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Introduction

In southwestern North America, riparian habitats have declined precipitously in the last century both within and outside protected areas such as national parks, U.S. Fish and Wildlife Service refuges, and Bureau of Land Management and biosphere reserve lands. These declines are primarily due to anthropogenic perturbations such as alterations in river flow regimes, agricultural conversion, livestock grazing, and urban expansion (Webb et al. 2003). In the southwestern United States and northwestern Mexico the decline of riparian habitat and loss of native cottonwood (*Populus fremontii*), willow (*Salix gooddingii*) gallery forests, and adjacent mesquite (*Prosopis* sp.) bosques has been accompanied by the invasion of non-native tamarisk (*Tamarisk* sp.), or salt cedar. This change has resulted in a dramatic shift towards the dominance of tamarisk in riparian vegetation communities within most protected areas (Shafroth et al. 2005). The reduction and shift in vegetation composition within riparian habitats in western North America has resulted in their classification as globally imperiled by The Nature Conservancy (Comer et al. 2003), and has had a tremendous impact on neotropical migrant birds. Although riparian habitat comprises less than one percent of the landscape in southwestern North America, it supports more breeding bird species than all other western habitat types combined (Anderson and Ohmart 1977). Riparian areas serve as critical breeding, winter, and stop-over habitat for birds, supporting 10 times greater bird numbers than surrounding uplands (Anderson et al. 2004). In fact, most wildlife within xeric environments of protected areas in Mexico and the United States depend on resources (e.g., water, cover, food) provided by riparian habitats during some time of their annual cycle (Rosenberg et al. 1991).

Vegetation species' composition is an important component of avian habitat selection (Anderson and Ohmart 1977), and several studies have examined the effects of tamarisk invasion in riparian areas on subsequent avian community structure (Rice et al. 1983; van Riper et al. 2007). These studies focused on comparing pure stands of tamarisk to native

dominated stands, and showed that tamarisk monocultures contained less diversity and lower absolute numbers of birds. The earlier studies resulted in the perception that tamarisk provides relatively unsuitable habitat for bird species, and that a negative relationship exists between avian diversity and tamarisk abundance. This perception helped to shape early restoration policies for southwestern riparian habitats, which commonly aim to eradicate tamarisk (e.g., Cohn 2005). The recent work by van Riper et al. 2007, who compared bird numbers in mixes of native and tamarisk habitats, suggests a suitability threshold for birds when 20–40% native trees occur in predominately tamarisk habitat.

In this study we compare the responses of neotropical migrant bird species' arrival and visual cues to differing sizes of vegetation patches within protected areas (e.g., Cibola and Bill Williams River national wildlife refuges) on the Lower Colorado River in the southwestern United States and northwestern Mexico. We developed research hypotheses that examined ways in which individual birds as well as avian communities respond to differing amounts of tamarisk and other vegetation within protected areas along the Colorado River. We will also discuss stop-over movement patterns and foraging in relation to plant phenology patterns and insect abundance. It is our hope that this information will allow land managers to re-examine present land configurations and more precisely address avian community needs within future restoration projects throughout southwestern North America.

Materials and methods

Study areas. Our studies were conducted along the entire length of the lower Colorado River, from the delta in Sonora, Mexico, to The Nature Conservancy reserve in Moab, Utah (Figure 1). Areas of most intense data collection were at Cibola National Wildlife Refuge (33°18'N, 114°41'W; elevation 60 meters) and Bill Williams River National Wildlife Refuge (34°18'N, 114°08'W; elevation 200 meters) in La Paz County, Arizona (Figure 1; nos. 2 and 3). Cibola is located adjacent to the main channel of the lower Colorado River, where intensive water management and land-use practices have resulted in large expanses of the landscape being dominated by tamarisk monocultures. The remaining native habitat patches presently found at Cibola are primarily the result of restoration efforts (Rosenberg et al. 1991). In contrast, the Bill Williams River is a perennial tributary of the lower Colorado River, and while tamarisk is a dominant tree species, the area contains some of the last remaining extensive stands of natural cottonwood and willow gallery forests within the lower Colorado River watershed. Honey mesquite (*Prosopis glandulosa*) and to a lesser degree screwbean mesquite (*Prosopis pubescens*) are other native tree species found at Bill Williams River, while common woody under-story species include seep willow (*Baccharis salicifolia*), arrow weed (*Tessaria sericea*), and saltbush (*Atriplex* sp.).

Field methods. We established point-count stations along the Colorado River corridor, following Reynolds et al. (1980). Each station was at least 300 meters from adjacent stations to minimize double counting. Over a five-year period (1998–2002), during March–May and August–November, we surveyed for birds every 7 to 10 days at our intensive study sites, located at Cibola and the Bill Williams River national wildlife refuges, and once each month (1998–1999) in Mexico, northern Arizona, and Utah. Surveys were conducted between sunrise and 1000 hours, except during rain or high winds. At each station, observers waited one



Figure 1. Protected areas in northwest Mexico and the southwestern USA that can serve as stop-over habitat for migrating birds. Large arrows depict major bird migration routes. National Park Service areas are indicated by squares. National Wildlife Refuge (NWR) areas are numbered as follows:

- California: (1) Klamath Basin; (2) Clear Lake; (3) Lower Klamath; (4) Tule Lake; (5) Modoc; (6) Humboldt Bay; (7) Sacramento; (8) Willow Creek-Lurline; (9) Delevan; (10) Butte Sink; (11) Colusa; (12) Sutter; (13) Stone Lakes; (14) San Pablo; (15) Antioch Dunes; (16) Farallon; (17) San Joaquin River; (18) Merced; (19) Grasslands; (20) San Luis; (21) Salinas River; (22) Blue Ridge; (23) Hem; (24) Bitter Creek; (25) Havasu; (26) Hopper Mountain; (27) Seal Beach; (28) Coachella Valley; (29) Cibola; (30) Sonny Bono Salton Sea; (31) San Diego; (32) Sweetwater Marsh A; (33) Tijuana Slough.
- Nevada: (1) Sheldon; (2) Anano Island; (3) Ruby Lake; (4) Fallon; (5) Lurline; (6) Still Water; (7) Pahranaqat; (8) Moapa Valley Desert; (9) Ash Meadows.
- Arizona: (1) Bill Williams River; (2) Kofa; (3) Imperial; (4) Cabeza Prieta; (5) Leslie Canyon; (6) San Bernadino; (7) Buenos Aires.
- Utah: (1) Big Bear; (2) Ouray; (3) Fish Springs.
- Colorado: (1) Arapaho; (2) Browns Park; (3) Rock Flats; (4) Rocky Mountain Arsenal; (5) Two Ponds; (6) Monte Vista-Alamosa.
- New Mexico: (1) Maxwell; (2) Las Vegas; (3) Sevilleita; (4) Grulla; (5) Bosque Del Apache; (6) Bitter Lake-San Andreas.

minute to minimize influences of disturbance, then recorded all birds heard or seen within a 100-meter radius for five minutes. Distance to each bird was recorded, and birds flying overhead were excluded. We also mist-netted birds on alternate days when counting did not occur.

To quantify vegetation characteristics we randomly selected two azimuths, and located two 11.3-meter radius plots 30 meters from the center of each station along those random directions. Vegetation parameters were measured during the spring of 1999 using a combi-

nation of vegetation sampling techniques from James and Shugart (1970) and the BBIRD protocol (Martin and Finch 1995).

To obtain an overall representation of arthropod abundance, we sampled all dominant riparian tree species. Insects were sampled twice during peak spring migration in 2003 with branch-bagged samples collected of foliage dwelling insects. This technique captures active and inactive insects likely to be hunted by the predominantly leaf-gleaning insectivores (after Johnson 2000). One branch sample was collected per tree. The branch was shaken into a sweep net, and insects collected from the net were transferred into one-gallon zip-lock bags. We controlled for foliage surface area by choosing branches with similar stem diameter. Samples were frozen immediately and brought to the laboratory for processing. From each sample, arthropods were sorted, counted, and identified. Voucher specimens from samples were mounted and placed in a reference collection at Northern Arizona University, Flagstaff, and the University of Arizona, Tucson. The remaining insects were stored by sample in 70 percent ethanol.

Results

Migrant arrival timing. We found that migrant bird species arrived asynchronously along the Colorado River, particularly neotropical migrant warblers which appear to partition their arrival times to minimize overlap with other species (Figure 2). Moreover, we found that the more northern breeding members arrive later and “leap-frog” over their southern breeding counterparts during migration (Paxton et al. 2007). Thus, we see that individuals who winter in northern Mexico arrive first and then move on to their breeding grounds in the southwestern United States. Birds that winter further south, arrive later and “leap” over the earlier arrivals to reach their more northern breeding grounds in Canada and Alaska. The Colorado River corridor appears to be a less important fall migration route, as seen in the differences between spring and fall numbers of migrant species and duration of stop-over (Figure 2).

Visual cues. When birds arrive during migration at areas along the Colorado River, we believe that they assess stop-over habitats at multiple scales (Figure 3). The coarsest scale (A) is the largest, and appears to be a genetically influenced corridor selection, coupled with weather frontal patterns. When following a migration route, a bird then selects specific stop-over habitat next on the basis of large-scale landscape features (B). Once the large-scale feature has been selected, the bird then decides on the type of vegetation patch (C). Finally, the bird makes microhabitat selection about specific foraging and roosting locations within the vegetation patch (D), selecting between native and introduced tamarisk vegetation. Over time, this selection process ultimately maximizes resources for each bird species during migration stop-over (Hutto 1985).

Movement and feeding. We have found that once a bird selects a stop-over location, daily movement is minimal. At Cibola National Wildlife Refuge for example, we found that birds rarely move more than 100 meters throughout a day. In fact, in 2006 some birds visited only a few trees for the entire stop-over period. Birds were preferentially choosing to forage in honey mesquite trees (Figure 4). This was due in a large part to the greater abundance of insects on flowering honey mesquite trees (McGrath and van Riper 2005).

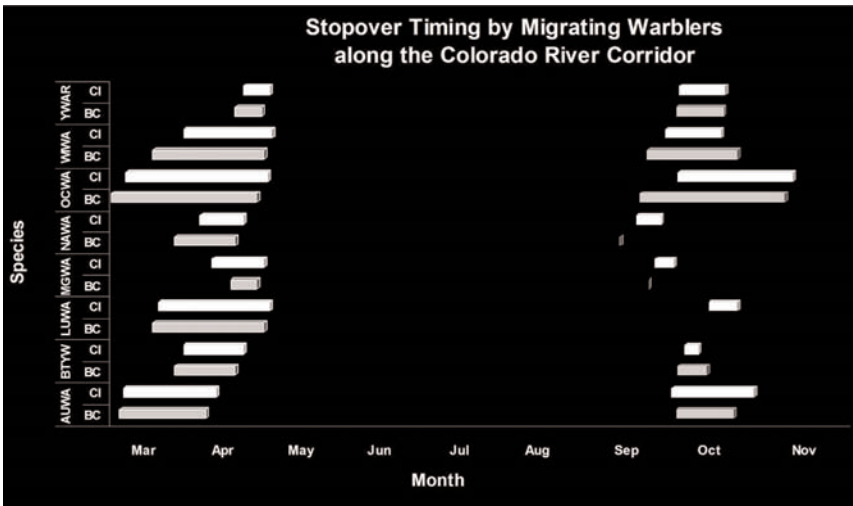


Figure 2. Arrival times and duration of stop-over during spring and fall migrations for neotropical warbler species. The horizontal axis is month of the year while the vertical axis lists bird species identified as being present: AUWA (Audubon's warbler), BTYW (black-throated grey warbler), LUWA (Lucy's warbler), MGWA (MacGillivray's warbler), NAWA (Nashville warbler), OCWA (orange-crowned warbler), WIWA (Wilson's warbler), and YWAR (yellow warbler).

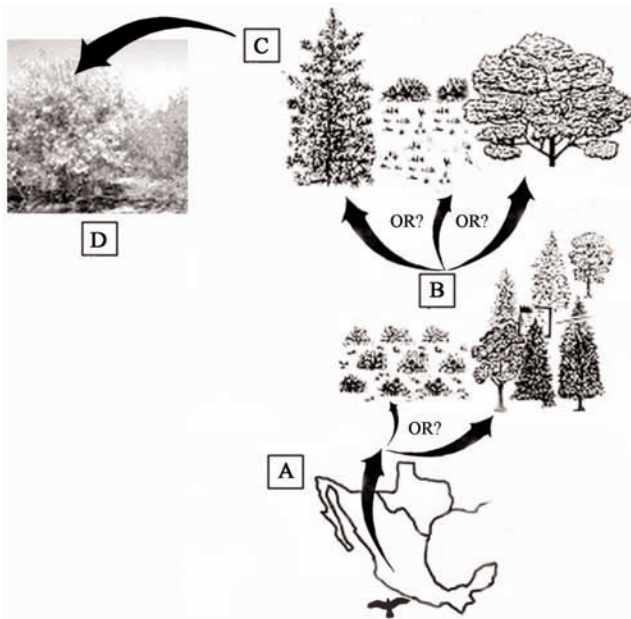
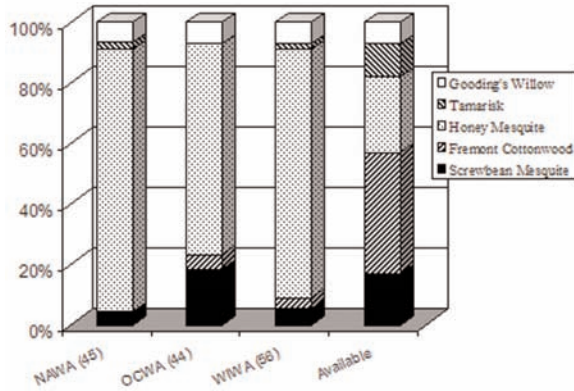


Figure 3. Figure depicting how migrant birds, passing from Mexico to the southwestern United States, assess stop-over habitat. The birds appear to assess migrant routes and stop-over habitats at four major scales. These scales correspond to the letters in the figures and are identified as: (A) genetically influenced corridor selection; (B) large-scale landscape features; (C) vegetation patches; and (D) micro-habitat selection within the vegetation patch.

Figure 4. Proportion of substrate used by some neotropical migrant birds during 2002 and 2003 at Cibola NWR on the lower Colorado River near Blythe, Arizona. Data are from observations of a single attack maneuver and the associated substrate that the bird foraged on. Amount available is the percentage of canopy coverage based on random point vegetative sampling. Species are: NAWA (Nashville warbler), OCWA (orange-crowned warbler), and WIWA (Wilson's warbler). Numbers in parentheses are sample sizes.



Phenology. When we correlated migration at protected areas with plant phenology data, the only significant correlation was that migrant arrivals coincided with honey mesquite flowering ($R=0.76$, $p=0.03$). In fact, we found that almost every warbler species preferentially chose honey mesquite as a foraging substrate and utilized this tree significantly more often than would have occurred by chance (Figure 4). Correlations were not significant for the other tree species' leaf cover and flowering compared to the relative abundance of migrants. Screwbean mesquite leaves emerged at the end of peak migration. Fremont cottonwood showed no pattern with migrant stop-over patterns, as there was no flowering and leaves were much older by the time the first migrants arrived (McGrath and van Riper 2005). Although peak tamarisk flowering occurred after spring migration, flowers were present and leafing was almost complete during the migration period. Gooding's willow also bloomed in spring, but no correlation with migrant arrival and tree phenology was detected by McGrath and van Riper (2005).

Tamarisk. The avian community structure at Cibola and Bill Williams River national wildlife refuges varied significantly across a gradient in tamarisk abundance. At both sites, van Riper et al. (2007) found a significantly high degree of avian community structure between tamarisk dominated and native dominated habitats. We found that avian communities associated with low and intermediate levels of tamarisk did not differ, while both differed significantly from avian communities associated with high tamarisk levels (ANOSIM: $r=0.52$, $p=0.003$). Thus, habitats with low and intermediate levels of tamarisk support similar avian communities, but contrast markedly to avian communities associated with higher tamarisk levels.

Discussion

Managers of protected areas throughout southwestern North America should realize that habitat selection by avian species varies seasonally as energetic demands and habitat requirements change with differing phases of the annual cycle (Anderson et al. 2004). Migrant birds partition their arrival times to maximize food resources and allow for prey recovery. Although birds generally arrive at more southern latitudes first during spring migration,

managers should be aware that a “leap-frog” migration pattern occurs in spring and fall for many neotropical bird species migrating along the Colorado River corridor. Thus, the longer-distance migrants come through most stop-over areas at a later date.

Both large and small protected areas are important for neotropical migrant bird stop-over sites. Birds appear to assess migrant routes and stop-over habitats at multiple scales, with larger protected areas providing the initial target for stopping. Once a location is chosen, at the smaller local scale phenological phases of major plant species strongly influence when and where birds stop. Smaller protected areas such as United States Fish and Wildlife Service refuges and state parks, provide important vegetation patches and suitable microhabitats for bird refueling during spring migration. Importantly, however, these areas must include areas with mixes of native vegetation. We found the greatest abundances of birds in habitats composed of 40–60% native vegetation with a tamarisk under-story (van Riper et al. 2007), and the lowest abundances in homogenous tamarisk stands. However, the selection by birds of habitats with small amounts of tamarisk, suggests that mixed native-tamarisk habitats can adequately meet avian requirements in protected areas along the Colorado River corridor in western North America.

Conclusions

We found that western migrant land bird species arrived at different times within protected areas along the Colorado River. The birds appear to assess migrant routes and stop-over habitats at multiple scales: (1) genetically influenced corridor selection; (2) large-scale landscape features; (3) vegetation patches; and, (4) microhabitat selection within a vegetation patch. Weather, vegetative species, structure, plant phenology patterns, and food resources variously influence migrating birds along the lower Colorado River. Species arrival dates and numbers of neotropical migrant warblers were variable among years, being largely influenced by large-scale weather patterns and plant phenology cycles. Protected areas are important stop-over sites because once selected, there was minimal movement by individual birds over the landscape during the stop-over period. Therefore, stop-over and bird foraging patterns were greatly influenced by plant species and phenological patterns of the selected microhabitat. Neotropical migrant bird species rely on protected areas in the southwest, as these habitats provide suitable stop-over and foraging habitat. It thus appears that larger protected (and unprotected) areas such as biosphere reserves and national parks, provide the appropriate landscape features that attract migrating birds, while smaller protected areas may play a more important role as micro-sites for stop-over habitat. Managers must recognize that within their protected areas, vegetation, structure, plant species, phenology, abundance, and food availability all play a role in structuring bird migration patterns along the lower Colorado River corridor.

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