

CHAPTER EIGHT

Phenological Synchrony of Bird Migration with Tree Flowering at Desert Riparian Stopover Sites*

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Abstract. Small-bodied songbirds replenish fat reserves during migration at stopover sites where they continually encounter novel and often unpredictable environmental conditions. The ability to select and utilize high-quality habitats is critical to survival and fitness. Vegetation phenology is closely linked with emergence of insect prey and may provide valid cues of food availability for stopover habitat selection. Climate change is disrupting phenological synchrony across trophic levels with negative impacts on bird populations. However, whether synchrony or mismatch indicates historic or disrupted systems remains unclear. Many Neotropical migratory songbirds of western North America must cross arid regions where drought conditions related to climate change and human water use are expected to increase. We studied migrant abundance and the diversity (niche breadth) and proportional use of vegetation species as foraging substrates and their synchrony with vegetation flowering during spring migration along the lower Colorado River in the Sonoran Desert of the United States and Mexico. Peak migrant abundance in late March–early April coincided with the period of narrowest

niche breadth. Abundance of migrants increased with willow and mesquite flowering, but significantly only in 2003, a severe drought year. Annual niche breadth was negatively correlated with flowering and with total monsoon precipitation. Birds proportionally foraged most in willow and mesquite, shifting from one species to the next, temporally synchronous with their flowering. The period of greatest overlap in willow and mesquite flowering and use also coincided with peak migrant abundance and narrowest niche breadth. Our results show that migration timing and foraging habitat selection is highly synchronized with flowering of large woody perennials, particularly in dry years. However, if food availability declines in dry years, increased selection of fewer species for foraging could result in greater competition and reduced fitness. Therefore, increased synchrony rather than mismatch could indicate negative climate-driven impacts on some systems.

Key Words: climate change, drought, mesquite, niche breadth, phenological mismatch, *Prosopis*, *Salix*, Sonoran Desert, willow, wood-warbler.

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Neotropical songbirds must make frequent stops to rest and feed during migration, a phenological period with potentially high mortality (Moore and Kerlinger 1987, Sillett and Holmes 2002, Seewagen and Guglielmo 2010). During stopover, birds repeatedly encounter novel habitats and unpredictable environmental conditions (Moore et al. 1990, Parrish 2000, Petit 2000). An ability to identify, select, and utilize high-quality stopover habitat elements across a wide range of habitat types and conditions would benefit reproduction and survival (Balbontin et al. 2009, Bauchinger et al. 2009, LaManna et al. 2012). Understanding factors that influence stopover habitat selection and use is important for improving migratory bird conservation (Faaborg et al. 2010a, b).

Food availability is an intrinsic component of stopover habitat quality (Rodewald and Brittingham 2007, Bauchinger et al. 2009, Carlisle et al. 2012), but can only be directly assessed once birds have entered a stopover site (Aborn and Moore 2004; Paxton et al. 2007, 2008). Songbirds rely on insect prey during spring migration (Aborn and Moore 1997, MacDade et al. 2011), and emergence and abundance of invertebrates often track the phenology of plant resources, resulting in phenological synchrony between both trophic levels (Visser and Holleman 2001; Visser et al. 2006; van Asch et al. 2007, 2010). Vegetation phenology may provide valuable cues of food availability and habitat quality that allow en route migrants to maximize stopover habitat selection among and within stopover sites (Buler et al. 2007, McGrath et al. 2009, Strode 2009). Bird migration can thus become spatially and temporally synchronized with plant phenology due to trophic relationships with prey. Climate-driven phenological mismatches have been linked to trophic cascades that disrupt migration patterns and induce population declines (Both et al. 2009, Thackeray et al. 2010, Saino et al. 2011).

The ecological consequences of phenological synchrony or mismatch are often unclear. Few studies directly assess synchrony of bird migration with vegetation phenology at stopover sites and the demographic impacts can be species and system dependent (Jones and Cresswell 2010, Miller-Rushing et al. 2010). It is easy to assume that climate-driven mismatch has necessarily negative consequences for populations (Both et al.

2006), but mismatch may be the historical condition or even be evolutionarily adaptive (Singer and Parmesan 2010, Visser et al. 2012). Many studies of bird migration and phenological mismatch have focused on how temporal patterns of bird abundance at a site coincide with resource phenology, such as correlations between the temporal peaks in migrant detections or capture rates with flowering of plants at seasonally used sites (Bertin 1982, Hart et al. 2011) or the correlation between onset dates of plant flowering and bird arrival (McKinney et al. 2012). Although these seasonal patterns provide an index of synchrony, they do not directly link use of specific foraging substrates with their phenology of flowering or other key resources. In addition to examining patterns of relative migrant abundance and plant phenology, we directly assessed how the use of vegetation species as foraging substrates was temporally correlated with flowering phenology to gain greater insight into the implications of observed levels of synchrony.

Many Neotropical migratory songbirds in the western United States must cross large regions of the arid Southwest (Kelly and Hutto 2005). Riparian forests and woodlands that border large river systems can provide vital stopover habitat to a range of species (Skagen et al. 2005). Under climate change models, arid lands of North America are expected to experience more extreme conditions, becoming increasingly hot and dry with extended severe drought periods (Seager et al. 2007, Weiss et al. 2009, Balling and Goodrich 2010). Bird migration can be synchronized by climate as well as food availability. The interactions of climate, plant phenology, and food availability could have important implications for birds that rely on riparian stopover habitat in desert regions (Jones et al. 2003, Kelly and Hutto 2005, Skagen et al. 2005).

Our goals were to examine temporal patterns and phenological synchrony of migrant abundance, the diversity and proportional selection of different plant species as foraging substrates, and the flowering phenology of these species at spring stopover sites along the lower Colorado River in southwestern Arizona and northwestern Sonora, Mexico. We also assessed the influence of annual variation in monsoon precipitation and drought on phenological synchrony.

METHODS

Study Sites

We assessed bird migration and vegetation phenology at four sites along the lower Colorado River (LCR) in the southern United States and northern Mexico. The LCR watershed includes a vast region of western North America and bridges the US and Mexican border en route to the Gulf of California. Like many large rivers, the waters of the Colorado River are intensively managed (Poff et al. 1997, Rajagopalan et al. 2009). Our study sites were located at Cibola and Bill Williams National Wildlife Refuges, Arizona, and El Doctor, Sonora, and Alto Golfo de California Biosphere Reserve, Baja California, Mexico (Figure 8.1).

Climate

We obtained climate data on precipitation and drought from the National Oceanic and Atmospheric Association National Climatic Data Center for Arizona Climate Division 5 (NOAA 2013). The majority of annual precipitation in this region falls during the North American monsoons (Adams and Comrie 1997), and we used the total amount of precipitation (millimeters) recorded over the monsoon season during July through September in the year prior to each spring migration season. We assessed annual drought conditions leading up to each migration season using the Palmer drought severity index (PDSI) for March through February (NOAA 2013).



Figure 8.1. Locations of four study sites (black dots) where we studied spring bird migration and plant phenology along the lower Colorado River in the southwestern United States and northwestern Mexico, 2000–2003.

TABLE 8.1
Focal species of neotropical migratory songbirds and the number of foraging observations made along the lower Colorado River in southwestern Arizona and northwestern Sonora, Mexico, during Spring migration, 2000–2003.

Common name	Scientific name	No. Foraging observations
Wilson's Warbler	<i>Cardellina pusilla</i>	3969
Orange-crowned Warbler	<i>Oreothlypis celata</i>	1935
Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	1207
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	1165
Warbling Vireo	<i>Vireo gilvus</i>	942
Yellow-rumped Warbler	<i>Setophaga coronata</i>	693
Townsend's Warbler	<i>Setophaga townsendi</i>	592
Lucy's Warbler	<i>Oreothlypis luciae</i>	562
Yellow Warbler	<i>Setophaga petechia</i>	338
MacGillivray's Warbler	<i>Oreothlypis tolmiei</i>	236
Hermit Warbler	<i>Setophaga occidentalis</i>	163
Ruby-crowned Kinglet	<i>Regulus calendula</i>	43
Bell's Vireo	<i>Vireo bellii</i>	21

Focal Bird Species and Surveys

We selected an assemblage of 12 species of insectivorous songbirds (Table 8.1). Of these birds, only Yellow Warbler (*Setophaga petechia*) and Lucy's Warbler (*Oreothlypis luciae*) breed at our study sites (Corman and Wise-Gervais 2005). We used point count transects to estimate relative migrant abundance (Reynolds et al. 1980). To determine niche breadth and proportional use of vegetation species as foraging substrates during each survey period, we walked the same transects used for point counts and recorded the tree species in which foraging activity was first observed for each individual of a focal bird species encountered (Remsen and Robinson 1990).

Vegetation Phenology

We measured the flowering phenology of mesquite (*Prosopis* sp.), Gooding's willow (*Salix goodingii*), Fremont cottonwood (*Populus fremontii*), and tamarisk (*Tamarix* sp.), which represent the dominant and largest species of trees and shrubs at our study sites. Along each survey transect where we performed point counts and bird foraging surveys, we also estimated the percentage of flowering of

100 individuals of each species (van Riper 1980, McGrath et al. 2009).

We performed point counts, foraging, and vegetation phenology surveys between 1 March and 31 May 2000–2003. We divided survey dates into eight 10-day periods within which no site was surveyed more than once. We were unable to conduct point-count surveys during periods 1 and 8 in 2002 and 2003 and foraging surveys during period 4 in 2001, period 2 in 2002, and periods 1–3 and 8 in 2003.

Analyses

We calculated relative migrant abundance as the mean number of migrants per point at each site per survey period. We used the Shannon and Weaver (1964) entropy statistic as a measure of niche breadth (\hat{H}) for individual focal bird species during each survey period using the following function:

$$\hat{H} = -\sum p_i \ln(p_i)$$

where p = the proportional use of plant species i as a foraging substrate (Strode 2009). We use the

term “niche breadth” to refer only to the diversity of vegetation species used as foraging substrates at the stopover sites we surveyed, recognizing that diversity represents only one dimension of a bird’s overall niche. We calculated mean values across study dates to assess annual patterns of relative abundance and niche breadth.

We used generalized linear models (GLMs) to examine variation in relative migrant abundance, niche breadth, and proportional use of focal tree species among years and across survey dates and to explore correlations of niche breadth with migrant abundance, monsoon precipitation, and tree flowering. To assess phenological synchrony, we also used GLMs to examine the relationships of migrant abundance and proportional tree use with percentage of flowering, including tree species and survey period as factors. We treated survey date as an integer to assess trends in abundance, niche breadth, and phenological synchrony through time and included second-order terms and two-way interactions in analyses. We examined differences among factor levels with Tukey’s multiple comparison tests with Bonferroni adjustments. We performed all analyses in program R 2.1.5 (R Development Core Team 2012).

RESULTS

Migrant Abundance

Relative migrant abundance per site did not differ among years ($F = 2.3$, $df = 3$, $P = 0.12$). Within years, relative abundance had a negative quadratic relationship with survey date ($F = 5.9$, $df = 1$, $P < 0.05$), whereby abundance generally peaked in early April (Figure 8.2).

Niche Breadth

Niche breadth was different among years ($F = 4.0$, $df = 3$, $P < 0.01$); it was broadest in 2000 ($z = 2.9$, $P < 0.01$) and narrowest in 2002 ($z = 2.3$, $P < 0.05$; Figure 8.3). Niche breadth had a positive quadratic relationship with survey date ($F = 4.9$, $df = 1$, $P < 0.05$; Figure 8.2), with birds foraging in the narrowest diversity of species in late March. Niche breadth was also inversely correlated with migrant abundance ($F = 5.7$, $df = 1$, $P < 0.05$; Figure 8.2).

Proportional Tree Use

Proportional use of focal tree species as foraging substrates was not different among years ($F = 2.5$, $df = 9$, $P = 0.12$). Birds disproportionately foraged

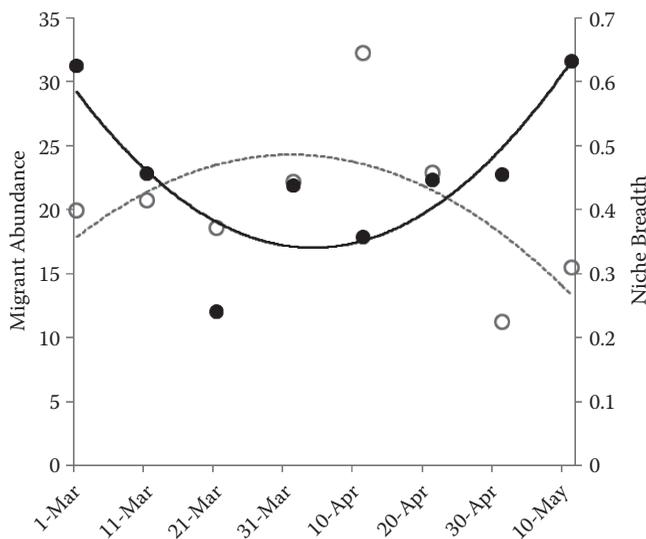


Figure 8.2. Abundance (circles) and niche breadth (dots) of 13 species of migratory birds combined during spring migration along the lower Colorado River in the southwestern United States and northwestern Mexico, plotted by 10-day time periods from 2000 to 2003. Niche breadth represents a Shannon-Weaver diversity index (0–1) of tree species birds used as foraging substrates during stopover; values closer to one indicate greater niche breadth and the use of more tree species. Best-fit polynomial lines are shown for abundance (dashed) and niche breadth (solid).

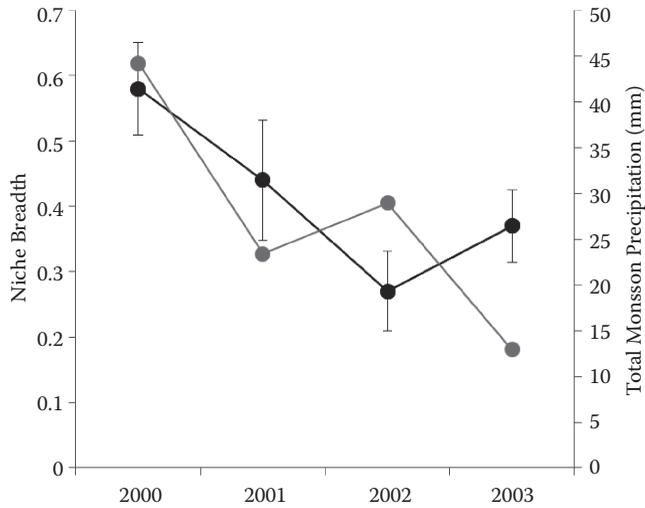


Figure 8.3. Annual mean niche breadth (black) \pm SE of migratory birds during spring migration (March–May) and total monsoon precipitation (July–September, gray) of the preceding year along the lower Colorado River in the southwestern United States and northwestern Mexico. Precipitation is for Arizona climate division 5 (NOAA 2013).

in tree species ($F = 33.0$, $df = 3$, $P < 0.0001$). Migrants used mesquite more than all other species ($z = 9.9$, $P < 0.0001$), and willow more than cottonwood and tamarisk ($z = 2.4$, $P < 0.05$; Table 8.2).

TABLE 8.2

Plant species used as foraging substrates for focal migratory bird species and the mean proportion of foraging observations (p) per 10-day survey period along the lower Colorado River in the United States and Mexico, March–May, 2000–2003.

Plant species	Common name	p
<i>Prosopis</i> sp.	Mesquite	0.72
<i>Salix gooddingii</i>	Gooding's willow	0.40
<i>Populus fremontii</i>	Fremont cottonwood	0.28
<i>Tamarix</i> sp.	Tamarisk	0.24
<i>Pluchea sericea</i>	Arrow weed	0.18
<i>Parkinsonia</i> sp.	Palo verde	0.12
<i>Baccharis</i> sp.	Baccharis	0.10
<i>Larrea tridentata</i>	Creosote	0.07
<i>Lycium berlandieri</i>	Wolfberry	0.02
<i>Typha latifolia</i>	Cattails	0.02
<i>Atriplex canescens</i>	Salt bush	0.01

NOTE: The four most used species represent our focal species for which flowering phenology was recorded.

Tree Flowering

Mean percent flowering was not different among years for willow and mesquite combined ($F = 1.5$, $df = 2$, $P = 0.24$) or for mesquite alone ($F = 0.5$, $df = 2$, $P = 0.63$). However, flowering of willow was greater in 2001 ($23.2 \pm 9.3\%$, $t = 2.7$, $P < 0.01$) than in 2002 ($3.9 \pm 1.3\%$) and 2003 ($8.1 \pm 2.8\%$). Flowering of willow and mesquite combined was significantly correlated with survey date ($F = 10.7$, $df = 1$, $P < 0.01$).

Phenological Synchrony

Migrant abundance was not correlated with the percentage of flowering of focal tree species combined ($F = 1.2$, $df = 1$, $P = 0.31$). However, there was an interaction of flowering and year ($F = 8.4$, $df = 2$, $P < 0.05$); only in 2003 was the positive linear increase in migrant abundance with flowering significant ($\beta = 2.2$, $F = 19.2$, $df = 1$, $P < 0.05$; Figure 8.4a). The relationship between abundance and flowering was also positive but not significant in 2001 ($\beta = 0.4$, $F = 1.0$, $df = 1$, $P = 0.36$) and 2002 ($\beta = 0.6$, $F = 1.3$, $df = 1$, $P = 0.33$; Figure 8.4a). Niche breadth had a negative linear relationship with percentage of flowering of willow and mesquite ($F = 12.2$, $df = 1$, $P < 0.05$; Figure 8.5).

Proportional use of mesquite and willow for foraging was highly correlated with the percentage

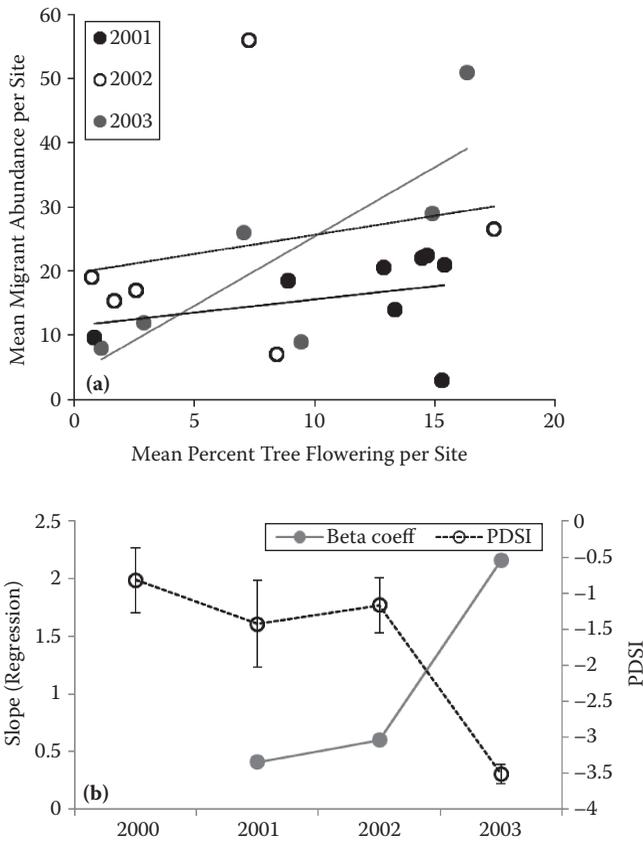


Figure 8.4. (a) The relationship between mean relative abundance of migratory birds and percentage of flowering of willow (*Salix gooddingii*) and mesquite (*Prosopis* sp.) at four sites along the lower Colorado River from 1 March–31 May, 2001–2003. Best-fit regression lines for each year are 2001 (solid black), 2002 (dashed), 2003 (solid gray). (b) The regression coefficients (β) from the annual fitted linear models in panel a (solid gray line and circles) and the mean Palmer drought severity index (PDSI) over a 12-month period (dashed black line with open circles) March through February.

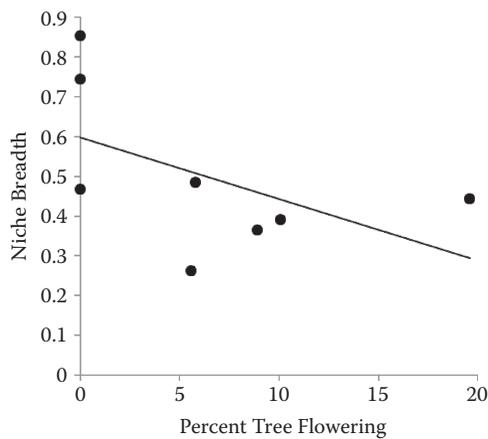


Figure 8.5. Relationship between niche breadth of migratory birds and percentage of flowering of willow and mesquite at stopover sites along the lower Colorado River in the southwestern United States and northwestern Mexico during spring migration, 2001–2003.

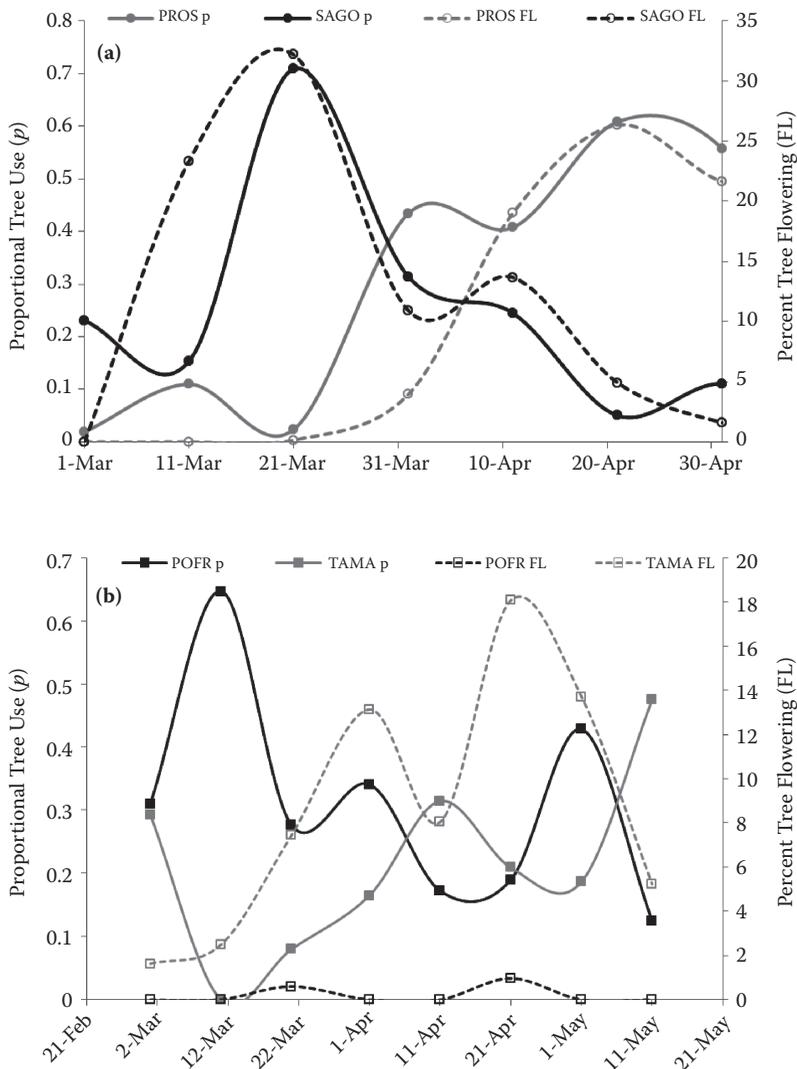


Figure 8.6. Phenological synchrony between mean percentage of flowering (FL) and the mean proportional use (p) as foraging substrates by migratory birds of (a) *Prosopis mesquite* species (PROS) and Gooding's willow (*Salix gooddingii*, SAGO) and (b) Fremont cottonwood (*Populus fremontii*, POFR) and tamarisk (*Tamarix* sp., TAMA) during spring migration at four sites along the lower Colorado River in the southwestern United States and northwestern Mexico, 2001–2003.

of flowering of these species ($F = 9.8$, $df = 1$, $P < 0.01$), and proportional use of each species was highly synchronized with flowering over the migration period (Figure 8.6a). There was an interaction of proportional use with survey date ($F = 5.0$, $df = 1$, $P < 0.05$), and mesquite use was negatively correlated with willow use ($F = 7.1$, $df = 1$, $P < 0.05$), representing a shift in foraging from willow to mesquite (Figure 8.6a). There was no significant relationship between proportional use of cottonwood and tamarisk and their

percentage of flowering ($F = 0.4$, $df = 1$, $P = 0.52$; Figure 8.6b).

Precipitation and Drought

Total monsoon precipitation was lowest the summer prior to the 2003 migration season (Figure 8.3) and had the lowest mean monthly PDSI value (Figure 8.4b), indicating a severe drought (NOAA 2013). Niche breadth had a positive linear relationship with total monsoon

precipitation the preceding summer ($F = 129.2$, $df = 3$, $P < 0.01$), with annual niche breadth and precipitation showing a decreasing trend from 2000 to 2003 (Figure 8.3). The broadest mean niche breadth occurred in 2000, following the highest total monsoon precipitation during our study (Figure 8.3), and the largest β coefficient for the relationship between migrant abundance and tree flowering was in 2003, following a severe drought ($PDSI < -3$, NOAA 2013, Figure 8.4b).

DISCUSSION

Temporal patterns of migrant abundance and the diversity (niche breadth) and proportional selection of plant species as foraging substrates were highly synchronized with flowering of these plant species during spring migratory stopover along the lower Colorado River. Peak migrant abundance during late March and early April coincided with the period of narrowest niche breadth when migrants were primarily foraging in willow and mesquite. Timing of migration further coincided with the greatest temporal overlap in willow and mesquite flowering, suggesting that this may be the period of peak flowering phenology and hence food availability and habitat quality for this riparian habitat (McGrath et al. 2009).

The strong patterns of phenological synchrony we observed—particularly between niche breadth, proportional substrate use, and flowering in relation to precipitation and climate—question whether synchrony in this case is always a benefit that represents the historic or unmodified condition of the ecosystem. High concentrations of migrants at stopover sites can rapidly decrease food abundance and limit birds' ability to replenish energy reserves (Moore and Yong 1991). In drier years, migrant abundance had a stronger positive correlation with willow and mesquite flowering, while niche breadth decreased as migrants concentrated their foraging within these few species, possibly abandoning more peripheral habitat areas that could contain fewer preferred prey under dry conditions. Increased selection of willow and mesquite for foraging could lead to greater densities of birds in these high-quality substrates and have negative density-dependent effects on migrants—resulting in greater competition for prey, decreased replenishment of energy reserves, and decreased fitness as birds'

ability to complete migration and breed successfully is compromised (Moore and Yong 1991, Smith and Moore 2003, Norris and Marra 2007). Furthermore, if the emergence of preferred prey were to become decoupled from flowering phenology, flowering would no longer represent a valid indicator of habitat quality (Johnson 2007). Unsuitable cues could result in a greater concentration of birds selecting foraging habitat that has less available food.

The concentration of proportional foraging on willow and mesquite trees and shrubs, especially during drier years, may indicate greater predictability of preferred prey availability in these species in addition to their synchronous timing of flowering. Variation in plant growth and productivity in arid lands is strongly influenced by precipitation, the majority of which comes during summer monsoons (Adams and Comrie 1997, Ogle and Reynolds 2004). Large, woody perennials such as willow and mesquite can access deeper ground water and may be less susceptible to annual variation in precipitation and thus could sustain greater densities of preferred prey species (Ehleringer et al. 1991, Stromberg et al. 1996, McGrath et al. 2009). Altered flood frequency, reduced water tables, and increased salinity have already drastically reduced the abundance of large woody perennials and riparian forest (Busch and Smith 1995). Increasing human demands on the limited water available in the Colorado River Basin due to climate change-induced drought and continued exurban development, agriculture, and recreation further threaten riparian habitat (Christensen et al. 2004). Maintaining sufficient willow and mesquite stopover habitat along the lower Colorado will likely require active management strategies that address flow regimes, forest restoration, and water conservation in the region (Stromberg 2001, Garfin et al. 2007, van Riper et al. 2008).

Latitudinal differences in phenology and synchrony among our sites was beyond the scope of this chapter. Spring phenology seems to be advancing most rapidly at more northern latitudes (Parmesan 2007, Ellwood et al. 2013); however, our most distant sites were only about 250 km apart, were within the same bioregion and climate zone, and had the same vegetation communities. Perhaps more important than latitude, our sites spanned the international border

between the United States and Mexico. Water policies in the United States strongly impact the amount of water in the Colorado River flowing into Mexico and the Gulf of California and thus the condition of riparian habitats there (Glenn et al. 2001, Zamora-Arroyo et al. 2001). Future research in the US–Mexican borderlands would benefit from international consideration of how political control and legislation of water use and access may affect the presence, distribution, and condition of riparian stopover habitats.

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