder; upon or under large rocks ≥ 0.5 m diameter, (2) crevice; cracks in solid rock < 5 cm width, (3) cavity; gaps in solid rock ≥ 5 cm width, (4) talus/rubble; upon or under smaller rocks < 0.5 m diameter, (5) open ground; non-rock areas with soil or grasses, and (6) vegetation; contacting a shrub or tree. We totaled foraging locations by

pair (Canyon Wren; $n = 12$ pairs, Rock Wren; $n = 15$ pairs) and transformed the totals into percentages before analysis. We used a Pearson's chi-square test to compare contingency tables of the proportions of foraging locations for each species, considering each foraging location as biologically independent. All statistics were performed in JMP, v.9 (SAS Institute Inc. 2010).

RESULTS

Home Ranges

We collected from 18–93 location points for each wren pair, with similar sampling effort for Canyon Wrens (mean = 49 \pm 18 locations) and Rock Wrens (mean = 52 \pm 18 locations). Home range area was not significantly correlated with the number of location points ($r^2 = 0.07$, $F_{33} = 2.3$, $P = 0.14$), or with sampling year among Rock Wrens ($t_{20} = 1.2$, $P = 0.23$). The kernel bandwidth values, based on the average distance between sequential sampling locations, were 49 m for Canyon Wrens and 42 m for Rock Wrens.

Home range estimates for Canyon Wren pairs in our study population using 95% fixed kernels were significantly larger than those for Rock Wrens, while 50% fixed kernel (core areas) tended to be similar in size (Table 1). Hetero-specific UDs overlapped in 68% of cases by a mean volume of 28%, indicating considerable spatial overlap between Canyon and Rock wren

TABLE 2. Summary of mean overlap between mapped Canyon and Rock wren home ranges and their nearest conspecific or heterospecific neighbor, measured from the intersection of 95% fixed kernels and 50% fixed kernel utilization distributions (UDs).

Species Pairing	Frequency of 95% fixed kernel UD intersection ^a	VI ^b of intersecting UDs	Frequency of 50% fixed kernel intersection ^a	VI ^b of intersecting core areas
CANW-CANW	0% (0/13)	0%	0% (0/13)	0%
CANW-ROWR	68% (23/34)	28%	17% (6/34)	18%
ROWR-ROWR	33% (7/21)	19%	0% (0/21)	0%

^a The bandwidths for fixed kernels were based on the average distance between contiguous sampling locations for each species (Canyon Wrens = 49 m, Rock Wrens = 42 m).

^b VI = Volume of Intersection Index values (from 0–1) converted to percentages.

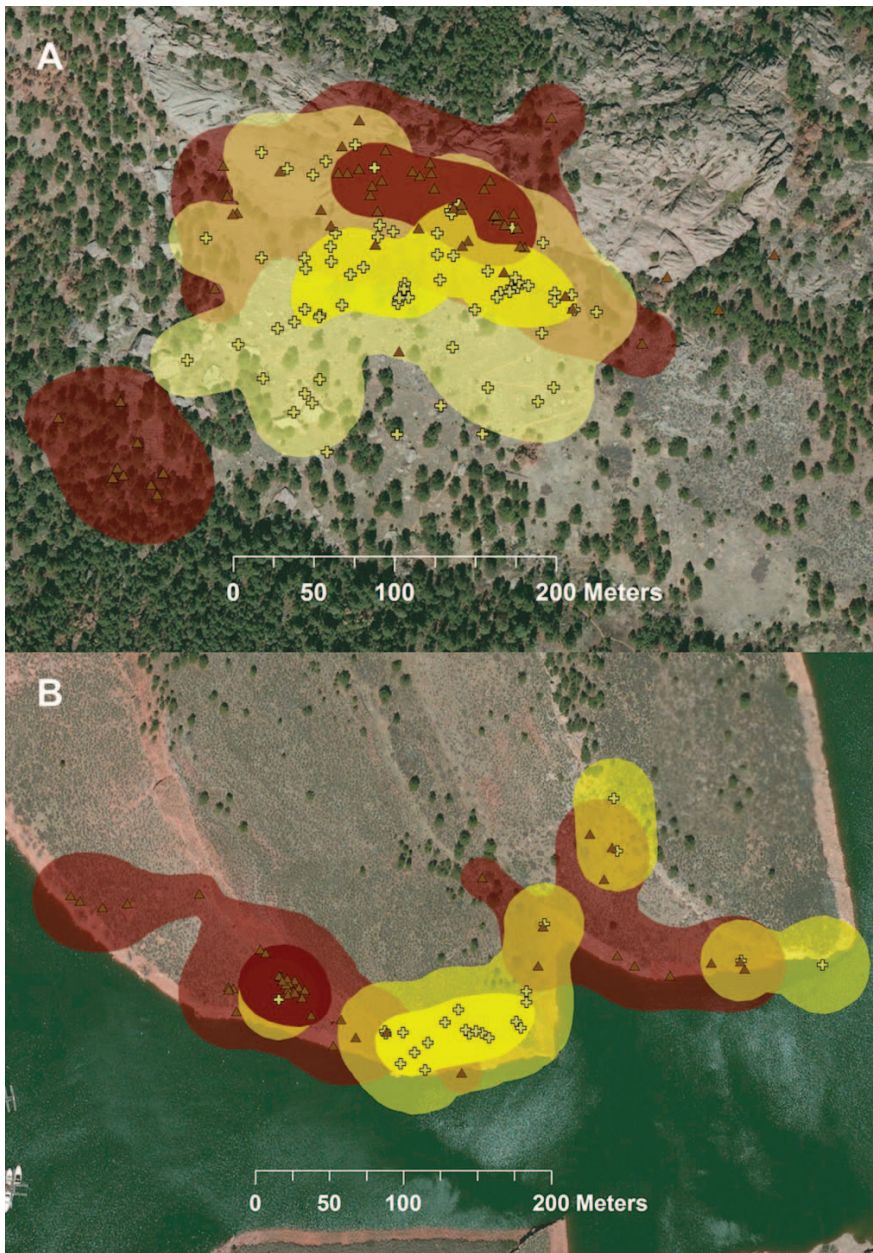


FIG. 1. Ninety-five percent fixed kernels and 50% fixed kernel utilization distributions for two different pairs of Canyon and Rock wrens in northern Colorado. Canyon Wren locations are shown as brown triangles, 95% kernels in light brown, and core use areas in dark brown. Rock Wren locations are shown as yellow crosses, 95% kernels in light yellow, and core areas in dark yellow. (A) Kernels overlap by 43%, and core areas overlap by 11%. (B) Kernels overlap by 36%, with non-overlapping core areas.

home ranges (Table 2). Within species, core use areas did not overlap, and between species they overlapped infrequently by an average of 18% volume (Table 2). In overlapping kernels, core

use areas typically differed between species, with Canyon Wrens using steeper cliff faces (3–30 m in height) and Rock Wrens using rock-strewn approach slopes with a less vertical component

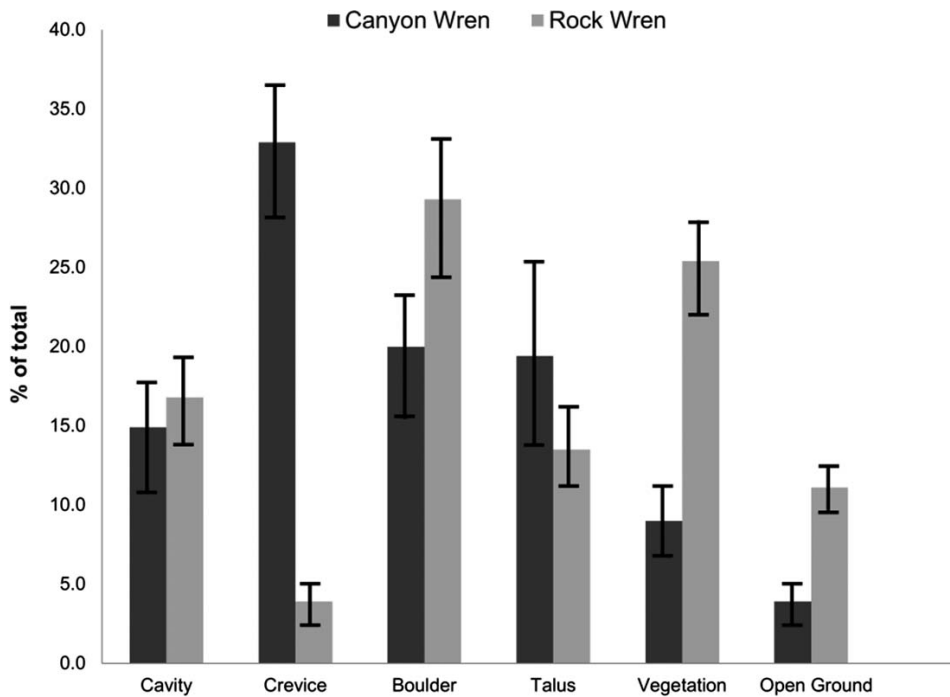


FIG. 2. Foraging microhabitat locations used by Canyon Wrens (dark grey bars; $n = 12$ pairs) and Rock Wrens (light grey bars; $n = 15$ pairs) from April–October 2012 expressed as mean percentages. Brackets indicate standard error. Overall foraging microhabitat use differed between species, $X^2_5 (n = 2,700) = 516, P < 0.001$.

(see Fig. 1 for examples). Core areas on average contained 46% of sampling points. Thus, non-core areas contained the majority of sampling points at which birds were observed.

Mean nearest neighbor distance was significantly different ($t_{18} = -4.2, P < 0.001$) between Canyon Wrens (986 m, SD = 638, $n = 5$) and Rock Wrens (216 m, SD = 96, $n = 14$). Mean interspecific nearest neighbor distance (between Canyon and Rock wrens) was 195 ± 148 m SD, $n = 11$.

Foraging Microhabitat

Both species were observed foraging in all six microhabitat types. Foraging comprised 53% of the location points recorded for Canyon Wrens, and 45% for Rock Wrens. In the remaining locations birds were recorded as either singing or perching. The percentages of foraging microhabitat locations used by Canyon and Rock wrens differed significantly between species ($X^2_5 = 516, P < 0.001$; Fig. 2).

DISCUSSION

Our 95% kernel density UD estimates revealed large, widely spaced Canyon Wren home ranges with no intraspecific overlap, and smaller, more

tightly spaced Rock Wren home ranges with minimal intraspecific overlap (Table 2). Patterns of overlap suggest that territory defense is expectedly strong within species (particularly within Canyon Wrens), but is weaker between species, since we had high rates of interspecific home range overlap. This result differs from results in similar systems, where closely related wren species do exclude each other from inter-specifically-defended territories (Farwell and Marzluff 2013, Battiston et al. 2015).

Core use areas (50% kernels) were similar in size between species, with very little overlap, suggesting that each species uses a similarly sized territorial core during the breeding season despite using different amounts of peripheral space around that principal area. Canyon Wrens may occupy larger home ranges because they are permanent residents who depend on their territories for winter as well as summer resources, while Rock Wrens need only defend enough space to provide resources during the breeding season (Lowther et al. 2000, Jones et al. 2002).

Our results suggest that Canyon Wren home ranges in Colorado are much larger than

previously reported (0.91 hectares in Jones and Dieni 1995), but are smaller than those reported in other locations (15–20 hectares in Miller and Stebbins 1964, Mirsky 1976). We expect that our results are more accurate than previous estimates, which were typically based on spacing between pairs rather than focal tracking of individuals. Our results provide the first estimates of Rock Wren home range sizes, and are consistent with previous reports of spacing between neighboring pairs. One limitation of our study is that it did not fully incorporate measures of the vertical component of Canyon and Rock wren home ranges (locations were highly accurate only in the x, y component), which may be an important measure of habitat use, particularly in areas containing very large cliffs and canyons. Recent advances in Lidar remote sensing may facilitate future studies that examine more precisely the full extent and partitioning of vertical space by these and other cliff-dwelling birds (Goetz et al. 2010, Broughton et al. 2012).

The partitioning of foraging locations suggests that Canyon and Rock wrens exploit shared resources in different ways. Although four of our six foraging categories included some type of rock microhabitat, they were used differently by members of the two species. Canyon Wrens are true rock specialists, expending roughly half of their foraging effort in crevices and cavities. Rock Wrens also foraged on all rocky substrates and supplemented that with nearly 40% of foraging events on open ground or in vegetation. Thus, the two species make use of these habitats in different ways, including by using the limited stands of vegetation that can be found in rock-strewn areas.

Competitive interactions tend to be proportional to the quality of the shared habitat (Sherry and Holmes 1988), and more research is needed to determine which habitat variables influence competition and home range formation in Canyon and Rock wrens. Migratory Rock Wrens settle territories after resident Canyon Wrens, but do not appear to avoid overlapping with them or settling in adjacent locations. This analysis provides an example of how different home range and foraging behaviors support coexistence in cliff-dwelling bird species with similar ecological demands.

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