Importance of the 2014 Colorado River Delta pulse flow for migratory songbirds: insights from foraging behavior

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Highlights

- Migrant songbirds foraged at higher rates in mesquite in 2000 and in willow in 2014
- Migrants used predominantly mesquite in 2000 and willow in 2014
- Wilson's warbler foraged more efficiently in willow than in other tree species
- Pulse flows may improve stopover habitat for spring migrant songbirds

Abstract

The Lower Colorado River provides critical riparian areas in an otherwise arid region and is an important stopover site for migrating landbirds. In order to reverse ongoing habitat degradation due to drought and human-altered hydrology, a pulse flow was released from Morelos Dam in spring of 2014, which brought surface flow to dry stretches of the Colorado River in Mexico. To assess the potential effects of habitat modification resulting from the pulse flow, we used foraging behavior of spring migrants from past and current studies to assess the relative importance of different riparian habitats. We observed foraging birds in 2000 and 2014 at five riparian sites along the Lower Colorado River in Mexico to quantify prey attack rates, prey attack maneuvers, vegetation use patterns, and degree of preference for fully leafed-out or flowering plants. Prey attack rate was highest in mesquite (*Prosopis* spp.) in 2000 and in willow (*Salix gooddingii*) in 2014; correspondingly, migrants predominantly used mesquite in 2000 and willow in 2014 and showed a preference for willows in flower or fruit in 2014. Wilson's warbler (*Cardellina pusilla*) used relatively more low-energy foraging maneuvers in willow than in tamarisk (*Tamarix* spp.) or mesquite. Those patterns in foraging behavior suggest native riparian vegetation, and especially willow, are important resources for spring migrants along the lower Colorado River. Willow is a relatively short-lived tree dependent on spring floods for dispersal and establishment and thus spring migrants are likely to benefit from controlled pulse flows.

Keywords: birds; migration; hydrology; restoration; foraging

1.1 Introduction

Habitat loss and degradation is one of the major causes of decline of many long-distance migrant songbird populations in North America (Carlisle et al. 2009; Terborgh 1989), and is the primary threat cited for the majority of bird species listed under the Endangered Species Act (Johnson 2007). Riparian habitats of the southwestern United States and northern Mexico are increasingly threatened by ongoing habitat alteration (e.g., Glenn et al. 1996; Krueper 1993) and have been the focus of many regional conservation and restoration actions (Carrillo-Guerrero et al. 2013; Glenn et al. 2001, 2008; Gerlak et al. 2013; Skagen et al. 2005). These riparian areas are of key importance to migrant songbirds traveling between their wintering grounds in Central or South America to their breeding grounds in the northern United States and Canada, because they provide critical food and shelter in an otherwise hostile arid landscape (Arizmendi et al. 2008; Kelly and Hutto 2005; Knopf et al. 1988; Skagen et al. 1998). Anthropogenic changes to hydrologic regimes can strongly influence the structure, composition, and phenology of riparian vegetation (Nagler et al. 2005, 2008; Stromberg 1998, 2001; Zamora-Arroyo et al. 2001), potentially influencing the quality of the habitat. Our current understanding of what constitutes quality stopover habitat, particularly in western North America, is poor relative to our understanding of breeding- and wintering-ground habitat requirements for many species (Moore et al. 1995; Skagen et al. 2005). An improved understanding of stopover ecology will be critical for guiding habitat restoration efforts with the goal of improving habitat quality for songbirds during a potentially limiting stage in their lifecycle (Carlisle et al. 2009).

The lower Colorado River in Mexico is an important region for migratory landbirds (Hinojosa-Huerta et al. 2008; Hinojosa-Huerta et al. 2013b; Zamora-Arroyo et al. 2005). The hydrology of this region has been greatly altered since the completion of Glen Canyon Dam in 1964, which prevented surface water from entering the lower reaches of the Colorado River Delta. Today surface water reaches the Gulf of California only during flood releases in high precipitation years associated with El Nino cycles (Zamora-Arroyo et al. 2005). These flows have been shown to improve riparian vegetation in subsequent years by encouraging establishment of new cohorts of native cottonwood and willow (Nagler et al. 2005). In fact, while much of the riparian corridor in Mexico is dominated by invasive tamarisk (*Tamarix* spp.) (Hinojosa-Huerta et al. 2013a), there remains greater cover of native trees and shrubs than in the neighboring U.S. reaches (Zamora-Arroyo et al. 2005). This important area remains under threat due to the paucity of surface water in most years, particularly in the face of recent (2002-2007) droughts, during which tamarisk cover increased with a corresponding decline in riparian breeding bird abundance (Hinojosa-Huerta et al. 2013a). To address those concerns, between March and May 2014, a pulse of water (hereafter “pulse flow”) was released from Morelos Dam and from two downstream points in Mexico (Km 18 and Km 27 spillways) into the extensive dry stretches of the Colorado River Delta, to assess the response of the Lower Colorado River Delta ecosystem to renewed flow (Daesslé et al. 2016; Flessa et al. 2014; Stokstad 2014). This pulse flow, through its influence on the survival and recruitment of native riparian vegetation, has the potential to improve habitat quality for breeding and migratory landbirds in the region.

Food availability is an important component of habitat quality because it can limit populations of bird species across diverse taxa (Arcese and Smith 1988; Johnson 2007; Lyons 2005; Rodenhouse and Holmes 1992; Rota et al. 2015). Food availability is especially critical

for small migratory songbirds, whose capacities for storing and carrying fuel reserves is far exceeded by the energy demands of long-distance migration (Blem 1990; Newton 2008). The presence of high quality stopover sites along the migration route, therefore, is crucial for survival, allowing birds to rest and replenish depleted fat reserves before resuming migration (Hutto 1998; Lindström 2003). Food availability, however, is difficult to measure directly or accurately, particularly for insectivores; most insect sampling methods do not capture all taxa equally, and furthermore, due to the diversity of insect forms, behaviors, and the preferences of different bird species, no sampling scheme will accurately reflect how food availability is perceived by a foraging bird (Hutto 1990; Wolda 1990). Instead, observing the behavior of a foraging bird can provide an index of food availability that can be used to compare the quality of different habitats (Lovette and Holmes 1995; Lyons 2005; Maslo et al. 2010; Rota et al. 2015). In particular, observational and experimental studies have demonstrated that the number of attack maneuvers (attempts to capture prey) per unit time is positively correlated with prey availability (Delestrade 1999; Hutto 1990; Loegering & Fraser 1995).

A cooperative international study was initiated to assess the hydrologic and environmental effects of the 2014 engineered pulse flow and to evaluate the potential for such practices to aid riparian restoration (e.g., Hinjosa-Huerta et al. 2013a, Ramírez-Hernández et al. 2013, 2015). While concurrent studies measured the direct effects of the flow on groundwater recharging and native plant recruitment patterns (Flessa et al. 2014), our objectives were to elucidate the relationships between vegetation and migrant birds, as evidenced by their foraging behavior. We assessed which riparian habitats and tree species were most important to migrant songbirds by: 1) comparing foraging attack rates among birds using different sites and tree species; 2) quantifying tree species use among multiple species of migrant songbirds; and 3)

comparing the use of different foraging maneuvers (indicative of potential prey quality and energetic expenditure) of a focal bird species observed foraging in several tree species.

2.1 Methods

2.2 Study Area

We visited four study areas along the lower Colorado River in eastern Baja California Norte state, Mexico, in 2000, 2001, and 2014, with a fifth study area visited in 2014 (Fig. 1). Baja California Native (BCN; 32.2217° N, -115.0828° W) and Baja California Tamarisk (BCT; 32.2271° N, -115.0584° W) were adjacent sites, both located in the riparian corridor on the west side of the Colorado River. BCN was a ~1-ha area within the larger Laguna Grande restoration site, comprising primarily native trees and shrubs: cottonwood (*Populus fremontii*), willow (*Salix gooddingii*), honey mesquite (*Prosopis glandulosa*) and screwbean mesquite (*P. pubescens*), whereas BCT was an area ~1.5 ha in size covered in >90% non-native tamarisk shrubs. Surface water from the pulse flow first reached these areas on 4 – 5 Apr 2014 (Flessa et al. 2014). The Ciénega de Santa Clara (CE; 32.0394° N, -114.9113° W) was a brackish 6000-ha wetland within the Colorado River Delta, fed by agricultural runoff and irrigation drainage from the Wellton-Mohawk Irrigation and Drainage District in southern Arizona (Glenn et al. 1992). Vegetation within the wetland was predominantly cattail (*Typha domingensis*) with some common reed (*Phragmites australis*) and bulrush (*Schoenoplectus americanus*). The wetland was surrounded by dry salt mudflats, with sparse cover of tamarisk and pickleweed (*Salicornia* spp.) immediately bordering the emergent vegetation. El Doctór (DR; 31.9260° N, -114.7185° W) was a slightly brackish spring-fed wetland area (864 ha) southeast of Ciénega de Santa Clara, with emergent vegetation in the wetland including bulrush, surrounded by a corridor of tamarisk, willow, and

mesquite (van Riper et al. 2008; Zamora-Arroyo et al. 2005). In 2014 observers also visited a fifth site, the riparian areas on the west side of the Colorado River at the border (“limitrophe”) between the U.S. and Mexico (Limitrophe – LT; $\sim 32.6258^{\circ}$ N, -114.7983° W). Vegetation in this area was $\sim 70\%$ tamarisk, with the remaining vegetation cover comprising mesquite, willow, and cottonwood trees. Surface water from the pulse flow passed through this area beginning on 23 Mar 2014 (Flessa et al. 2014).

2.3 Field Data Collection

Observers conducted foraging observations at each site between 29 Mar – 11 May 2000, 29 Mar – 26 Apr 2001, and 14 – 24 Apr 2014, corresponding with peak spring migration of Neotropical passerines (Paxton et al., 2008; Hinojosa-Huerta et al. 2013a) and in 2014 occurring after surface water from the pulse flow had reached the river corridor study sites. Observers conducted focal observations on migrant warblers and vireos, following birds with binoculars until the bird moved out of sight (van Riper et al. 2008). Eight species were observed, all of which were small insectivores that typically glean prey from live or dead foliage in trees and shrubs: warbling vireo (*Vireo gilvus*), orange-crowned warbler (*Vermivora celata*), Nashville warbler (*Leiothlypis ruficapilla*), yellow warbler (*Setophaga petechia*), yellow-rumped warbler (*Setophaga coronata*), black-throated gray warbler (*Setophaga nigrescens*), Townsend’s warbler (*Setophaga townsendi*), and Wilson’s warbler (*Cardellina pusilla*). During observations, observers classified foraging and search behaviors continuously using the classification scheme of Remsen and Robinson (1990), dictated into hand-held voice recorders in 2000 and 2001 and written directly onto datasheets in 2014. For a comparison of foraging maneuver use in different substrates, we subsequently lumped maneuvers into aerial/high energy (sally-strikes and hover-gleans) and non-aerial/low energy (perch-glean and reach-glean). During observation we noted

duration of each behavior and the plant species in which bird was foraging. In 2014, we also recorded phenology of plant species by noting the extent of leaf-out, flowering, and fruiting of the foraging substrate (McGrath et al. 2009; van Riper 1980). Separate from the foraging observations, observers visually sampled up to 100 individual trees of each dominant tree or shrub species (mesquite, tamarisk, cottonwood, and willow) throughout the study area once per week. At each tree the observer assessed phenology by visualizing a full crown and estimating the proportion of the tree covered in leaves, flowers, and fruits. This visual estimation method produces similar results to more rigorous measures using a digital camera (McGrath et al. 2009).

2.4 Data Analysis

2.4.1 Foraging Rates

Early data exploration revealed that data collected using tape recorders vs. data written directly onto datasheets produced estimates of foraging rates that were not directly comparable, with attack rate nearly an order of magnitude greater in 2014 (pooled mean attack rates in no. attacks per sec: 0.09 in 2000, 0.07 in 2001, and 0.32 in 2014); this is because while observation time was measured directly in 2000 with tape recorders, duration of each foraging maneuver was estimated in the field in 2014. However, the same observer conducted all observations in 2014, so within-year comparisons should not be biased; thus we conducted separate analyses for the data collected in each time period. We combined data from 2000 and 2001 for analysis because there were only 11 observations in 2001. For both datasets, we modeled attack rate as a Poisson-distributed random variable with observation length (sec) as an offset and bird species as a random-effects intercept using the *glmer* function in package *lme4* (Bates et al. 2015) in R version 3.2.2 (R Core Team 2015). We built a candidate set of models for each time period with combinations of site and substrate effects on attack rate, and for 2014 we also included the

effects of percent green leaf, percent flower, and the interactions green leaf*substrate and flower* substrate. We ranked models using AIC_c (Aikake's information criterion corrected for small sample sizes) with the assumption that models ≤ 2 AIC_c from the top model have strong support (Burnham and Anderson 2002).

2.4.2 *Tree Species Use*

We did not have detailed data on tree species composition at each of the sites, and the proportion of observations obtained from each site differed between time periods; thus we could not estimate tree species selection indices or quantify preference. Instead, we report broad qualitative patterns of tree species use among sites and among bird species sampled in each time period.

Phenological characteristics can serve as important cues for migrants because they can be reliable indicators of food availability (McGrath et al. 2009), therefore we included an analysis relating phenology to probability of use to determine if migrants selected individual trees based on such characteristics. We used logistic regression, separately for each tree species, to compare phenology characteristics of used trees (from the 2014 foraging observation data) and available trees (from the phenology assessments of 100 sampled trees of each species). For mesquite we modeled percent green leaf and percent flowers; for tamarisk, we modeled all four phenology characteristics (green leaf, brown leaf, flower, fruit), and for willow we modeled green leaf, flower, and fruit. There were too few observations of cottonwood to include in this analysis, and at the time of visit, cottonwoods had already completed flowering and fruiting.

2.4.3 *Foraging Behavior of Wilson's warbler*

Resources may vary in the energy required to exploit them, for instance whether they require the use of powered flight or can be reached from a perch. Warbler species differ in their

habitual use of different foraging maneuvers, so for inferring patterns of foraging maneuvers as a function of substrate use, we restricted this analysis to observations of Wilson's warbler. This species had the greatest number of observations ($N = 173$), and the next-most common species (orange-crowned and Nashville warblers) showed limited diversity in foraging maneuvers. We conducted an analysis with all years combined and for 2014 only. In both analyses, we calculated the total frequency that aerial and non-aerial maneuvers were used among the three predominant substrates (mesquite, willow, and tamarisk), and conducted a chi-squared test to determine if relative frequencies of high- and low-energy attack maneuvers varied among substrates.

3.1 Results

3.1.1 Foraging Rates

The top model ($\Delta AIC_c \leq 2$) for attack rate in both time periods included only tree species in the linear predictor (Table 1). All other variables occurred in models with low support and exhibited non-significant effects (Table 2). In 2000, attack rate was highest in mesquite and lowest in miscellaneous natives (Table 2, Fig. 2), while in 2014, attack rate was highest in willow (Table 2, Fig. 2).

3.1.2 Tree Species Use

Tree species use varied among sites (Fig. 3) and among bird species (Fig. 4). Willow was the predominant tree used at BCN during both time periods, and mesquite use was high at DR in both time periods. Mesquite was used heavily at BCT in 2000 but not in 2014. Tamarisk was the predominant tree used at BCT and LT in 2014. Use of miscellaneous natives occurred primarily at Ciénega de Santa Clara, which had sparse woody cover. Patterns of tree species use

among bird species differed between years (Fig. 4). All species except orange-crowned warbler used mesquite in > 50% of observations in 2000, while mesquite use exceeded 25% only for Townsend's warbler in 2014. Most species used tamarisk in at least 25% of observations, except for yellow warbler, which was observed in tamarisk in 10% of observations in 2000 and no observations in 2014, despite increased effort at the tamarisk-dominated BCT in 2014. Most species used willow in 2014, with few observations of willow use for most species in 2000.

There was no significant effect of phenology characteristics (% flower and % green) on probability of use of individual mesquite trees based on 55 observations of use and 100 observations of availability (Table 3). For tamarisk (N = 106 used, 200 available), percent green leaf and percent brown leaf both had negative effects on probability of use, while percent fruit and flower had no effects (Table 3). For willow (N = 51 used, 100 available), percent green leaf had no effect on use while flower and fruit both had small positive effects on use (Table 3).

3.1.3 Foraging Behavior of Wilson's warbler

Wilson's warbler used low energy maneuvers more frequently in willow than in tamarisk or mesquite (Table 4) in 2014 ($\chi^2 = 9.49$, $df = 2$, $p = 0.009$) and in all years combined ($\chi^2 = 15.26$, $df = 2$, $p < 0.001$).

4.1 Discussion

Spring passerine migrants exhibited the highest prey attack rates when foraging in mesquite in 2000-2001 and when foraging in willow in 2014. There was a tendency for lower attack rates at tamarisk-dominated sites (LT and BCT) in 2014 compared to native-dominated sites, but model-averaged effects were non-significant, with variance better explained by foraging tree choice and

the random effect of bird species. These results suggest that native trees and shrubs provide superior habitat for spring migrants than tamarisk, at least with respect to food availability. Tamarisk-dominated habitats may support lower arthropod diversity (Yard et al. 2004) and thus reduced food availability for spring migrants than native vegetation. Honey mesquite was a preferred foraging substrate for spring migrants along the San Pedro River in Arizona, particularly when trees were in flower and thus had greater arthropod abundance (McGrath et al. 2009). Willow has been shown to be an important resource for spring migrants elsewhere in the arid southwest, and willow-cottonwood habitats have more arthropod biomass than tamarisk-dominated sites during spring migration (Cerasale and Guglielmo 2010; Kelly et al. 2000). The relative change in attack rates among tree species between time periods highlights the importance of maintaining structural and taxonomic diversity of riparian vegetation; habitat preferences of migrants can change within or among years as a result of phenologically-mediated changes in food availability (Rodewald & Brittingham 2007; Strobe 2009).

Migrants appeared to prefer mesquite in 2000-2001 and willow in 2014, which corresponded to the tree species with the highest prey attack rate in each time period and suggests that migrants may preferentially choose tree species with the greatest food availability. These patterns must be interpreted with caution because we lack data on tree species composition and because the proportion of foraging observations collected among the study sites varied between time periods. Region-wide, however, overall vegetation cover did not change during this time period, tamarisk and mesquite cover increased slightly, and willow and cottonwood cover decreased (Hinojosa-Huerta et al. 2013a). When tree species use within sites was compared between time periods, mesquite use within sites decreased (especially at El Doctór and

BCT) despite the region-wide increase in mesquite cover. This suggests that at least some of the observed variation was a result of a true change in use patterns.

The observed changes in foraging behavior between 2000/2001 and 2014 cannot necessarily be attributed to an immediate positive effect of the 2014 pulse flow, especially given that the study areas have surface water in most years and we lack detailed data on surface water and vegetation conditions prior to the pulse flow. However, the apparent shift toward using more willows in 2014 and the observed increased attack rate in willows in 2014 could reflect a short-term change in relative food availability mediated by surface flow. Satellite imagery revealed a 17% increase in vegetation greenness by June 2014 compared to June 2013 (C. J. Jarchow, personal communication), which likely resulted in increased arthropod abundance (Bang et al. 2012). It is difficult to say how much of this change coincided with the timing of spring migration, but due to complex interactions among water availability, habitat type, and arthropod abundance and diversity (Bang et al. 2012), as well as different phenological differences among plant species, it is possible that food availability increased more rapidly in willow-dominated habitats that line the river corridor than in the slightly more xeric mesquite-dominated habitats.

Wilson's warblers used relatively fewer energetically expensive aerial maneuvers when foraging in willow than when foraging in other plant species. Aerial maneuvers are typically directed at small-bodied flying insects, while non-aerial maneuvers such as gleaning from a perch are more often directed at larger, soft-bodied insects such as lepidopteran larvae (Lovette and Holmes 1995). Thus, in addition to supporting potentially greater prey availability, willows may have provided better quality prey for migrating warblers in 2014. While it is possible that the change in foraging maneuvers used by Wilson's Warbler among substrates was related to

structural differences among tree/shrub species (Whelan 2001), it may still result in greater foraging efficiency by allowing individuals to maintain or increase food intake while decreasing the use of more costly aerial maneuvers.

Migrants tended to select willows that were flowering or fruiting at the time of data collection in 2014. We expected but did not see a similar selection pattern for mesquites; spring migrants in Arizona used mesquite flowers as settlement cues for selecting individual trees with high arthropod abundance relative to trees with fewer flowers (McGrath et al. 2009). This discrepancy may be due to differences in the relative timing of flowering of these species in Mexico compared to further north in Arizona; willow flowering had peaked but mesquite flowering was still in the early phase during the 2014 visit (unpublished data). Willows are predominantly wind-pollinated, yet most species rely secondarily on insect pollination and produce nectar to attract insects (Fox 1992; Karrenberg et al. 2002). A hypothesized increase in arthropod abundance in actively reproducing willows is also consistent with the observed increase in prey attack rates by migrants foraging in willows compared to other plant species. A second possibility is that migrants were selecting willows in certain microhabitats where reproduction happened to be elevated. The spatial distribution of reproductive female cottonwoods has been shown to correlate with water availability (Hultine et al. 2007), although this is not often observed in willows because they are more strictly limited to the riparian corridor (Alliende and Harper 1989).

4.1.1 Conclusions

Based on the high prey attack rates in mesquite and willow compared to tamarisk or less predominant native species, reduced use of aerial attack maneuvers in willows by Wilson's warbler, and an apparent preference for either mesquite or willow in years when those plants

might provide increased prey availability, native vegetation and especially willows appear to provide important food resources for spring passage migrants along the Lower Colorado River in Mexico. Spring floods are critical to the germination of both willow and cottonwood seedlings, and once established the plants can sustain growth to maturity without recurrent flooding (Zamora-Arroyo et al. 2001). However, future pulse flows, increased environmental flows, and active restoration will be important for the germination of new cohorts of cottonwood and willow, and for keeping soil salinity low enough for the continued survival of native plants (Glenn et al. 1998, Nagler et al. 2008). Even a small proportion of native plants within a tamarisk-dominated landscape has been shown to increase diversity and abundance of migrant landbirds (Fischer et al. 2015). Thus, environmental flows will be a key component in the restoration of the Lower Colorado River.

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Figure 1. Location of five study areas along the Colorado River and adjacent wetlands in Mexico (LT = Limitrophe, BCT = tamarisk site along the river, BCN = native site along river, CE = Ciénega de Santa Clara, DR = El Doctór wetlands) where spring passerine migrants were observed foraging in 2000, 2001, and 2014.

Figure 2. Attack rates by spring passerine migrants in four vegetation types (ME = mesquite, TA = tamarisk, ON = other natives, WI = willow) along the lower Colorado River in Mexico in 2000 and 2014.

Figure 3. Proportion of foraging observations (eight species pooled) that occurred in each of four tree or shrub species (ME = mesquite, TA = tamarisk, ON = other natives, WI = willow) at five sites (BCN = Baja California native, BCT = Baja California tamarisk, CE = Ciénega de Santa Clara, DR = El Doctór wetlands, LT = limitrophe) along the lower Colorado River in Mexico in 2000 and 2001 (combined) and 2014.

Figure 4. Proportion of foraging observations of 7 species of spring migrants (BTYW = black-throated gray warbler, NAWA = Nashville warbler, OCWA = orange-crowned warbler, WAVI = warbling vireo, WIWA = Wilson's warbler, YEWA = yellow warbler) in each of 4 dominant tree species (CO = cottonwood, ME = mesquite, TA = tamarisk, WI = willow) along the lower Colorado River in Mexico in 2000 and 2001 (combined) and 2014.

Table 1. Model selection results* of spring migrant prey attack rate as a function of site, vegetation type, and percent leaf-out and flowering along the Lower Colorado River in Mexico in 2000 and 2001 (combined) and 2014.

Model**	K	AIC_c	ΔAIC_c	w	cw	LL
<i>2000</i>						
veg	5	623.21	0.00	0.77	0.77	-306.43
veg+site	8	625.86	2.64	0.20	0.97	-304.51
site	5	629.74	6.53	0.03	1.00	-309.70
intercept	2	636.94	13.73	0.00	1.00	-316.44
<i>2014</i>						
veg	5	734.68	0.00	0.86	0.86	-362.21
flower*veg	9	739.71	5.03	0.07	0.93	-360.45
site+veg	9	741.08	6.40	0.04	0.96	-361.13
green*veg	9	741.47	6.79	0.03	0.99	-361.33
intercept	2	746.88	12.20	0.00	1.00	-371.41
site	6	747.25	12.57	0.00	1.00	-367.44
green*veg+site	13	748.04	13.37	0.00	1.00	-360.19
green	3	748.64	13.97	0.00	1.00	-371.27
flower	3	748.92	14.24	0.00	1.00	-371.41
global	17	752.86	18.18	0.00	1.00	-358.00

*AIC_c = Aikake's Information Criterion, w = model weight, cw = cumulative weight, LL = negative log likelihood

**veg = vegetation type, site = site, intercept = only random effect intercept for bird species included in model, green = percent green leaf of foraging substrate, flower = percent flowering of foraging substrate, global = all terms included in model

Table 2. Model-averaged standardized regression coefficients for covariate effects on prey attack rate of spring migrants foraging along the Lower Colorado River in Mexico in 2000-2001 (combined) and 2014.

Coefficient*	Effect	SE	95% CI
<i>2000</i>			
UN	-0.60	0.20	-0.99, -0.21
DR	0.57	0.36	-0.14, 1.28
CE	0.44	0.45	-0.43, 1.32
WI	-0.43	0.33	-1.08, 0.23
BCT	0.25	0.48	-0.69, 1.2
TA	-0.03	0.10	-0.22, 0.15
<i>2014</i>			
WI	0.53	0.15	0.23, 0.83
LT	-0.22	0.21	-0.64, 0.19
Green*WI	0.19	0.15	-0.12, 0.49
Green*UN	0.19	0.17	-0.14, 0.51
TA	0.18	0.14	-0.09, 0.44
Flower*UN	-0.17	0.18	-0.52, 0.18
Green	-0.13	0.13	-0.38, 0.13
Green*TA	0.11	0.16	-0.20, 0.41
UN	-0.10	0.19	-0.48, 0.28
Flower*TA	0.09	0.13	-0.16, 0.34
Flower*WI	-0.07	0.13	-0.33, 0.19
BCT	-0.05	0.22	-0.49, 0.38
Flower	0.02	0.10	-0.17, 0.22
CE	0.02	0.27	-0.51, 0.56
DR	-0.01	0.18	-0.36, 0.34

*UN = other natives, WI = willow, TA = tamarisk, Green = percent green leaf, Flower = flower,

BCT/CE/DR = site codes

Table 3. Means, standard errors (SE), and results of logistic regression comparing phenological characteristics of trees used by foraging migrant songbirds (“used”) and randomly selected (“available”) trees along the Lower Colorado River in Mexico in 2014.

Species & Trait*	Used		Available		Coefficient Estimate	SE	z	p
	Mean	SE	Mean	SE				
<i>Mesquite</i>								
Green	91.8	2.4	87.2	2.4	0.010	0.010	1.040	0.290
Flower	33.6	5.1	26.4	3.5	0.005	0.005	0.980	0.320
<i>Tamarisk</i>								
Green	78.4	0.9	87.8	2.2	-0.040	0.009	-4.170	<0.001
Brown	2.0	0.8	3.2	0.6	-0.050	0.020	-2.600	0.009
Flower	19.0	2.9	16.4	2.1	0.002	0.004	0.450	0.650
Fruit	26.9	3.0	34.7	2.8	-0.005	0.004	-1.260	0.210
<i>Willow</i>								
Green	88.8	1.2	88.4	3.6	-0.003	0.010	-0.330	0.740
Flower	23.9	5.7	14.6	3.0	0.010	0.005	2.610	0.009
Fruit	37.8	6.5	21.1	3.3	0.010	0.005	3.190	0.001

*Trait values presented as percents; green = % of whole tree in green leaf, brown = % of whole tree in brown leaf, flower = % of maximum flowering, fruit = % of maximum fruit.

Table 4. Relative frequencies of high energy (aerial) and low energy foraging maneuvers used by Wilson's Warbler foraging in 3 tree species (ME = mesquite, TA = tamarisk, WI = willow) along the Colorado River in 2000, 2001, and 2014.

Substrate	High Energy	Low Energy	# Obs
<i>All Years</i>			
ME	0.48	0.52	233
TA	0.61	0.39	177
WI	0.32	0.68	53
<i>2014</i>			
ME	0.59	0.41	41
TA	0.61	0.39	71
WI	0.33	0.67	48