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A comparison of avian use of high- and low-elevation sites during autumn migration in central New Mexico

John P. DeLong,[1,3] Steven W. Cox,[2] and Nancy S. Cox[2]

[1] *HawkWatch International, Inc., 1800 South West Temple, Suite 226, Salt Lake City, Utah 84115 USA*
[2] *Rio Grande Bird Research, Inc., 4426 San Isidro NW, Albuquerque, New Mexico 87107 USA*

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ABSTRACT. We compared the migratory bird assemblage at a high-elevation site in central New Mexico (Capilla Peak in the Manzano Mountains) with the bird assemblage at a low-elevation riparian corridor site (Rio Grande Nature Center State Park in Albuquerque). During fall 2001–2003, we used mist nets to sample these bird assemblages. We found greater species richness at the low-elevation site than at the high-elevation site, both overall and for most migratory and resident subgroups. However, at the high-elevation site we captured more species that may have had local origins at high elevations. Over the course of the study, capture rates were similar between sites, but there was greater annual variation in capture rates at the high-elevation site than at the low-elevation site. Several species were captured at higher rates at one site versus the other, and some were captured strictly at one or the other site. Our data showed that both sites supported many species in large numbers, and both riparian and montane habitats in the southwestern U.S.A. should be recognized for their importance as potential stopover sites for migrating birds.

SINOPSIS. **Comparación de localidades a elevaciones altas y bajas durante la migración otoñal en la parte central de New México**

Comparamos el ensamblaje de aves migratorias en una localidad de alta elevación en la parte central de New México, (pico Capilla en las montanas Manzano) con el ensamblaje en una localidad baja del corredor ripario en el Rio Grande Nature Center State Park, en Albuquerque. Durante el otoño de 2001–2003, utilizamos redes de niebla para estudiar las aves. Encontramos mayor riqueza de especies a elevaciones bajas, que en las altas, tanto entre aves migratorias como en aves locales (residentes). Sin embargo, a mayor elevación capturamos más especies de la localidad (residentes). A lo largo del estudio, la tasa de captura fue igual para ambas localidades, pero hubo mayor variación anual en la tasa de captura en los lugares más elevados, al compararlos con los bajos. Algunas especies fueron capturadas con mayor frecuencia en una localidad que en la otra, y algunas fueron estrictamente capturadas en una de estas. Nuestros datos muestran que ambas localidades mantienen muchas especies y en números altos, y ambos tipos de hábitats deben ser reconocidos, por su importancia, como lugares de parada por parte de migratorios.

Key words: migration, migration strategy, neotropical migrant, stopover, stopover habitat

Migratory birds make use of a variety of habitats during their journey between breeding and non-breeding areas. These stopover sites are places where birds may forage and accumulate energy reserves prior to making additional migratory flights (Alerstam and Hedenström 1998). Consequently, habitats used as stopover sites may be of critical importance to the survival or health of migrating birds (Hutto 2000). Some habitats may be relatively important for particular species, while other habitats may have little value in providing necessary food resources or protection from predators (Yong et al. 1998). Mortality rates of migratory birds may be relatively high during the migration period (Sillett and Holmes 2002), so identifying and conserving key stopover habitats is a critical component of migratory bird conservation (Finch and Yong 2000; Hutto 2000).

In the deserts of the American Southwest, major riparian corridors may provide important stopover habitats for migrating songbirds. Data from several studies demonstrate that there are diverse and abundant migratory bird communities in riparian corridors during both spring and fall migration (Skagen et al. 1998; Yong et al. 1998; Finch and Yong 2000; Yong and Finch 2002; Krueper et al. 2003). Migrating birds also may use relatively xeric riparian areas such as desert washes (Hardy et al. 2004). It has been suggested that migrating songbirds

[3] Corresponding author. Current address: Eagle Environmental, Inc., 2314 Hollywood Avenue NW, Albuquerque, New Mexico 87104 USA. Email: jpdelong@comcast.net

funnel into major riparian corridors from drier, less hospitable upland habitats, causing major riparian corridors to harbor relatively high densities of migratory songbirds (Yong and Finch 1997). In Arizona, Stevens et al. (1977) found a greater abundance of migrating songbirds in riparian habitats than in neighboring upland habitats.

Yet, the distribution of migrating songbirds across the southwestern landscape has been studied relatively little, and the abundance of migrating songbirds in southwestern upland habitats (particularly forested uplands) is poorly understood (Hutto 1985). A few studies have documented the presence of migrating songbirds in southwestern upland areas (Swarth 1908; Austin 1970; Blake 1984; Hutto 1985; Puschock 1998), but much remains to be learned about migratory songbird stopover outside of riparian areas in the southwest.

Upland habitats such as grassland, shrub-steppe, and montane forest cover large portions of the southwestern landscape (Dick-Peddie 1993). If migrating birds stop over in these habitats at even relatively low densities, significant portions of the migratory songbird populations could be using upland habitats. If so, upland habitats may merit significant conservation attention in terms of managing for migratory bird populations. Yet, even coarse-scale data comparing migratory bird use of upland and riparian valley habitats is lacking (Stevens et al. 1977), so there is little basis for assigning conservation priorities to any particular stopover habitat in the southwestern U.S. Here we describe and compare the avian communities at a high-elevation montane stopover site and a low-elevation riparian corridor in central New Mexico. We describe species richness, species similarity, and capture rates for the two sites to evaluate the possibility that montane habitats also could provide important migratory stopover areas for passerines.

METHODS

High-elevation site. The high-elevation study site was located at Capilla Peak (34°42′N, 106°24′W) in the Manzano Mountains in the Cibola National Forest, approximately 56 km south-southeast of Albuquerque, New Mexico. The study site is centered on an approximately 4.3-ha grazed montane grassland meadow straddling the ridge just south of Capilla Peak. Surrounding the meadow are stands of trees and shrubs, primarily ponderosa pine (*Pinus ponderosa*), Gambel's oak (*Quercus gambeli*), quaking aspen (*Populus tremuloides*), white pine (*Pinus* sp.), and Douglas-fir (*Pseudotsuga menziesii*). There is a small, ephemeral spring on the northeast side of the study area, located within an approximately 0.1-ha meadow and surrounded by a mixture of oak, pine, and Douglas-fir woodland. This spring is the only natural source of water in the study area, and it usually is not running. Average elevation at the site is approximately 2800 m. Human activity at the site is high for this type of location, with a gravel road dissecting the site and a fire-lookout tower, campground, and astronomical observatory all located within 0.5 km of the center of our study site.

Low-elevation site. The low elevation site was located at the Rio Grande Nature Center State Park (Nature Center; 35°07′N, 106°41′W) in Albuquerque, New Mexico. The site is a disturbed riparian woodland, consisting primarily of cottonwood (*Populus deltoides*) with Russian olive (*Elaeagnus angustifolia*), New Mexico olive (*Forestiera neomexicana*), and willow (*Salix exigua* shrubs and *S. gooddingii* trees) understory and edge thickets. The site also includes agricultural fields to the east of the woodland areas. There are drainage ditches and additional cottonwood gallery forest to the west. There are two human-made ponds within the woodland area and two additional ponds in the adjacent agricultural habitat. Average elevation at the site is approximately 1500 m. Human activity at this site is very high, with heavy foot traffic along the paths to the Nature Center and vehicle traffic entering and exiting the parking lot. There is also a foot and bicycle path along the west edge of the site that is heavily used. The Nature Center site is well known for its abundance of migrating birds during spring and fall (Yong and Finch 1997; Yong et al. 1998; Kelly et al. 2000).

Field methods. During fall 2001–2003, we conducted mist-netting programs at both sites. We opened mist-nets (30–36 mm mesh nets) two consecutive days per week from late August through late October (Saturday and Sunday at the low-elevation site and Monday and Tuesday at the high-elevation site), except during periods of rain, snow, fog, or high

winds. Closure of nets due to bad weather conditions occurred more often at the high-elevation site than at the low-elevation site. At the high-elevation site, nets were placed in each of five distinguishable vegetation types in the area (aspen, ponderosa pine, oak, Douglas-fir, and meadow), along the forest/meadow edge, and along the inside edges of the spring meadow. Standard net distribution across habitat type was aspen (three), ponderosa pine (two), oak (five), fir (one), meadow (three), forest/meadow edge (one), and spring (three). At the low-elevation site, nets were placed in the two major habitat types: woodland (15) and agricultural fields (5). We logged 5865 net-hours at the high-elevation site and 7773 net hours at the low-elevation site. Nets were checked approximately every half-hour. Captured birds were banded with numbered aluminum bands provided by the Bird Banding Laboratory of the U.S. Geological Survey. We identified birds to species and determined age and sex where possible with the aid of Pyle (1997).

Data analysis. Mist-netting operations are limited in their ability to sample some important parts of the migratory bird community, although some individuals of poorly represented species may be captured. Most notable in this category are raptors and owls, which we removed from our data set prior to analysis. In addition, mist-netting studies poorly sample species in overstory vegetation, but similar vegetative structure between sites (understory shrubs with scattered overstory trees) and similar net distribution indicates our sampling scheme should be adequate for a comparison between these two sites. We attempted to use a similar number of nets over a similar area in order to reduce potential sampling differences between sites.

We compared capture rates, calculated as birds captured/100 mist-net hours, between the two sites. Between-site differences in vegetation structure, net placement, and weather disturbance may have strong effects on capture rates, so caution is needed when interpreting capture rates between sites. In particular, greater average wind speeds at the high-elevation site may have depressed capture rates there, and our capture rates at that site may be low relative to the number of birds actually present. Therefore, we do not make statistical comparisons in capture rates between sites and instead focus on the extent of general similarity in capture rates between sites.

We also compared species richness between the two sites. We used the species diversity module in Ecosim v. 7.0 (Gotelli and Entsminger 2001) to calculate median species richness and 95% confidence intervals for each site with rarefaction curves. In short, Ecosim creates simulated species diversity by abundance curves by taking multiple (1000 iterations) random samples of various sizes (e.g., samples of 1, 5, . . . , 200 individuals) from the original data set and calculating the median richness and confidence intervals for each sample size. Then, different samples can be compared using the simulated medians and confidence intervals for equivalent abundances. Samples where confidence intervals do not overlap can be said to differ in species richness.

We refined our site comparisons by condensing species into two sets of functional guilds: migratory status and breeding locality. Migratory status classes were neotropical migrants (species that breed in North America and winter primarily south of the U.S.), temperate migrants (species that breed in North America with a portion of the population wintering in North America), and permanent residents (species that both breed and winter primarily in North America). We followed the Partners in Flight preliminary list as used by Yong and Finch (2002) and made our own determinations of migratory status based on range maps in field guides (Sibley 2003).

Breeding locality refers to the areas where a particular species breeds, and more specifically whether it could be found breeding at or near either site. We designated these categories as high-elevation species (i.e., species that could be found breeding at or in the mountains near Capilla Peak), low-elevation species (i.e., species that could be found breeding at or in the riparian habitat near the Nature Center), and high/low-elevation species (i.e., species that could be found breeding at or near both sites). This categorization was to help clarify where the species diversity at the banding sites might be originating. We also included a designation for species that were strictly passage migrants. We use species as the lowest taxonomic designation, except for Dark-eyed Juncos (*Junco hyemalis*) because the gray-headed form is a local breeder at the high-elevation site and the

Table 1. Species richness (95% confidence intervals) estimated, using simulated diversity-abundance curves, by migration status and locality category for birds captured at the high-elevation site (Capilla Peak) and the low-elevation site (Rio Grande Nature Center State Park), central New Mexico, during fall 2001–2003.

	Simulated abundance level	High-elevation site	Low-elevation site
All species	2140	55 (54–55)	76 (71–79)
Migratory status category			
Neotropical migrant	940	26 (25–26)	34 (30–37)
Temperate migrant	930	17 (16–17)	25 (25–29)
Permanent resident	185	12 (10–12)	14 (12–14)
Locality category			
High-elevation species	650	25 (23–27)	21 (20–21)
Low-elevation species[a]	—	4	17
High/low-elevation species	190	12 (11–12)	17 (15–19)
Passage species	560	11 (9–11)	16 (13–19)

[a] Inadequate sample size at Capilla Peak for a simulated comparison, total unadjusted species richness shown.

Oregon form is a strictly passage migrant and winter resident. The complete list of captured species, the classification scheme, and data on capture rates for each site for each species is available in electronic form from J.P.D.

RESULTS

Our results indicate that species richness was greater at the low-elevation site than at the high-elevation site, yet many species were present at both sites. There were more species of neotropical migrants, temperate migrants, permanent residents, low-elevation species, high/low-elevation species, and strictly passage migrants captured at the low-elevation site than at the high-elevation site (Table 1). There were more high-elevation species captured at the high-elevation site than at the low-elevation site (Table 1). There was some variation in species composition between sites, with 43% of all species captured at both sites, 42% captured only at the low-elevation site, and 15% captured only at the high-elevation site. Species captured only at the high-elevation site included predominantly high-elevation species, and species captured only at the low-elevation site included predominantly low-elevation species and temperate migrants, especially those that winter in lowland areas of central New Mexico.

Over the course of this study, we had similar capture rates at the low-elevation site and the high-elevation site, but there was more annual variation in capture rates at the high-elevation site. From 2001 to 2003, the range in annual capture rates was greater at the high-elevation site (16.9–56.1 birds/100 net hours) than at the low-elevation site (34.2–48.6 birds/100 net hours). Capture rates were greater at the low-elevation site for neotropical migrants and for low-elevation species, high/low-elevation species, and for strictly passage migrants (Table 2). Capture rates were greater at the high-elevation site for temperate migrants, permanent residents, and high-elevation species (Table 2).

Differences in capture rates between sites were large for some species, with more species showing greater capture rates at the low-elevation site than at the high-elevation site than vice versa. Species that were captured at greater rates at the low-elevation site included the Willow Flycatcher (*Empidonax traillii*), Bewick's Wren (*Thyromanes bewickii*), House Wren (*Troglodytes aedon*), Yellow Warbler (*Dendroica petechia*), Green-tailed Towhee (*Pipilo chlorurus*), Spotted Towhee (*P. maculatus*), Chipping Sparrow (*Spizella passerina*), Brewer's Sparrow (*S. breweri*), Song Sparrow (*Melospiza melodia*), Lincoln's Sparrow (*M. lincolnii*), White-crowned Sparrow (*Zonotrichia leucophrys*), Lazuli Bunting (*Passerina amoena*), House Finch (*Carpodacus mexicanus*), and Lesser Goldfinch (*Carduelis psaltria*). Species that were captured at greater rates at the high-elevation site included the Northern Flicker (*Colaptes auratus*), Hammond's Flycatcher (*Empidonax hammondii*), Steller's Jay (*Cyanocitta stel-*

Table 2. Total captures and capture rates (birds/100 net hours) for birds captured at the high-elevation site (Capilla Peak) and the low-elevation site (Rio Grande Nature Center State Park), central New Mexico, during fall 2001–2003.

	High-elevation site		Low-elevation site	
	Total captures	Capture rate	Total captures	Capture rate
Migratory status				
Neotropical migrant	979	16.7	1739	22.4
Temperate migrant	982	16.7	1223	15.7
Permanent resident	227	3.9	217	2.8
Locality				
High-elevation species	1344	22.9	683	8.8
Low-elevation species	11	0.2	474	6.1
High/low-elevation species	213	3.6	839	10.8
Passage species	616	10.5	1179	15.2

leri), Mountain Chickadee (*Poecile gambeli*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), Ruby-crowned Kinglet (*Regulus calendula*), Orange-crowned Warbler (*Vermivora celata*), Yellow-rumped Warbler (*Dendroica coronata*), Black-throated Gray Warbler (*D. nigrescens*), Townsend's Warbler (*D. townsendi*), Dark-eyed Junco (gray-headed form), and Red Crossbill (*Loxia curvirostra*).

DISCUSSION

We found that both the low-elevation and high-elevation sites supported diverse and abundant communities of migrating songbirds during fall migration. The diversity and abundance of migrants at the low-elevation site reinforce the importance of major riparian corridors like the Rio Grande as stopover habitats for migrating songbirds in the southwestern U.S. Overall avian diversity, and the diversity for most categories, was greater at the low-elevation site than at the high-elevation site. Overall capture rates were similar between the two sites, but the capture rates for species that were strictly passage migrants and neotropical migrants were greater at the low-elevation site. Both of these results point to the importance of riparian habitats as stopover sites for migratory birds in the southwest. Yet, the high-elevation site supported greater capture rates for temperate migrants, shared many migratory species with the low-elevation site, and was used by several species to a greater extent than at the low-elevation site. Additional differences were evident at a species level. Of the 10 most frequently captured species at each site, only four species were common to both: the Wilson's Warbler (*Wilsonia pusilla*), Chipping Sparrow, MacGillivray's Warbler (*Oporornis tolmiei*), and Dark-eyed Junco. In total, these results demonstrate that migratory stopover is occurring at significant levels outside of the lowland riparian corridors and that the migratory community is different in montane and riparian habitats in central New Mexico.

Our results are important for two reasons. First, these data demonstrate that important stopover habitats occur outside of major low-elevation riparian corridors in the southwestern U.S., and that conservation of these habitats will be important for the management of migratory bird populations. If montane habitats are used to a similar degree elsewhere in the southwest, then it is possible, given the greater spatial extent of these higher-elevation habitats, that the importance of montane habitats on a bird population level exceeds that of the riparian habitat. Much additional work needs to be conducted to determine if migratory bird stopover in montane habitats is widespread and which montane habitats appear to be most important. In particular, work should be conducted to determine to what degree other southwestern montane habitats, such as montane riparian areas, mature pine forests, or pinyon-juniper woodlands, also could be used as stopover sites. Casual observations indicate that these other habitats may be used as stopover sites (J. P. Delong, S. W. Cox, and N. S. Cox, pers. obs.; S. W. Cox, unpubl. data).

Our data also reveal that stopover site selec-

tion in New Mexico is more complex than previously suggested, and there may be multiple migration strategies at play in this region. Migrating songbirds are not simply funneling into major riparian corridors from upland areas (Yong and Finch 1997), although this process may be occurring at some level. Avian species migrating south through New Mexico are in some cases spreading out across a wide range of habitats (e.g., the Wilson's Warbler, which was the most frequently captured species at both sites) and in other cases consistently selecting one area over another (e.g., the Yellow Warbler at the low-elevation site and the Townsend's Warbler at the high-elevation site). Our results may suggest that these three warbler species are using different migration strategies, at least as they pass through New Mexico. One hypothesis is that Wilson's Warblers use a broad-front migration strategy, Yellow Warblers follow riparian corridors, and Townsend's Warblers make flights from mountain range to mountain range. Because migration strategies are essentially rules for finding food and avoiding predation during the migratory journey (Alerstam and Lindström 1990), such clear differences in the spatial patterning of stopover habitat use across the landscape may indicate that species are organizing their migratory journeys in several different ways.

The availability of food is an important factor in the selection of stopover habitat sites by migrating birds (Alerstam and Lindström 1990). Migrating birds in the southwest may choose riparian corridors as stopover sites because riparian areas contain mesic deciduous habitats of willow and cottonwood with an abundance of food (Yong et al. 1998). Some upland habitats do not appear as attractive in this regard, in particular the desert grassland and shrubland habitats. With little water, dry vegetation, and presumably fewer insects, many migrating songbirds may avoid these habitats during migration. High-elevation montane areas, however, may be fairly wet during the late summer and fall because of intense monsoon rains, and insect abundance may be very high during that part of the year (J. P. Delong, S. W. Cox, and N. S. Cox, pers. obs.). Hence, some migratory songbirds may select montane habitats because of heightened food availability during the fall. Additional study is needed to determine if food availability is a factor in the use of montane habitats as stopover sites.

Another potentially important factor in the selection of stopover habitats by migratory songbirds is the avoidance of predation (Alerstam and Lindström 1990). In the western U.S., many migrating raptors follow mountain ridges as they migrate south during the fall (Kerlinger 1989). The Capilla Peak study site harbors a well-studied concentration of migrating bird-eating raptors (Hoffman and Smith 2003), suggesting that the risk of predation for stopping-over songbirds could be high. On any particular day in September, there may be up to several hundred individual bird-eating hawks and falcons passing within easy foraging distance of the mist-netting area at Capilla Peak (J. P. Delong, S. W. Cox, and N. S. Cox, pers. obs.). In contrast, the Rio Grande riparian forests harbor a dense population of nesting Cooper's Hawks (*Accipiter cooperii*), but the number of bird-eating raptors found in the low-elevation areas during fall migration is much lower (J. P. Delong, S. W. Cox, and N. S. Cox, pers. obs.). Despite greater potential predation risk at the high-elevation site, many migrating songbirds use high-elevation areas for stopover. We can think of two possible reasons why they may do this. First, it may be that the high elevation habitats are easy to access for birds that are migrating at high altitudes. Upon finishing a nocturnal flight, the ease of reaching mountaintops may outweigh the benefits of traveling 1300 m down slope to the riparian corridors (and presumably having to regain that altitude at the start of the next migratory flight). Second, although many songbirds are passing through the site during the peak of raptor passage in late-September through early October (DeLong and Hoffman 1999), it appears that much of the songbird passage occurs two to three weeks before the major peak in raptor passage (J. P. Delong, S. W. Cox, and N. S. Cox, pers. obs.). Hence, songbirds may be able to reduce the predation risk by traveling ahead of the potential predators.

Some of the variation in species composition between the low-elevation and the high-elevation sites may result from species' selecting migratory stopover habitats that are similar to their breeding or natal habitats (e.g., Parnell 1969). For example, montane breeders may select montane habitats for stopover, and riparian

breeders may select riparian habitats for stopover. Parnell (1969) found this type of habitat selection in spring migrant parulid warblers in North Carolina. Our data seem to provide support for this phenomenon. Far more Townsend's Warblers, Black-throated Gray Warblers, and Yellow-rumped Warblers, all montane forest breeders, were captured at the high-elevation site than at the low-elevation site. Likewise, riparian breeders such as Willow Flycatchers, Lincoln's Sparrows, and Song Sparrows were captured at greater rates at the low-elevation site than at the high-elevation site. Our data also indicate that preferences for stopover habitats that look like a species' breeding habitat are not universal, with many species using both montane and riparian habitats regardless of the type of habitat in which they breed. For example, Green-tailed Towhees, a shrubsteppe and montane meadow breeder, were captured at greater rates at the low-elevation site than at the high-elevation site. Several common neotropical migrants such as Virginia Warblers (*Vermivora virginiae*), Wilson's Warblers, and Warbling Vireos (*Vireo gilvus*) were captured at similar rates at both sites. This result does not necessarily suggest that Green-tailed Towhees and other species common at both sites are not selecting habitats within stopover areas that share physiognomies with their breeding habitats. Alternatively, it is possible that some species are willing to use whatever habitat is available for foraging and predator evasion, and perhaps even move through many habitat types during their stopovers.

In summary, we found that migratory songbirds used both a low-elevation riparian corridor and a high-elevation mountaintop site to a similar degree, but that there were important differences and similarities in species composition between sites. We conclude that efforts focusing on managing habitats and birds in riparian corridors should be continued, but that a real understanding of songbird migration in the southwest will require additional focus on upland, particularly montane forest, habitats.

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