RESEARCH ARTICLE

Cliff Attributes and Bird Communities in Jefferson County, Colorado

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ABSTRACT: Bird communities associated with differing cliff variables in Jefferson County, Colorado, were sampled using point counts. Species-specific density estimates and community diversity values were compared among four cliff types: small cliffs, medium cliffs, large cliffs, and non-cliff sites. A model selection was run to determine if cliff variables were associated with changes in species richness. Cliff variables included cliff height, cliff length, cliff verticality, cliff surface roughness, and distance to the nearest cliff. None of the cliff variables were good predictors of variability in species richness. Although no differences existed for bird community diversity estimates, there were significant differences in densities among cliff types for particular bird species. The rock wren (*Salpinctes obsoletus* Say), canyon wren (*Catherpes mexicanus* Swainson), violet-green swallow (*Tachycineta thalassina* Swainson), and white-throated swift (*Aeronautes saxatalis* Woodhouse) were detected more frequently at the large cliffs than the other cliff types (the differences for the canyon wren were not statistically significant). Larger cliffs appear to be necessary for these cliff-obligate species.

Index terms: bird communities, cliff ecology, cliffs, Colorado

INTRODUCTION

The Colorado Front Range, from Fort Collins to Colorado Springs, is one of the premier rock climbing areas in the United States. It is also one of the fastest growing regions in the country. With the increased popularity of rock climbing (Pyke 1997, Krajick 1999), as well as increasing recreation in general, land management agencies are now developing management plans to protect the plants and wildlife associated with cliff areas (Baker 1999). Despite the recreational pressures placed on cliffs, little is known of the role that cliffs play in defining the bird species diversity or species composition of the Colorado Front Range.

The presence of cliffs and rocky outcrops has been found to influence the composition of plant and animal communities (Rumble 1987, Ward and Anderson 1988, Camp and Knight 1997, Camp and Knight 1998, Matheson and Larson 1998, Larson et al. 2000). Indeed, cliffs and rocky outcrops may be classified as "keystone ecosystems," portions of landscapes that are particularly important for a given ecological or management issue (Stohlgren et al. 1997). Furthermore, because cliffs have largely been inaccessible to humans, they may serve as important refuges for native species (Larson et al. 1999, Larson et al. 2000).

Cliff environments, including escarpments, cliff faces, rocky outcrops, and talus at the base of cliffs, provide a unique habitat for wildlife (Maser et al. 1979, Larson et al. 2000). Ledges and pockets, as well as cracks, caves, and crevices, provide a variety of nesting and foraging areas for birds. Some species of birds are restricted to cliffs for critical periods of their annual cycle (e.g., nesting white-throated swifts (*Aeronautes saxatalis* Woodhouse) (Dobkin et al. 1986) and peregrine falcons (*Falco peregrinus* Tunstall) (Ratcliffe 1980).

In addition, because cliff ecosystems add structural heterogeneity to landscapes, they promote a biodiversity different from areas without cliffs (Camp and Knight 1997). Structural heterogeneity can be defined as different degrees of structural complexity of habitat (Stenseth 1980), including both horizontal and vertical variability (Roth 1976, Kolasa and Rollo 1991). Studies have found that bird species richness usually increases with increasing habitat heterogeneity (Roth 1976, Boecklen 1986, Finch 1989). Recent studies have shown that cliffs increase avian species diversity and alter species composition in structurally homogeneous areas such as the Mojave Desert (Camp and Knight 1997), sagebrush steppe (Ward and Anderson 1988), and continuous forest (Matheson and Larson 1998).

The Colorado Front Range is a topographically complex landscape with steep canyons leading into the Rocky Mountains. Elevation changes rapidly and the canyons form ridges with sharply contrasting plant communities. Because of varying environmental gradients, the forests and shrub communities are patchy (Berry and Bock 1998). Included in these Front Range forests and shrub communities are varying amounts of cliffs, ranging from large escarpments to smaller rock outcrops. These cliff ecosystems may differ from those of previous cliff studies, and the role of cliffs in more topographically diverse landscapes is unclear. Thus, it is difficult to apply generalizations from cliff studies done in more homogeneous landscapes to systems like the foothills of the Colorado Front Range (Hansen and Urban 1992).

The objectives of our study were to: (1) determine if species diversity and composition of bird communities associated with cliffs differed from bird communities in non-cliff areas, and (2) determine if cliff features were associated with changes in avian species richness and composition.

METHODS

Study Site and Design

All sites were located on Jefferson County Open Space properties, Jefferson County, Colorado, USA (39° 45'N, 105° 15'W). The climate was continental with an average daily temperature in Evergreen, Colorado, of 20.5 C° in the summer and 0 C° in the winter (Price and Amen 1983). The average yearly precipitation was 46 cm with 70% falling in April through September (Price and Amen 1983). The elevation for all sites was between 1900 m and 2400 m.

Our study sites were located on the southern-facing hillsides of canyons running west into the mountains. Both elevation and aspect are variables known to affect vegetation composition (Peet 1988) and were therefore restricted to minimize variation among cliff sites and non-cliff sites. These south-facing slopes were xeric with mountain mahogany (*Cercocarpus montanus* Raf.), Rocky Mountain juniper (*Sabina scopulorum* Sarg.), and some ponderosa pine (*Pinus ponderosa* Doug.). Detailed vegetation information can be found in Graham and Knight (2004).

The study design followed a non-replicated randomized complete block (Zar 1999) with six canyons representing the blocks. Four cliff types were sampled within the canyons: small cliffs (>5 m and <10 m high), medium cliffs ($\geq$10 m and <20 m high), large cliffs ($\geq$20 m high), and non-cliff sites. The sample size was five small cliffs, five medium cliffs, six large cliffs, and six non-cliff sites (*n* = 22 sites). The unbalanced nature of this design resulted because it was not possible to locate a small or medium cliff in Ralston Canyon, which only had a non-cliff site and Ralston Buttes as a large cliff site. Ralston Buttes is approximately 800 m long and was therefore magnitudes larger than the other large cliffs, with the next largest cliff only 108 m long. Therefore, sampling was slightly different at Ralston Buttes (see below). Cliffs were defined as an exposed rock face greater than 5 m high with a minimum overall verticality of 50°. Non-cliff sites were defined as the nearest slope at least 100 m from cliffs with a similar aspect (southeast to southwest) and elevation. The large cliffs represent a census of all possible south-facing large cliffs on Jefferson County Open Space properties. Small and medium cliffs were chosen randomly from all possible cliffs with a southern aspect. There was no evidence of rock climbing on any of the cliffs.

Bird Sampling

Sampling of birds took place in May and June of 1998 and 1999 using variable-distance point counts truncated at 50 m. Point counts were 8-minutes long following an initial 4-minute settling period. The species and distance to all birds seen or heard within 50 m of the point were recorded. Point counts were conducted between 0600 and 1000 MST when the birds were most active (Bibby et al. 1992). Counts were not conducted during periods of precipitation or high wind. Points at cliff sites were located 20 m down slope from a random point along the cliff base. Sampling points at non-cliff sites were located using a random compass bearing and distance upon entering the site. All cliff sites and non-cliff sites were sampled with one point count location, except for Ralston Buttes (due to its length) which was sampled by eight point count locations 100 m apart along the base.

Two observers in 1998 and 1999 conducted the counts. Points were revisited three times in 1998 and five times in 1999. To avoid biases associated with early and late breeding season or time of day, the order of the first series of counts was chosen randomly and later visits reversed the order in which each point was revisited. To reduce problems with observer bias, we practiced identification and distance estimation for two weeks prior to data collection for each field season. Known distances were flagged 20 m and 40 m away from the sampling points to aid in distance estimation.

Measurement of Cliff Variables

Five variables (cliff length, height, verticality, cliff surface roughness, and mean nearest-neighbor distance) were measured for all cliff sites (Table 1). The variables cliff length, height, verticality, and cliff surface roughness were defined a priori. Nearest-neighbor distance among cliffs was recognized as a variable of interest after realizing that cliff sites did not occur in isolation. Thus, nearest-neighbor distance was used as a measure of proximity of the sites to other cliffs. Cliff length was measured by walking the base of the cliff with a GPS unit (Trimble Pro XRS) and calculating the length in ArcView GIS. Using a GPS, cliff height was calculated as the maximum difference between the minimum base elevation and maximum top elevation. Cliff verticality was measured with a clinometer at intervals along the cliff base. A mean verticality was then calculated. Cliff surface roughness was measured while on rappel using the methods of Matheson and Larson (1998). A measuring tape was held parallel to the cliff surface and the distance from the measuring tape to the surface was measured at 1-m intervals. This process provided a profile of cliff topography along each rappel transect. Three rappel transects were sampled for the large cliffs, two for medium cliffs, and one for small cliffs. Rappel transects were chosen randomly from all possible safe anchor locations. The percent coefficient of variance (%CV) was calculated for each transect, and then a mean was calculated for each cliff. A sample with a high %CV indicates a more heterogeneous surface relative to a sample

Table 1. Cliff variable measurements (mean ± SE) for small, medium, and large cliffs studied in association with bird communities in Jefferson County, Colorado, 1998-1999.

	Cliff Variable				
Cliff-type	Height (m)	Length (m)	Verticality (°)	Surface-roughness (%CV)	Nearest-neighbor (m)
Small	7.20 ± 0.86	12.43 ± 2.23	61.53 ± 5.20	94.71 ± 14.09	81.32 ± 29.78
Medium	15.20 ± 0.80	31.80 ± 6.97	61.17 ± 2.76	101.23 ± 20.55	27.12 ± 4.76
Large*	39.80 ± 8.11	77.24 ± 13.74	68.12 ± 4.71	110.60 ± 5.98	49.04 ± 13.38

* Data for Ralston Buttes are not included.

with a low %CV. Nearest-neighbor distance was defined as the mean nearest-neighbor distance to the five closest cliffs larger than 5-m high. Distances were measured using a laser rangefinder (Bushnell YardagePro Laser Rangefinder 400).

Statistical Analyses

Bird species richness and species densities were assessed for each point. Detailed descriptions of how richness and density were calculated can be found in Graham (2000). Detection rates may vary among bird species (Boulinier et al. 1998); therefore, species-specific detection functions and densities (D_i) were estimated using distance-sampling methods (Buckland et al. 1993). Detection functions and densities were calculated using Program DISTANCE 3.5 (Thomas et al. 1998). Program DISTANCE was only used for those species, or groups of species with similar detection functions, with more than 40 detections over the two years. Data were entered as "exact," but were grouped in distance categories within the analyses to reduce bias associated with distance estimation.

Pooling across all species, there were sufficient detections of birds (excluding violet-green swallows (*Tachycineta thalassina* Swainson), white-throated swifts, and broad-tailed hummingbirds (*Selasphorus platycercus* Swainson)) to estimate separate detection functions (with associated effective detection radii, densities, and confidence intervals) for observers, cliff types, and canyons. Detection functions were also estimated for each cliff type and each canyon. Densities were then estimated for all possible species at each point count location except for Ralston Buttes. An average species density was calculated across the eight Ralston Buttes point counts and then included in the analysis as a data point for the large cliff type.

Densities of violet-green swallows and white-throated swifts were not estimated because these species do not fit the assumptions of distance sampling (Buckland et al. 1993). These birds were most often detected flying in a group overhead making it impossible to estimate an exact distance to the initial detection location. Therefore, the total number of point count visits on which these birds were detected was recorded. For Ralston Buttes, a detection was recorded if at least one bird was observed at any one of the eight point count sites. Because some of the frequency values were less than five, a Fisher's exact test (Zar 1999) was conducted on the observed versus expected counts of the violet-green swallow and the white-throated swift detections using PROC FREQ (SAS Institute 1990) in SAS version 6.12 for Windows. Pairwise comparisons were then made between cliffs, also using Fisher's exact tests. These analyses do not adjust for differences among canyons and may have violated the assumption of independence because of repeated measures within a canyon.

Hill's family of diversity numbers (N_0, N_1, and N_2) (Hill 1973) was used to describe community diversity as recommended in Ludwig and Reynolds (1988). All the diversity numbers calculated for this study represent within-habitat (alpha) diversity. Species richness corresponds to Hill's N_0. N_2 is a dominance measure whereas N_1 weights the abundances of rare species more (Magurran 1988, Krebs 1999). All diversity numbers were calculated for each of the 22 sites.

Species richness was calculated in two ways: observed species richness and estimated species richness. Observed species richness was defined as the number of species within 50 m of the plot center; the effective detection radius for 9 of 11 of the species or species groups with similar detectability was 50 m. The species richness of Ralston Buttes was calculated as all species detected at the eight count sites along the base of the cliff. Species richness was also estimated to account for the fact that not all species were detected at each point count because of possible differing species detectabilities (Boulinier et al. 1998).

To test for differences in diversity and in species densities among cliff types, ANOVA analyses were run in PROC MIXED (Littell et al. 1996). The data were analyzed using a two-factor mixed model with cliff type as the fixed effect and canyon as a random effect. An $\alpha = 0.10$ was chosen a priori to reduce the likelihood of committing a Type II error. Committing a Type II error, or concluding no difference when in fact a difference does exist, can be more costly than committing a Type I error when management will be based on the conclusions. Mean values and 90% confidence intervals by cliff type were calculated using

LSMEANS in PROC MIXED (Littell et al. 1996). These data are more meaningful than p-values alone (Johnson 1999). Based on F-protected pairwise t-tests, pairwise comparisons were made only if the overall ANOVA F-test was significant. N_0, N_1, N_2 and density estimates were natural logs transformed to better meet the assumption of homogeneity of variance and normality. However, ANOVA analyses are robust to violation of normality and homogeneity of variance (Zar 1999).

To determine if the measured cliff features were associated with increased species richness, a multiple regression was run with estimated species richness as the response variable and the canyon dummy variables, cliff height, length, verticality, cliff surface roughness, and nearest-neighbor distance as the predictor variables. Model selection with the same predictor variables was also completed for the rock wren (*Salpinctes obsoletus* Say), and the canyon wren (*Catherpes mexicanus* Swainson), both of which showed a difference in densities (birds/ha) among cliff types. Model selection was completed in SAS with PROC REG (SAS Institute 1990). Data from Ralston Buttes were excluded because the length data point (800 m) is an outlier and could have influenced the multiple regression.

RESULTS

A total of 1631 detections of birds within 50 m of the survey points were recorded for 41 species in 1998 and 45 species in 1999.

Species Composition

There were sufficient observations to estimate the detection functions for 11 species (Table 2). Two of these species had significantly different densities among cliff types, while nine did not differ among the three different cliff types and non-cliff sites (Table 2). Rock wrens were detected at higher densities on the medium and large cliffs (MIXED ANOVA: $F_{3,13}$ = 4.05, P = 0.03). Although not significant at α = 0.10, canyon wrens were also found at higher densities at the large cliffs (MIXED ANOVA: $F_{3,13}$ = 2.16, P = 0.14). With the

Table 2. Mean bird species density (birds/ha) with 90% confidence intervals by cliff type, in Jefferson County, Colorado, 1998-1999. The densities were estimated by Program DISTANCE 3.5 (Thomas et al. 1998) and then means and confidence intervals estimated in PROC MIXED LSMEANS in SAS 6.12 (SAS Institute 1990). The data, which are presented back-transformed from natural log (density + (0 to 0.5)), are biased low, but are less variable than natural log values. Densities from Ralston Buttes are included in the means for the large cliffs.

	Cliff Type			
Species	Non-cliff	Small	Medium	Large
Species combined	7.40 (5.76, 9.51)	7.21 (5.47, 9.52)	6.49 (4.92, 8.57)	5.79 (4.51, 7.44)
American robin				
Turdus migratorius (Linnaeus)	0.36 (0.13, 0.73)	0.23 (0.04, 0.53)	0.21 (0.03, 0.51)	0.17 (0.01, 0.43)
Blue-gray gnatcatcher				
Polioptila caerulea (Linnaeus)	0.25 (0.00, 0.75)	0.37 (0.01, 1.23)	0.30 (0.02, 0.85)	0.24 (0.00, 0.73)
Canyon wren	0.00 (0.00, 0.15)	0.03 (0.00, 0.21)	0.00 (0.00, 0.17)	0.29 (0.11, 0.53)
House wren				
Troglodytes aedon (Vieillot)	0.15 (0.00, 0.47)	0.22 (0.00, 0.65)	0.12 (0.00, 0.47)	0.10 (0.00, 0.38)
Green-tailed towhee				
Pipilo chlorurus (Audubon)	0.44 (0.18, 0.90)	0.72 (0.31, 1.49)	1.03 (0.47, 2.08)	0.69 (0.32, 1.34)
Lazuli bunting				
Passerina ameona (Say)	0.31 (0.01, 0.98)	0.13 (0.00, 0.65)	0.18 (0.00, 0.77)	0.30 (0.00, 0.96)
Rock wren*	0.00 (0.00, 0.15)	0.08 (0.00, 0.28)	0.36 (0.14, 0.64)	0.38 (0.18, 0.64)
Spotted towhee*	1.20 (0.48, 2.65)	0.84 (0.28, 1.99)	0.48 (0.10, 1.25)	0.47 (0.11, 1.19)
Steller's jay				
Cyanocitta stelleri (Gmelin)	0.16 (0.01, 0.40)	0.50 (0.20, 1.00)	0.20 (0.02, 0.51)	0.15 (0.00, 0.39)
Virginia's warbler				
Vermivora virginiae (Baird)	0.48 (0.20, 0.92)	0.57 (0.23, 1.12)	0.76 (0.35, 1.46)	0.25 (0.06, 0.56)
Western tanager				
Piranga ludoviciana (Wilson)	0.20 (0.05, 0.39)	0.11 (0.00, 0.29)	0.07 (0.00, 0.24)	0.14 (0.01, 0.32)

* MIXED ANOVA fixed effects F-Test significant at α = 0.1

exception of one detection at a small cliff, the canyon wren was only found at the large cliffs. On the other hand, the spotted towhee (*Pipilo maculatus* Swainson) was found in higher densities at non-cliff sites (MIXED ANOVA: $F_{3,13} = 3.01$, $P = 0.07$). In addition, a mixed model ANOVA was run on the total densities of all birds combined (excluding violet-green swallows, white-throated swifts, and broad-tailed hummingbirds). There were no significant differences among total bird densities at different cliff types (MIXED ANOVA: $F_{3,13} = 0.64$, $P = 0.60$).

Violet-green swallows were not detected equally among cliff types (PROC FREQ, Fisher's Exact Test: $P < 0.001$). Swallows were detected more at the large cliffs (Figure 1) than other cliff types. White-throated swifts were also detected in unequal numbers among cliff types (PROC FREQ, Fisher's Exact Test: $P < 0.001$). With the exception of two detections, swifts were only detected at the large cliffs (Figure 1).

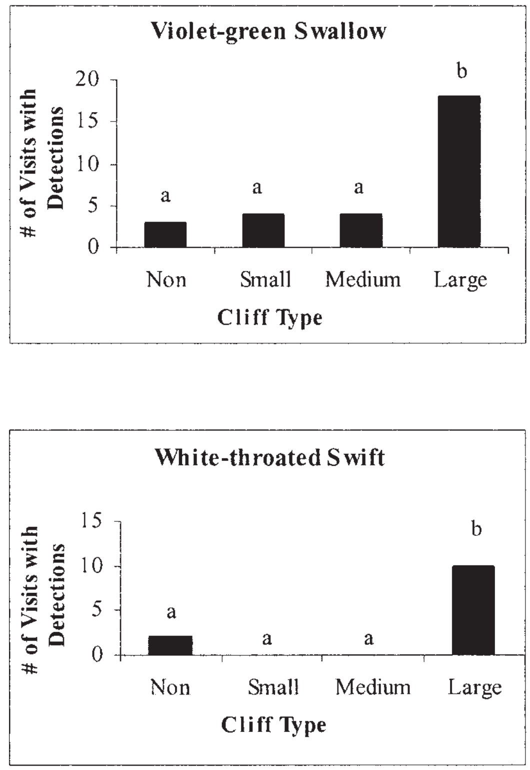

Figure 1. Number of point count visits on which violet-green swallows or white-throated swifts were detected by cliff type in Jefferson County, Colorado, 1998-1999. A detection was recorded for Ralston Buttes if at least one bird was detected at any of the eight count sites. Letters indicate a difference at $\alpha = 0.1$.

Community Diversity

In mixed model two-factor ANOVAs with cliff type as the fixed factor and canyon as the random factor, there were no significant differences by cliff type for any of the Hill's (1973) diversity values (Table 3). Ralston Buttes is included in the mean for the large cliffs. Mean species richness (N_0) did not differ among cliff types for either observed species richness (MIXED ANOVA: $F_{3,13} = 0.15$, $P = 0.93$) or estimated species richness (MIXED ANOVA: $F_{3,13} = 0.19$, $P = 0.90$). N_1 diversity values did not differ among cliff types (MIXED ANOVA: $F_{3,13} = 0.12$, $P = 0.95$). Nor did N_2 diversity values differ among cliff types (MIXED ANOVA: $F_{3,13} = 0.42$, $P = 0.74$).

The analyses were also run without the Ralston canyon data for two reasons. First, it was not possible to locate a small or medium cliff in this canyon; thus, the variance associated with this canyon is only estimated with two sites. Second, with a length over 800 meters long, the large cliff was much larger than the other large cliffs. However, excluding Ralston did not change the results (Table 4). Mean species richness (N_0) did not differ among cliff types for either observed species richness (MIXED ANOVA: $F_{3,12} = 0.96$, $P = 0.44$) or estimated species richness (MIXED ANOVA: $F_{3,12} = 1.01$, $P = 0.42$). N_1 diversity values did not differ among cliff types (MXED ANOVA: $F_{3,12} = 0.47$, $P = 0.71$). Finally, N_2 diversity values did not differ among cliff types (MIXED ANOVA: $F_{3,12} = 0.47$, $P = 0.71$).

Model Selection on Cliff Variables

A model selection on cliff variables was run to determine if cliff features were associated with increasing species richness. The unit of analysis was each cliff and the response variable was estimated species richness. The predictor variables were canyon dummy variables (Bear Creek (BC), Coal Creek (CC), Mount Falcon (MF), and Mount Morrison (MM)), cliff length, height, verticality, cliff surface roughness, and nearest-neighbor distance. The model chosen included only nearest-neighbor distance (PROC REG: ln(richness) = 2.769 – 0.002*nearest-neighbor, $R^2 = 0.07$). However, this model only explains 7% of the variability in species richness. Thus, none of the cliff variables were good predictors of avian species richness.

Separate model selections were also completed with the rock wren densities (birds/ha) and canyon wren densities (birds/ha) as response variables and the canyon dummy variables, cliff length, height, verticality, cliff surface roughness, and nearest-neighbor distance as the predictor variables. The model selected for the rock wren included the canyon dummy variables, verticality, surface roughness, and nearest-neighbor distance (PROC REG: ln(density + 0.5) = –2.181 + 0.366*BC + 0.691*CC – 0.003*MF + 0.660*MM

Table 3. Mean Hill's (Hill 1973) diversity numbers N_0 (observed and estimated), N_1, and N_2 by cliff-type with 90% confidence intervals for birds in Jefferson County, Colorado, 1999. Estimated N_0 values were estimated according to Boulinier et al. (1998). Means and confidence intervals were estimated by PROC MIXED LSMEANS and are presented back-transformed from a natural log transformation, thus they are biased low but less variable. The means for the large included Ralston Buttes.

	Hill's Numbers			
Cliff-type	Observed N_0	Estimated N_0	N_1	N_2
Non-cliff	10.40 (7.97-13.57)	14.98 (10.26-21.88)	19.76 (13.25-29.46)	6.21 (4.75-8.12)
Small	10.44 (7.78-14.01)	13.81 (9.06-21.06)	21.71 (14.00-33.68)	6.98 (5.20-9.37)
Medium	11.88 (8.85-15.94)	17.31 (11.35-26.40)	23.81 (15.35-36.93)	7.89 (5.88-10.60)
Large	10.98 (8.42-14.32)	14.77 (10.11-21.58)	22.85 (15.33-34.09)	7.38 (5.64-9.65)

+ 0.021*verticality + 0.006*roughness – 0.006*nearest-neighbor, R^2 = 0.83). The model selected for the canyon wren included all variables: the canyon dummy variables, length, height, verticality, surface roughness, and nearest-neighbor distance (PROC REG: ln(density + 0.5) = 0.814 + 2.234*BC – 0.053*CC + 0.718*MF + 0.520*MM – 0.017*length + 0.044*height – 0.015*verticality – 0.007*surface roughness – 0.008*nearest-neightbor, R^2 = 0.98). These models suggest that no variable alone is a good predictor of rock wren or canyon wren densities.

DISCUSSION

Species Composition

Our study confirms that certain birds are associated with cliffs. These birds include the canyon wren, rock wren, white-throated swift, and violet-green swallow. In our study, canyon wrens were primarily detected at the larger cliffs. Rock wrens are also known to be associated with cliffs and rocky outcrops (Rumble 1987, Merola 1997). Rock wren densities were significantly higher at the medium and large cliffs than the small cliffs and non-cliff sites. Rumble (1987) also found higher rock wren densities at sites with larger rock outcrops than small outcrops. White-throated swifts, which were also detected more at the large cliffs, are cliff obligates (Kingery 1998). Violet-green swallows nest in trees as well as cliffs (Brown et al. 1992); however, in the open habitats of our study, they were detected more at large cliffs than the other cliff types or non-cliff sites.

Community Diversity

Our results showed no differences for Hill's (1973) family of diversity numbers (observed N_0, estimated N_0, N_1, and N_2) among cliff types. Furthermore, in a model selection with estimated species richness (N_0) as the response variable, the best model (minimum AIC) included only nearest-neighbor distance, which is a measure of cliff isolation from other cliff sites. Thus, the model chosen includes more of a landscape measure than variables directly associated with cliff size; however, this model only explains 7% of the variability.

The result of no difference in species diversity among cliff sites and non-cliff sites differs from other studies. For example, Ward and Anderson (1988), Camp and Knight (1997), and Matheson and Larson (1998) all found enhanced bird species richness at cliff sites as opposed to non-cliff sites. These authors suggested that cliffs added structural diversity to a landscape, which then increased bird species richness. In more homogeneous environments like the Mojave Desert (Camp and Knight 1997) or sagebrush steppe (Ward and Anderson 1988), cliffs would likely add both vertical and horizontal structure. The foothill canyons of Jefferson County, Colorado, however, are both vertically complex, with rapidly increasing elevation and forest structure, and horizontally complex, with a

Table 4. Ralston Canyon data excluded, mean Hill's (Hill 1973) diversity numbers N_0 (observed and estimated), N_1, and N_2 by cliff-type with 90% confidence intervals for birds in Jefferson County, Colorado, 1999. Estimated N_0 values were estimated according to Boulinier et al. (1998). The means and confidence intervals were estimated by PROC MIXED LSMEANS and are presented back-transformed from a natural log transformation, thus they are biased low but are less variable.

	Hill's Numbers			
Cliff-type	Observed N_0	Estimated N_0	N_1	N_2
Non-cliff	11.25 (8.79-14.41)	17.44 (11.79-25.82)	22.75 (15.63-33.11)	6.75 (5.25-8.67)
Small	10.04 (7.80-12.94)	13.40 (8.97-20.03)	20.71 (14.11-30.39)	6.94 (5.39-8.92)
Medium	12.22 (9.48-15.74)	18.00 (12.05-26.90)	24.91 (16.97-36.55)	7.94 (6.17-10.21)
Large	9.39 (7.33-12.03)	13.00 (8.78-19.24)	18.41 (12.65-26.79)	6.33 (4.93-8.13)

matrix of mixed forests and shrublands.

Management Implications

Humans have largely neglected cliff environments because of their inaccessibility. For this reason, Larson et al. (1999, 2000) believe that cliffs may serve as important refuges for native species. With the increased popularity of rock climbing, these vertical ecosystems are experiencing a marked increase in use. Canyon wrens, rock wrens, and white-throated swifts were particularly associated with larger cliffs in our study. In addition, these birds were found in relatively low densities as compared with other species. Our results agree with studies in different environments that found regional scarcity in several bird species that use a rare and local habitat type (Kolasa 1989, Haney 1999). Thus, large cliffs may be necessary for the presence of these species along the Colorado Front Range. In addition, the fact that canyon differences were important in the regression models for the canyon wren and rock wren suggests that canyons are not simple replicates of each other, but need to be considered as a collective resource. In addition, because the canyons are different in terms of species richness and species composition, management should focus at a larger scale than simply a cliff-by-cliff perspective. A larger scale would actually be more appropriate considering that trails leading to cliffs and human presence in the general vicinity would affect a much larger area than a single cliff. Furthermore, humans can help spread non-native plant species. McMillan and Larson (2002) found a much higher proportion of exotic species at climbed cliffs than non-climbed cliffs. It would be prudent for managers to continue to assess cliff habitat ecology as well as the possible impacts of rock climbing on cliff-obligate species.

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