Spring migrant use of native and saltcedar-dominated riparian areas along the lower Colorado River in Arizona

SPRING MIGRANT USE OF NATIVE AND SALTCEDAR-DOMINATED RIPARIAN AREAS ALONG THE LOWER COLORADO RIVER IN ARIZONA

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ABSTRACT—Riparian systems in the western United States provide essential stopover habitat to en-route migrant birds, and there is concern that the invasion and dominance of saltcedar (*Tamarix*) in many areas may inhibit use by some species. However, evidence from recent studies is challenging the widely held belief that invasive plants universally reduce habitat quality. Moreover, where many studies have compared avian use of riparian habitats dominated by saltcedar with those comprised primarily of native trees, few have investigated how birds use shrub communities, which are becoming more prevalent in western riparian zones because of widespread hydrologic modifications. We compared spring migrant use of 125-m sections of riparian habitat dominated by five different habitat types in southwestern Arizona in 2006 and 2007. We found that migrant abundance, species richness, and community assemblages were all influenced by the composition of riparian vegetation. Habitats completely dominated by saltcedar supported fewer migrants and migrant species than any other habitat type, but the presence of small amounts of native vegetation as a part of the overall riparian plant community greatly bolstered habitat use. Habitats dominated by native shrubs tended to support the greatest total migrant abundance, total species richness, and abundance of many individual species. Our findings suggest that riparian areas dominated by saltcedar are avoided by many western migrant species and have relatively low value as stopover habitat. In places where this species is a predominant component of the riparian plant community, restoration of at least a portion of native riparian vegetation may be effective for encouraging use by stopover migrants.

RESUMEN—Los sistemas riparios del oeste de los Estados Unidos proveen un hábitat de parada crítico para las aves migrantes en tránsito, y existe la preocupación de que la invasión y dominancia del cedro salado (*Tamarix*) en muchas áreas pueda inhibir su uso por parte de algunas especies. Sin embargo, evidencia de estudios recientes está desafiando la creencia ampliamente sostenida de que las especies invasivas reducen la calidad de hábitat de forma universal. Aún más, mientras que muchos estudios han comparado el uso por parte de las aves de hábitats riparios dominados por el cedro salado con aquellos compuestos principalmente por árboles nativos, pocos han investigado cómo las aves usan las comunidades arbustivas, las cuales están volviéndose más prevalentes en las zonas riparias del oeste debido a extendidas modificaciones hidrológicas. Comparamos el uso primaveral por parte de aves migrantes en secciones de hábitat ripario de 125 m de largo en el sudoeste de Arizona en el 2006 y 2007. Estas secciones estaban dominadas por cinco tipos diferentes de hábitat. Encontramos que la abundancia, riqueza de especies, y composición de la comunidad de los migrantes fueron influidas por la composición de la vegetación riparia. Los hábitats dominados completamente por el cedro salado sostuvieron menos individuos y especies migrantes que cualquier otro tipo de hábitat, pero la presencia de pequeñas cantidades de vegetación nativa reforzó el uso del hábitat enormemente. Los hábitats dominados por arbustos nativos tendieron a sostener la mayor abundancia total de migrantes, riqueza total de especies, y abundancia de muchas especies individuales. Nuestros resultados sugieren que las áreas riparias dominadas por el cedro salado son evitadas por muchas especies migrantes occidentales y tienen relativamente poco valor como hábitat de parada. En lugares donde esta especie es un componente predominante de la comunidad vegetativa riparia, la restauración de por lo menos una parte de la vegetación nativa puede ser efectiva para promover el uso por migrantes de paso.

In recent decades the majority of the research on factors limiting populations of migratory bird species has focused on stressors encountered on either their breed-ing or wintering grounds (e.g., Sherry and Holmes, 1995, 1996; Sillett and Holmes, 2002; Nagy and Holmes, 2005; Holmes, 2007). However, migration is energetically

expensive, and along the migration route, birds must endure numerous constraining factors including high nutritional requirements, unfamiliar habitats, geographic barriers, environmental stochasticity, and man-made structures (Moore et al., 1995, 2005; Carlisle et al., 2009). The quality of available en-route stopover habitat may have a significant influence on such parameters as survival and body condition upon arrival on breeding grounds (Russell et al., 1994, Moore et al., 1995), and there is evidence to suggest that much of the mortality endured by some species occurs during migration (Ketterson and Nolan, 1982; Sillett and Holmes, 2002; Paxton et al., 2007). Thus, comprehensive conservation plans for migrant birds should take into account resource and habitat requirements throughout the migratory process (Moore et al., 1995) as part of full life-cycle conservation.

Migrants passing through the American Southwest encounter many habitat types that support relatively low bird densities (e.g., deserts, xeric shrublands), and consequently, riparian systems in this region play a significant role in supporting transient migrant birds. Riparian communities comprise less than 1% of the landscape here, yet can support spring migrant abundances over 10 times greater than those found in surrounding uplands (Stevens et al., 1977), and 14 times more migrant species in the fall (Hehnke and Stone, 1979). Though riparian width can influence migrant use in other parts of North America (Fischer, 2000), Skagen et al. (1998) concluded that all riparian systems in southeast Arizona provide important stopover habitat regardless of width or extent, and some species may even adjust their migratory routes to maintain proximity to riparian areas (Skagen et al., 2005). Whereas the importance of riparian areas to seasonal bird communities in the arid southwest is unquestionable, Carlisle et al. (2009) and Ruth et al. (2012) recently focused attention on identifying important stopover habitats other than riparian communities. Though our understanding of relative use of different habitats has recently improved from these investigations, there is far less information available as to how migrants respond to finer-scale differences in habitat variables within riparian areas such as vegetation structure and community composition (Carlisle et al., 2009). It is especially important to understand the influence of such variables on migrant assemblages in this region where human effects have eradicated or heavily degraded natural riparian systems and available stopover habitat on a broad scale.

Historically, riparian plant communities in the arid and semiarid western United States were dominated by native willow (*Salix*) and cottonwood (*Populus*) trees (Webb et al., 2007). However, most of these ecosystems have been significantly fragmented and degraded, with losses approaching 99% in some areas (Briggs, 1996). In addition, hydrologic modifications such as dams and water withdrawals for irrigation on many rivers and streams have heavily altered their natural functions and processes, creating ideal conditions for the invasion of saltcedar (*Tamarix* spp.; Stromberg et al., 2007). Saltcedar is native to Eurasia and was introduced into the United States in the 1800s as a firewood source and for erosion control. Saltcedar is now the second most dominant woody riparian tree in the western United States (Friedman et al., 2005), and its range continues to expand (Sexton et al., 2006).

The influence of saltcedar on avian communities has recently received a significant amount of attention from researchers, yet thus far there is little evidence to suggest that it is detrimental to birds (Fleishman et al., 2003; Durst, 2004). At least 49 different bird species have been documented utilizing saltcedar during the breeding season in the southwestern United States (Sogge et al., 2008). Moderate invasions can actually increase structural and compositional complexity, providing resources for species with diverse life-history characteristics, and possibly reducing interspecific competition (Van Riper et al., 2008; Cerasale and Guglielmo, 2010). Sogge et al. (2005) showed a positive link between saltcedar coverage and the abundance and diversity of breeding bird communities, and Walker (2008) found the highest migrant abundances along the Rio Grande in areas dominated by saltcedar. Additionally, it has been suggested that regeneration of native riparian plants, such as cottonwoods, would be challenging in parts of the Southwest because of widespread hydrologic alterations, and thus many riparian habitats would actually be dominated by upland shrub communities (and consequently have less value for birds) were it not for the presence of saltcedar (Livingston and Schemnitz, 1996; Sogge et al., 2008).

The emergence of such information is challenging the widely held belief that all invasive species systematically reduce habitat quality, and suggests that, in some instances, complete removal of invasive plants may be neither necessary nor immediately beneficial (Van Riper et al., 2008; Stromberg et al., 2009). To further our understanding of the ecological ramifications of saltcedar invasion and expansion, we investigated how assemblages of spring migrants utilizing riparian habitats along the lower Colorado River vary in response to dominant plant communities. Specifically we were interested in identifying differences in migrant abundance, richness, and species assemblages among river sections dominated by native riparian plants, shrub habitat, and with varying degrees of saltcedar composition.

MATERIALS AND METHODS—*Study Area*—Our study took place within the Lower Colorado Subdivision of the Sonoran Desert, a region characterized by very low precipitation and high summer temperatures. In early 2006 we used WSR-88D radar data from Yuma, Arizona to identify two sites along the Colorado River and one along the All-American Canal that appeared to be heavily used by stopover migrants (see Fischer et al., 2012*a*, 2012*b* for

TABLE 1—Distribution and vegetation composition of 125-m transect sections from three riparian sites[a] near Yuma Proving Ground, Arizona surveyed for spring migratory birds in 2006 and 2007.

Habitat[b]	AAC	YUMA	IMP	Total	Dominant woody vegetation
NS	13	0	9	22	Palo verde and mesquite with or without creosote bush
ND	2	0	2	4	Palo verde and mesquite with or without creosote bush; some saltcedar present but <50% dominance
NND	4	3	8	15	Saltcedar >50% in dominance with some willow, mesquite, or creosote bush
NNI	9	8	1	18	Saltcedar-dominated community
NT	0	11	4	15	Cottonwood, willow

[a] Sites represent three geographically unique locations associated with the Colorado River: All-American Canal (AAC), Yuma (YUMA), and Imperial (IMP).

[b] Sections were categorized according to dominant vegetation and were classified as either native shrub (NS), native-dominated with nonnatives (ND), nonnative/invasive dominant with some natives (NND), nonnative/invasive shrub and tree community (NNI), or native tree (NT).

details). The first site (YUMA) was located within the Colorado River floodplain in the city limits of Yuma. The second (IMP) was located along a 48-km reach of the Colorado River that bisects the United States Fish and Wildlife Service Imperial National Wildlife Refuge. The last site (AAC) occurred adjacent to the All-American Canal (a water supply channel that transports water diverted directly from the Colorado River to the Imperial Valley of California) and was within an abandoned floodplain of a former Colorado River tributary. We established either six or seven 500-m-long transects at each site, placed within or directly adjacent to the floodplain of each system. We placed transects end to end in most cases, but some were separated by short distances because of fragmented riparian habitats. Width of riparian vegetation along each transect varied, and in nearly all cases was >100 m in width (AAC, mean = 557 m; IMP, mean = 205 m; YUMA, mean = 140 m).

Although vegetation dominance varied among sites and transects, vegetation was fairly typical of present-day Colorado River riparian communities. Each site included either streamside riparian areas or dry washes (or both) comprised of riparian vegetation such as palo verde (*Circidium*), saltcedar, willow, and cottonwood. Water diversions and levees have significantly altered hydrology and reduced overbank flooding that historically maintained native riparian plant communities at our sites. Thus, other species that are not typically considered riparian plants (e.g., mesquite [*Prosopis*] and creosote bush [*Larrea tridentate*]) were also present. Two transects at the YUMA site traversed an approximately 4-ha cottonwood restoration area and most trees were <5 m in height.

Bird Surveys—In 2006 and 2007 three experienced birders attempted to survey all transects on every morning between 3 April 2006 and 10 May 2006 and between 3 April 2007 and 15 May 2007. Unfortunately, one field technician left at the start of the 2006 season, and we did not sample any transects in the IMP site that year. In addition, weather occasionally prohibited us from sampling one or more transects on a given morning. Transects sampled or not sampled on days affected by weather were random, and we assumed this did not introduce any bias into our habitat comparisons. Thus all data collected before or

after weather events were included in analyses. Ultimately, each YUMA and AAC transect was sampled between 26 and 33 times in 2006, and transects at all three sites were sampled between 37 and 42 times each in 2007.

On each morning one crew member was assigned to a specific site. Observers began surveying transects at approximately local sunrise, and all surveys were completed by 1000h. Observers used handheld global positioning system units preloaded with numbered waypoints that denoted the beginning and end of each 500-m transect, and strived to complete each transect within 30 min. The data sheets for 500-m transect surveys were subdivided into 125-m longitudinal sections, and surveyors recorded the number and species of all birds detected within each transect section. Observers were trained to record only the first detection of each individual in the section in which it was initially detected. This helped avoid double counting birds that might flush farther down the transect as a result of the approaching observer. Birds that were not identifiable to species were classified to the lowest taxonomic level possible to help identify all likely migrants. We rotated observers among sites daily to minimize the impact of any observer bias on bird counts.

Vegetation Classification—The 125-m sections within each transect were the smallest units for which we had collected bird abundance and richness data, so in 2007 a single observer (RAF) identified the dominant vegetation types at each section along the AAC, YUMA, and IMP transects. For each section, the first and second most dominant shrubs or tree species were identified, which included varying combinations of palo verde, cottonwood, willow, creosote bush, and saltcedar. We then classified each section into one of five habitat categories: native trees (NT: cottonwood/willow), native shrubs (NS: mesquite/creosote bush, palo verde/creosote bush; palo verde/mesquite), native-dominated with nonnatives (ND: mesquite/saltcedar, palo verde/saltcedar), nonnative/invasive shrub and tree community (NNI: saltcedar), or nonnative/invasive dominant with some natives (NND: saltcedar/mesquite, saltcedar/creosote bush, saltcedar/palo verde; Table 1). Because of the broad nature of these habitat categories and the fact that annual changes in vegetation cover and dominance are

TABLE 2.—Mean abundance per kilometer for all migrant species recorded at 125-m transect sections of various habitat types during spring migration near Yuma Proving Ground, Arizona in 2006 and 2007. The 20 most abundant species are indicated with an asterisk, and were tested for statistical differences among habitat types. Habitat types that were not statistically different from one another with regard to abundance of a species share the same letter. We were not able to construct appropriate habitat models for orange-crowned warbler or Bullock's oriole because the likelihood optimization routine used by PROC GLIMMIX (SAS Institute Inc., Cary, North Carolina) could not produce parameter estimates.

Species	Scientific name	NT[a]		NS		ND		NND		NNI		Total counted
Wilson's warbler*	Wilsonia pusilla	4.22 (0.65)	AC	8.73 (1.14)	B	4.32 (0.96)	ABC	5.36 (1.07)	AB	2.68 (0.4)	C	2,817
Common yellowthroat*	Geothlypis trichas	9.16 (1.43)	A	2.13 (0.55)	B	1.97 (1.51)	AB	5.61 (1.75)	A	5.1 (1.52)	AB	2,396
Brewer's sparrow*	Spizella breweri	0.03 (0.03)	AB	10.29 (4.25)	B	10.63 (10.44)	AB	0.94 (0.32)	A	0.59 (0.35)	A	2,069
Ash-throated flycatcher*	Myiarchus cinerascens	0.77 (0.14)	A	4.73 (0.47)	B	4.22 (1.35)	BC	3.16 (0.78)	BC	2.39 (0.33)	C	1,617
Unknown warbler	—	2.6 (0.49)		2.61 (0.34)		1.86 (0.44)		3.31 (0.81)		1.67 (0.2)		1,255
Western flycatcher*	—	1.02 (0.16)	A	3.85 (0.33)	B	3.81 (0.62)	BC	1.96 (0.36)	AC	1.08 (0.18)	A	1,230
Warbling vireo*	Vireo gilvus	1.28 (0.3)	A	3.21 (0.44)	B	2.44 (0.79)	AB	2.66 (0.57)	B	1.05 (0.16)	A	1,128
Orange-crowned warbler*	Vermivora celata	2.29 (0.4)		2.84 (0.3)		1.49 (0.45)		1.84 (0.42)	–	1.45 (0.24)	–	1,066
Yellow-headed blackbird*	Xanthocephalus xanthocephalus	6.48 (2.31)	A	0.3 (0.12)	B	0 (0)	AB	0.62 (0.36)	B	0.49 (0.22)	B	781
Nashville warbler*	Vermivora ruficapilla	0.5 (0.1)	AC	1.9 (0.27)	B	1.59 (0.59)	ABC	1.14 (0.26)	AB	0.43 (0.11)	C	600
Unknown empidonax	—	0.27 (0.06)		1.47 (0.2)		1.17 (0.27)		1.15 (0.32)		0.41 (0.08)		460
Yellow-rumped warbler*	Dendroica coronata	0.46 (0.14)	A	1.07 (0.15)	A	0.31 (0.15)	A	0.74 (0.17)	A	0.74 (0.16)	A	406
Western kingbird*	Tyrannus verticalis	0.72 (0.18)	A	1.23 (0.35)	A	0.6 (0.37)	A	0.53 (0.14)	A	0.49 (0.13)	A	390
Western tanager*	Piranga ludoviciana	0.34 (0.1)	A	1.2 (0.24)	B	0.53 (0.23)	AB	0.86 (0.23)	AB	0.36 (0.06)	A	385
Black-throated gray warbler*	Dendroica nigrescens	0.53 (0.11)	AB	1.08 (0.21)	A	1.19 (0.48)	AB	0.75 (0.18)	AB	0.19 (0.04)	B	380
Lucy's warbler*	Vermivora luciae	0.01 (0.01)	A	0.81 (0.21)	A	0.92 (0.49)	A	1.36 (0.51)	A	0.33 (0.13)	A	365
MacGillivray's warbler*	Oporornis tolmiei	0.41 (0.08)	A	0.86 (0.12)	A	1.05 (0.42)	A	0.67 (0.17)	A	0.18 (0.07)	A	328
Yellow warbler*	Dendroica petechia	0.5 (0.12)	A	0.85 (0.13)	A	0.37 (0.15)	A	0.44 (0.1)	A	0.38 (0.09)	A	320
Blue grosbeak*	Passerina caerulea	0.94 (0.16)	A	0.15 (0.05)	B	0.51 (0.15)	AB	0.63 (0.2)	A	0.64 (0.16)	AB	265
Townsend's warbler*	Dendroica townsendi	0.49 (0.12)	AB	0.71 (0.12)	A	0.38 (0.1)	AB	0.59 (0.14)	AB	0.16 (0.04)	B	260
Bullock's oriole*	Icterus bullockii	0.38 (0.12)		0.93 (0.17)		0.1 (0.07)		0.28 (0.06)	–	0.24 (0.08)		239
Unknown hummingbird	—	0.31 (0.12)		0.58 (0.12)		0.38 ± (0.2)		0.44 ± (0.09)		0.51 ± (0.14)		237
Black-chinned hummingbird*	Archilochus alexandri	0.14 (0.05)	A	0.66 (0.17)	A	0.1 (0.04)	A	0.42 (0.14)	A	0.2 (0.07)	A	204
Black-headed grosbeak	Pheucticus melanocephalus	0.27 (0.09)		0.39 (0.07)		0.45 (0.13)		0.38 (0.07)		0.26 (0.07)		179
Western wood-pewee	Contopus sordidulus	0.09 (0.03)		0.52 (0.06)		0.35 (0.06)		0.46 (0.1)		0.1 (0.03)		175
White-crowned sparrow	Zonotrichia leucophrys	0.08 (0.06)		0.51 (0.12)		0.66 (0.32)		0.12 (0.04)		0.22 (0.07)		160
Yellow-breasted chat	Icteria virens	0.36 (0.1)		0.19 (0.09)		0.41 (0.26)		0.76 (0.22)		0.04 (0.02)		160
Chipping sparrow	Spizella passerina	0 (0)		0.37 (0.22)		0.24 (0.16)		0.31 (0.2)		0.41 (0.25)		152

TABLE 2—Continued.

Species	Scientific name	NT[a]	NS	ND	NND	NNI	Total counted
Lazuli bunting	*Passerina amoena*	0.18 (0.07)	0.3 (0.07)	0.35 (0.25)	0.18 (0.07)	0.09 (0.03)	111
Bell's vireo	*Vireo bellii*	0 (0)	0.2 (0.13)	0 (0)	0.26 (0.18)	0 (0)	67
Blue-gray gnatcatcher	*Polioptila caerulea*	0.05 (0.02)	0.18 (0.05)	0.03 (0.03)	0.05 (0.03)	0.08 (0.03)	50
Ruby-crowned kinglet	*Regulus calendula*	0.1 (0.03)	0.1 (0.03)	0.22 (0.11)	0.05 (0.03)	0.07 (0.02)	45
Olive-sided flycatcher	*Contopus cooperi*	0.03 (0.02)	0.07 (0.02)	0.1 (0.07)	0.11 (0.04)	0.06 (0.02)	41
Hermit warbler	*Dendroica occidentalis*	0.07 (0.03)	0.05 (0.02)	0.03 (0.03)	0.13 (0.05)	0.1 (0.04)	40
Cassin's vireo	*Vireo cassinii*	0.03 (0.02)	0.11 (0.03)	0.06 (0.06)	0.11 (0.04)	0.01 (0.01)	38
Green-tailed towhee	*Pipilo chlorurus*	0.03 (0.02)	0.12 (0.03)	0.06 (0.06)	0.07 (0.03)	0.02 (0.01)	35
Unknown flycatcher	—	0.04 (0.02)	0.07 (0.02)	0.13 (0.09)	0.03 (0.02)	0.04 (0.01)	33
House wren	*Troglodytes aedon*	0.02 (0.02)	0.12 (0.04)	0.1 (0.07)	0.04 (0.03)	0.02 (0.01)	32
Unknown vireo	—	0.04 (0.02)	0.1 (0.03)	0 (0)	0.05 (0.02)	0.03 (0.01)	32
Summer tanager	*Piranga rubra*	0 (0)	0.03 (0.01)	0 (0)	0.18 (0.1)	0.01 (0.01)	26
Say's Phoebe	*Sayornis saya*	0.01 (0.01)	0.06 (0.03)	0 (0)	0.02 (0.02)	0.01 (0.01)	13
Unknown myiarchus	—	0 (0)	0.02 (0.01)	0 (0)	0.06 (0.02)	0.01 (0.01)	12
Swainson's thrush	*Catharus ustulatus*	0.02 (0.02)	0.03 (0.01)	0 (0)	0.02 (0.01)	0.01 (0.01)	10
Unknown thrush	—	0.02 (0.02)	0.02 (0.01)	0.03 (0.03)	0.02 (0.01)	0.01 (0.01)	10
Hermit thrush	*Catharus guttatus*	0.02 (0.02)	0.02 (0.02)	0 (0)	0.01 (0.01)	0.01 (0.01)	8
Hooded oriole	*Icterus cucullatus*	0 (0)	0.05 (0.03)	0 (0)	0 (0)	0 (0)	8
Unknown oriole	—	0 (0)	0.03 (0.02)	0 (0)	0 (0)	0 (0)	6
Northern parula	*Parula americana*	0 (0)	0.02 (0.02)	0 (0)	0 (0)	0 (0)	4
Willow flycatcher	*Empidonax traillii*	0 (0)	0.02 (0.01)	0 (0)	0 (0)	0.01 (0.01)	4
Sage thrasher	*Oreoscoptes montanus*	0.03 (0.02)	0 (0)	0 (0)	0 (0)	0.01 (0.01)	3
Calliope hummingbird	*Stellula calliope*	0.01 (0.01)	0.01 (0.01)	0 (0)	0 (0)	0 (0)	2
Clay-colored sparrow	*Spizella pallida*	0 (0)	0.01 (0.01)	0 (0)	0.01 (0.01)	0 (0)	2
Gray flycatcher	*Empidonax wrightii*	0 (0)	0.01 (0.01)	0.04 (0.04)	0 (0)	0 (0)	2
Hammond's flycatcher	*Empidonax hammondii*	0 (0)	0.01 (0.01)	0 (0)	0.01 (0.01)	0 (0)	2
Lincoln's sparrow	*Melospiza lincolnii*	0 (0)	0 (0)	0.03 (0.03)	0.01 (0.01)	0 (0)	2
Plumbeous vireo	*Vireo plumbeus*	0 (0)	0 (0)	0 (0)	0.01 (0.01)	0 (0)	1
Rufous hummingbird	*Selasphorus rufus*	0 (0)	0.01 (0.01)	0 (0)	0 (0)	0 (0)	1
Unknown tanager	—	0 (0)	0 (0)	0.03 (0.03)	0 (0)	0 (0)	1

[a] Habitat types are native shrub (NS), native-dominated with nonnatives (ND), nonnative/invasive dominant with some natives (NND), nonnative/invasive shrub and tree community (NNI), or native tree (NT).

very minimal in this region, we were able to use this information to compare abundance and richness data collected both in 2006 and 2007. Habitat within two surveyed 125-m sections was too heterogeneous to classify and thus removed from further analyses.

Data Analyses—Each bird species encountered was classified as either a Neotropical migrant, a Nearctic migrant, or a permanent resident of the region by referencing the Birds of North America Online (Poole, 2005). Because we were interested in terrestrial migrant habitat use, permanent residents were eliminated from analyses, as were all swifts and swallows because most were detected as flyovers, and we could not determine if these birds were actually using the habitat. Pacific-slope flycatchers (*Empidonax difficilis*) and Cordilleran flycatchers (*Empidonax occidentalis*) were grouped as western flycatchers because of the difficulty in distinguishing them in the field. Last, because the majority of the NT sections (11 of 15) were located in cottonwood restoration sites, we eliminated the four sections located in mature cottonwood stands because they were deemed too structurally different from the others, were only sampled in one year (2007), and represented a sample size too small for analyses.

We calculated total migrant abundance per kilometer, individual species abundance per kilometer, and total migrant species richness per section for each date a section was sampled. To account for the possibility of counting a single individual multiple times on different days, we averaged each metric across dates within years. Individuals not identified to species were removed from the data before calculating species richness. Although our study was not designed in such a way that allowed us to construct species-specific detection functions, we are confident in our detection of nearly all birds present because our sites were relatively open with scattered patches of shrubs and small trees.

As previously mentioned, all three sites had been specifically selected because radar data strongly suggested that each served as a migratory stopover hot spot; thus, we chose to ignore variability in bird community metrics among sites and focus on modeling the effects of vegetation at the section level. We first modeled total abundance per kilometer and species richness per section as a function of habitat, including year as a fixed block effect. We then selected the 20 most abundant species (83% of detections; Table 2) and investigated whether or not habitat influenced composition of migrant assemblages by including a species and species-by-habitat interaction term in the model. Results from this analysis indicated that habitat affected species differently, so we also modeled abundance of each of those 20 species individually as a function of habitat blocked by year. All modeling was conducted using PROC GLIMMIX (SAS Institute Inc., Cary, North Carolina). Abundance variables were best modeled by assuming a negative binomial distribution, and all richness data were best modeled assuming a normal distribution. When there was evidence that habitat significantly affected any of our response variables ($\alpha = 0.05$), we investigated all pair-wise comparisons of habitat types using a Tukey–Kramer adjustment of the P values.

RESULTS—We used data from 70 different 125-m sections in our analyses, where over the 2 years we recorded 20,665 migrant detections from 49 unique species (Table 2). In 2006 we conducted 1,496 bird
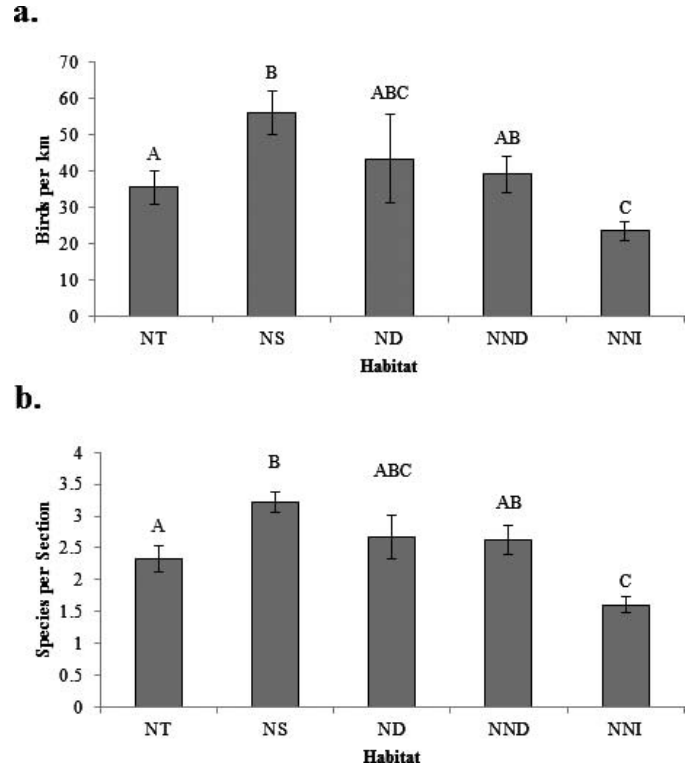
a.

b.

FIG. 1—a) Mean ($\pm SE$) total migratory bird abundance per kilometer and b) migratory bird species richness per transect section recorded at 125-m riparian transect sections of five different habitat types near Yuma Proving Ground, Arizona during spring migration in 2006 and 2007. Sections were classified as either native tree (NT), native shrub (NS), native-dominated with nonnatives (ND), nonnative/invasive dominant with some natives (NND), or nonnative/invasive shrub and tree community (NNI). Response variables with the same letter above the bar were not significantly different between those habitat types (*t*-test with Tukey–Kramer adjustment).

surveys (26–33 surveys per section) and in 2007 we conducted 2,896 bird surveys (37–42 per section). Yearly estimates of mean daily total migrant abundance for individual sections ranged from 5.9 birds/km to 178.4 birds/km and yearly estimates of mean daily migrant species richness ranged from 0.5 species/section to 5.7 species/section.

There was a significant overall habitat effect on both total migrant abundance ($F_{4,110} = 15.89$, $P < 0.01$) and migrant species richness ($F_{4,110} = 15.64$, $P < 0.01$), and the results from the analyses of these metrics were remarkably similar (Fig. 1). We encountered the greatest abundance and richness values in NS habitats, followed respectively by ND, NND, NT, and NNI habitat sections. In both cases NNI habitats had significantly lower values than all but ND habitats, and NT habitats had significantly lower values than NS sections.

There was strong evidence that individual species differed in their response to habitat type ($F_{76,2295} = 5.31$, $P < 0.01$). Of the 20 species we investigated

individually, the abundance of 12 differed significantly among habitats, whereas 6 did not (Table 2). We were unable to construct models for two species in PROC GLIMMIX because the likelihood optimization routine could not produce parameter estimates. Nineteen of these species were found in all habitat types, whereas yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) were found in all but ND habitats. We found peak densities of nearly 75% of species analyzed in NS communities, and no species peaked in NNI communities. In fact, abundances were lowest in NNI habitats for 40% of bird species.

DISCUSSION—We found that spring migrant abundance, species richness, and species assemblage were all affected by riparian vegetation composition. Our results indicated that riparian habitats completely dominated by invasive saltcedar supported fewer migrants and migrant species in the spring than other riparian habitat types in our study area. Presence of native vegetation, even as a minor component of a saltcedar-dominated riparian plant community, appeared to greatly increase migrant use at this time of year, though interestingly, many species tended to prefer habitats comprised entirely or partially of native shrubs (which here includes some shrubs more typical of upland systems), rather than riparian trees.

NNI habitat sections supported significantly fewer migrants and species than almost all other habitat types. Though the difference between NNI and ND habitats was not significant, this is more likely due to the small sample size and correspondingly large standard error associated with ND sections. Paxton et al. (2008) found that stopover location use by Wilson's warblers (*Wilsonia pusilla*) was heavily influenced by plant flowering phenology. It seems likely, then, that many migrants in our study area are avoiding habitats dominated by saltcedar because these plants tend to flower much later than native trees and shrubs (Paxton et al., 2008). Previous investigations into migrant use of saltcedar have produced mixed results. In the middle Rio Grande Valley of New Mexico, Kelly et al. (2000) recorded greater spring and fall migrant capture rates in riparian areas dominated by willows than by other plants. Walker (2008), however, found that migrant abundance and energy consumption were actually highest in saltcedar habitats during the fall. Avian use of saltcedar may be influenced by climatic variables (Hunter et al., 1988), but in our study region, high concentrations of the invasive plant appear to be relatively unattractive to spring migrants. However, distribution data are not necessarily indicative of habitat quality, and saltcedar-dominated riparian areas can actually be superior refueling habitat for migrants precisely because densities of heterospecific competitors is low (Cerasale and Guglielmo, 2010). Future research should focus on understanding the differences in resource availability and foraging and refueling rates among these habitat types to evaluate the true impacts of saltcedar proliferation on the suitability of habitat for migrating birds.

Van Riper et al. (2008) surveyed bird communities throughout the year just north of our study area and found that abundance of many bird species was highest at intermediate values of saltcedar cover. These researchers suggested that there may be a threshold for saltcedar composition above and below which avian habitat value is reduced. Our results somewhat support this hypothesis; however, though NND sections, which included low levels of native vegetation, did attract more migrants than NNI sections, we also found that habitats completely dominated by native shrubs supported the greatest abundance and richness of migrant birds. Van Riper et al. (2008) did not focus their investigation on avian use of habitats dominated by shrub vegetation, but rather on plants that have historically been more typical of southwestern riparian communities. It is important to consider avian use of hydrologically altered shrub-dominated habitats as well, given that it may not be realistic to expect natural regeneration of cottonwood and willow in systems that have been affected by significant water withdrawals (Livingston and Schemnitz, 1996; Sogge et al., 2008).

Though both NS and ND sections supported greater migrant richness, total migrant abundance, and abundance of several individual species than NT sections, it is important to remember that all of the NT sections that we included in our analyses were located at cottonwood restoration sites comprised of young (<5 yr old) trees with sparse understory. When we looked at spring migrant assemblages from the four mature cottonwood sections surveyed in 2007, we found that they also supported lower numbers of migrants (46.33 ± 10.61 birds per kilometer) than NS sections. However, they had substantially greater species richness (3.69 ± 0.80 species per section) than any other habitat type. These results should be interpreted with caution because we only sampled a small number of mature cottonwood sections (because of lack of this type of habitat in the region) in one of the sample years. Indeed, Szaro and Jakle (1985) found that bird densities and species richness values in areas dominated by riparian trees were greater than or similar to those found in adjacent shrub communities. Rehabilitation efforts along the Lower Colorado River currently include saltcedar removal and numerous small-scale cottonwood and willow replanting projects. These efforts should continue, though future monitoring should aim to compare migrant habitat use between mature native riparian tree communities and those dominated by native shrubs, as our data indicate that complete eradication of saltcedar and subsequent rehabilitation of traditional native riparian plant communities may not be necessary to support migrants. Furthermore, to further investigate the influence of varying percentages of native and nonnative shrubs and trees on migrant assemblages in western arid riparian systems, manipulative studies in saltcedar-domi-

nated riparian plant communities that reduce saltcedar cover and include pre- and postmanipulation monitoring of seasonal avian communities are needed. These types of investigation would assist in determining the costs and resulting ecological benefits of full versus partial saltcedar removal during ecological rehabilitation projects.

The United States Department of Agriculture recently halted its saltcedar biological control program over concerns that it was destroying federally endangered willow flycatcher critical nesting habitat. Yet nearly half of the migrant species we detected, including willow flycatchers, were found in greatest abundance in shrub habitats. By contrast, almost 35% of species had lowest abundance in NNI shrub habitats. Our data indicate that riparian areas dominated by saltcedar have relatively low value as stopover habitat, and that in places where this plant is a predominant component of the vegetation, restoration of native riparian or upland vegetation may be effective for encouraging use by stopover migrants. Fortunately, our results also suggest that complete restoration of hydrologic processes to support native riparian tree communities may not be necessary to provide habitat that will be preferred by en-route birds.

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