Flower power: tree flowering phenology as a settlement cue for migrating birds

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Summary

1. Neotropical migrant birds show a clear preference for stopover habitats with ample food supplies; yet, the proximate cues underlying these decisions remain unclear.

2. For insectivorous migrants, cues associated with vegetative phenology (e.g. flowering, leaf flush, and leaf loss) may reliably predict the availability of herbivorous arthropods. Here we examined whether migrants use the phenology of five tree species to choose stopover locations, and whether phenology accurately predicts food availability.

3. Using a combination of experimental and observational evidence, we show migrant populations closely track tree phenology, particularly the flowering phenology of honey mesquite (*Prosopis glandulosa*), and preferentially forage in trees with more flowers. Furthermore, the flowering phenology of honey mesquite reliably predicts overall arthropod abundance as well as the arthropods preferred by migrants for food.

4. Together, these results suggest that honey mesquite flowering phenology is an important cue used by migrants to assess food availability quickly and reliably, while in transit during spring migration.

Key-words: foraging, habitat selection, migration, phenology, stopover

Introduction

Migration is an energetically demanding period in the annual cycle of many species of birds, and can impose strong selection on individuals and represent an important limitation to population viability (Lindström 1989; Marra, Hobson & Holmes 1998; Sillet & Holmes 2002; Heglund & Skagen 2005; Lind & Cresswell 2006). Because of their small size and long-distance migration, Neotropical migrant songbirds are unable to carry sufficient energy reserves to migrate nonstop and must select habitats en route to stop and refuel (Moore & Aborn 2000). Stopover site selection directly influences survival and has cascading effects on future reproduction (Piersma 1990; Moore et al. 1995; Moore, Smith & Sandberg 2005); yet during migration, most individuals are in unfamiliar surroundings and have limited time and energy to sample habitats (Hutto 1985a; Loria & Moore 1990; Moore, Kerlinger & Simons 1990; Moore & Yong 1991; Moore & Aborn 2000; Petit 2000). Food limitation, predation, competition, and unfavourable weather all represent important costs associated with selecting stopover locations (Moore et al. 1995, 2005; Petit 2000) and theory would predict that birds should choose locations that minimize these costs (Fretwell & Lucas 1970; Fretwell 1972; Houston 1998).

However, despite clear evidence that migrants exhibit habitat preference during stopover (Hutto 1985a; Moore et al. 1995, 2005), we know little about the ecological cues individuals use to select stopover locations (Petit 2000). Variation in food resources, for example, can profoundly affect risk of starvation, exposure to predation, breeding energy budgets, and timing of breeding (Lima & Dill 1990; Piersma 1990; Moore et al. 1995, 2005; Newton 2006). Birds clearly prefer habitats that maximize the availability of food resources (Hutto 1985a; Moore et al. 1995), yet the cues that birds use to select these habitats remain largely unknown. Although direct sampling of food availability is the most accurate method of determining habitat suitability, the time and energy constraints migrants face may limit them to using vegetative and structural cues (Moore & Aborn 2000). Available foliage is generally correlated with the diversity and abundance of herbivorous insects (Marques, Price & Cobb 2000; Murakami, Hirao & Ichie 2007); therefore, changes in tree phenology (e.g. flowering, leaf flush, and leaf loss) may present insectivorous migrant birds with structural cues that reliably predict food availability.

Here we used observational and experimental evidence to examine whether insectivorous Neotropical migrant birds use tree phenology to choose stopover locations and if phenology accurately predicts food availability. Specifically, we asked: (i) Are macrohabitat patterns of avian diversity and abundance...
correlated with seasonal variation in tree phenology? (ii) Do migrant birds prefer particular phenological cues when selecting foraging microhabitats? and (iii) Do these cues accurately predict food availability?

Methods

STUDY SYTEM AND SPECIES

We examined the role of tree phenology in avian habitat selection between March and May of 2001 to 2004 at Cibola National Wildlife Refuge along the lower Colorado River. We established a study site along the riparian corridor, dominated by five tree species (40% FRCO, 25% HOME, 17% SCME, 7% GOWI, 11% TAMA) and seasonally occupied by >100 species of migrant birds of which we focused on 28 species of insectivorous Neotropical migrant songbirds (Table 1).

MACROHABITAT PREFERENCE

To assess the ability of the avian community to use tree phenology as a settlement cue, we established two 1-km transects through the middle of the study area, separated by 300 m. Transects did not differ in vegetation and are not considered independent samples, but rather a means of assuring overlap between estimates of avian abundance and stand phenology. Each week, the same observer walked both transects visually sampling 100 trees of each species found within 50 m. At each tree, we calculated phenology by visualizing a full crown and estimating the proportion of the tree currently covered by leaves, flowers, and fruits. We then averaged data for each species to obtain weekly stand conditions (after van Riper 1980). To increase rigor, we also documented phenology using a digital camera, but since both methods produced similar results ($t = 14.38, P = 0.17$), we present the larger samples based on visual estimates. Simultaneously, we conducted 25-m fixed-radius point counts (Hutto, Pletschet & Hendricks 1986) from sunrise to 09.00 h at eight points along each transect. To minimize bias, we reversed starting points for avian counts and tree phenology weekly. We tested for correlations between phenology and raw estimates of avian diversity and abundance using a combination of Pearson correlations and general linear models (GLM) that included migrant species, year, and transect as factors and date as a covariate. We excluded nonsignificant interactions from trial models and corrected for multiple tests using a Bonferroni correction.
MICROHABITAT PREFERENCE

To assess microhabitat preferences, we sampled individual birds along the same transects used for point-count sampling and compared the tree species and phenological conditions of migrant foraging locations against the average weekly phenology (see above) and availability of that tree species based on percentage coverage (i.e. use vs. availability). We compared the location of the first-attack maneuver, as opposed to the location of first detection, because attack maneuvers specifically identify foraging location, serve as independent observations (Bell, Hejl & Verner 1990), and reduce bias associated with variation in tree architecture, (Sturman 1968;
Hertz, Remsen & Zones 1976; Bradley 1985). We tested for differences in tree species preferences using a GLM that included migrant species and year as factors and date as a covariate with least significant difference (LSD) post-hoc tests to identify differences among tree species. We also tested for differences in tree species use vs. availability using a paired t-test of the average preferences and availability of each tree species for each sampling period in each year. We examined phenophase preferences for all tree species and each tree species individually using a binary logistic regression, where selected tree vs. nonselected tree was the dependent variable, the three phenophase traits and date were continuous factors, and year and migrant species were included as categorical factors. We excluded nonsignificant interactions from trial models and corrected for multiple tests using a Bonferroni correction.

FOOD AVAILABILITY AND USE

We compared food availability among tree species by sampling branches from the five dominant tree species for arthropods three times in 2003 (April 3, 18; May 6). Branches (1–2.5 cm diameter, 50–70 cm long) were selected within the preferred foraging height of migrants within each tree species (van Riper, unpublished data), and selected branches were removed from the tree, vigorously shaken into a large plastic bag, and visually inspected for hidden arthropods (after Johnson 2000). Because migrants do not forage on all arthropods, we identified preferred species by sampling the diet of a subset of migrants captured by passive mist netting, using a modified lavage technique which has been proven effective in sampling both hard- and soft-bodied arthropods (Moody 1970; Tombback 1975; Rosenberg & Cooper 1990; Poulin, Lefebvre & McNeil 1994). We tested for the influence of tree species and phenology on total arthropod and preferred arthropods abundance using a combination of Pearson correlations and a GLM that included date as a covariate with LSD post-hoc tests to identify differences among tree species. We performed all tests at the lowest taxonomic identification (e.g., morpho-species) and excluded nonsignificant interactions from trial models.

EXPERIMENTAL MANIPULATION OF PHENOLOGY

The timing of leafing, flowering, and fruiting are highly correlated and their relative importance as cues for habitat selection are difficult to discern from observational data alone. For example, in honey mesquite the timing of leafing and flowering often overlap, limiting our ability to identify which cue birds may use to choose foraging locations. To separate among alternative cues, in 2003 we experimentally manipulated the flowering phenology of one of two paired honey mesquite trees. We randomly selected 17 pairs of honey mesquite in full bloom (<10 m apart) and reduced flower coverage on one, creating two phenology categories: light flower (<5% coverage) and heavy flower (>30% coverage). Trees were deflowered by pulling petals by hand, being careful to remove the cue (i.e. the flower), but not the available arthropods, and were continually manipulated throughout the sampling period to maintain light flowering levels.

For each experimental pair, we measured migrant preference by recording the number of birds that visited each tree within a 15-min observation period between sunrise and 09.00 h. We monitored...
All five tree species expressed unique patterns of phenology, but generally phenological traits were positively correlated (Fig. 1; all leaf—all flower: Pearson_{xy} = 0.809, P < 0.001; all leaf—all fruit: Pearson_{xy} = 0.583, P = 0.002; all flower—all fruit: Pearson_{xy} = 0.499, P = 0.009). Migrant diversity and abundance were positively correlated with the combined flower phenology of all tree species (Fig. 1; diversity: all flower: F_{5,26} = 4·693, P = 0·012; abundance: all flower: F_{5,26} = 8·024, P = 0·010; date F_{5,26} = 0·406, P = 0·531; year: F_{5,26} = 1·998, P = 0·147). However, when examined independently, only the flowering phenology of honey mesquite correlated with both diversity and abundance of migrants (Fig. 1; diversity: HOME flower: F_{5,26} = 18·447, P < 0·001; date F_{5,26} = 0·566, P = 0·461; year: F_{5,26} = 5·099, P = 0·009; abundance: HOME flower: F_{5,26} = 9·622, P = 0·006; date F_{5,26} = 0·085, P = 0·773; year: F_{5,26} = 1·916, P = 0·159), although the flowering phenology of screwbean mesquite did correlate with diversity (diversity: SCME flower: F_{5,26} = 13·418, P = 0·002; date F_{5,26} = 2·131, P = 0·161; year: F_{5,26} = 2·741, P = 0·072).

**MICROHABITAT PREFERENCE**

At the microhabitat level, tree species also significantly influenced migrant foraging decisions (tree: F_{5,26} = 21·540, P < 0·001; year: F_{5,26} = 0·621, P = 0·15), as migrants were found on honey mesquite more than other species (Fig. 2a) and more than availability would predict (Fig. 2b; HOME: t_{30} = 5·299, P = 0·013; FRCO: t_{30} = −6·587, P = 0·008; TAMA: t_{30} = 7·87, P = 0·006). Migrants also preferred trees of all species that had more leaves and flowers (Fig. 2c; all leaf: Wald_{1,26} = 28·143, P < 0·001; all flower: Wald_{1,26} = 40·254, P < 0·001; all fruit: Wald_{1,26} = 0·914, P = 0·339; year: Wald_{1,26} = 4·426, P = 0·035; date: Wald_{1,26} = 16·748, P < 0·001; tree species: Wald_{1,309} = 20·502, P < 0·001; migrant species: Wald_{1,309} = 5·253, P = 0·096), but similar to macrohabitat patterns, when examined independently, only the phenology of honey mesquite was positively correlated with microhabitat preferences (Fig. 2d; HOME leaf: Wald_{1,26} = 14·598, P < 0·001; HOME flower: Wald_{1,26} = 16·599, P < 0·001; HOME fruit: Wald_{1,26} = 1·441, P = 0·230; year: Wald_{1,26} = 0·772, P = 0·380; date: Wald_{1,26} = 6·320, P = 0·012; migrant species: Wald_{1,26} = 0·781, P = 1·000).

**FOOD AVAILABILITY AND USE**

We collected 172 different morpho-species representing 12 orders; however, migrant stomach contents included only nine orders of which five morph-species (preferred arthropods) made up >25% of their total diet. Tree species (Fig. 3) and phenology (Fig. 4) influenced both total (tree species: F_{4,309} = 3·514, P = 0·008; leaf: 1·399 = 1·311, P = 0·253; flower: 1·399 = 61·274, P < 0·001) and preferred arthropod abundance (tree species: F_{4,309} = 5·962, P < 0·001; leaf: 1·399 = 2·757, P = 0·098; flower: 1·399 = 50·139, P < 0·001); however, only preferred arthropod abundance differed between tree species (Fig. 3b). When examined independently, total arthropod abundance was positively correlated with the flowering phenology of three of the five tree species (HOME flower: F_{5,26} = 18·549, P < 0·001; GOWI flower: F_{5,26} = 30·929, P < 0·001; TAMA flower: F_{5,26} = 21·771, P < 0·001), but preferred arthropod abundance was only correlated with the flowering phenology of honey mesquite (Fig. 4d; HOME flower: F_{5,26} = 30·752, P < 0·001).

EXPERIMENTAL MANIPULATION OF PHENOLOGY

Experimental manipulations significantly reduced flower coverage (Fig. 5a; treatment: $F_{1,128} = 530.226$, $P < 0.001$; tree pair: $F_{16,128} = 2.430$, $P = 0.004$; date: $F_{1,128} = 14.231$, $P < 0.001$), but not leaves (Fig. 5a; treatment: $F_{1,128} = 1.253$, $P = 0.265$; tree pair: $F_{16,128} = 4.015$, $P < 0.001$; date: $F_{1,128} = 91.801$, $P < 0.001$) and resulted in a significant decrease in visitation rate of migrants (Fig. 5b; treatment: $F_{1,128} = 28.094$, $P < 0.001$; tree pair: $F_{16,128} = 1.757$, $P = 0.047$; date: $F_{1,128} = 2.142$, $P = 0.146$).

Discussion

Migration is an important component of the life history of migratory birds, and for species that do not migrate continuously, where they stop to rest and refuel can have important implications for future survival and reproduction (Piersma 1990; Moore et al. 1995, 2005; Petit 2000). Yet, despite the importance of stopover decisions to avian life-history evolution and migratory bird conservation, we know little about how birds select stopover habitats. Predation and competition may shape stopover decisions, but food availability likely determines habitat preference (Hutto 1985a; Petit 2000; Moore et al. 2005). Birds are sensitive to food availability (Morris et al. 1958; MacArthur & Pianka 1966; Zach & Falls 1976) and can preferentially settle in food-rich environments (e.g. Hutto 1980; Yard et al. 2004); yet, the cues underlying these decisions remain unclear. Using both observational and experimental evidence, we show for the first time that the flowering phenology of a common tree species, honey mesquite, acts as a reliable settlement cue for insectivorous Neotropical migrant birds at both the macro- and micro-habitat levels.

Although we examined the phenology of all five major tree species along the Lower Colorado River, only the flowering phenology of honey mesquite consistently predicted seasonal variation in migrant diversity and abundance (Fig. 1). Mesquite flowers are highly visible and therefore may reduce search time in unfamiliar habitats. Furthermore, total and preferred arthropod abundance correlated with the flowering phenology of honey mesquite (Fig. 4), indicating the reliability of flowers as a settlement cue and implying that migratory timing and routes may have evolved to exploit this readily available and explicitly advertised resource. Indeed, exploitation of high elevation and monsoon-dependent habitats by fall migrant populations (e.g. DeLong, Cox & Cox 2005) suggests that stopover habitat preferences may be highly dependent upon area phenology. Alternatively, since
Empirical studies demonstrating the ability of birds to track greater availability of food (Fig. 4); indeed, there are many trees with more flowers (Fig. 2) is not surprising given the mesquite with more flowers (Fig. 2). That migrants prefer honey mesquite to other tree species, and particularly honey mesquite trees with more flowers independent of other vegetative cues (Fig. 5) or actual food availability. Alternatively, by manipulating flower abundance, we may have inadvertently reduced arthropod abundance, leading to changes in migrant habitat preferences based on food availability and not flower phenology; however, this is unlikely. First, although flower availability likely influences the distribution of pollinating arthropods, a minor component of migrant diet, herbivorous arthropod are more dependent on leaf phenology (e.g. Murakami et al. 2007), which was unchanged (Fig. 5a). Second, migrants primarily persist on small cryptic arthropods, thus even if we did alter food availability, it is unlikely that birds could directly assess differences before visiting each tree. Indeed, the failure of previous studies to affect migrant abundance and concentration of migrants during spring migration may create a positive feedback loop whereby herbivory, increasing survival and reproduction of host plants (reviewed in Schmitz, Hambäck & Beckerman 2000). That honey mesquite had the greatest abundance of arthropods (Fig. 3), and > 25% of the diet of migrants consisted of herbivorous insects, suggests such a possibility. The extreme abundance and concentration of migrants during spring migration may create a positive feedback loop whereby migrants reduce the costs of herbivory enabling honey mesquite trees to invest more in reproduction, producing more flowers, and thus a stronger signal to attract more migrants. In either case, the close tie between the timing and distribution of Neotropical migrants and the flowering phenology of honey mesquite suggests a strong co-evolutionary relationship.

Similar to the macrohabitat patterns, migrants preferred honey mesquite to other tree species, and particularly honey mesquite with more flowers (Fig. 2). That migrants prefer trees with more flowers (Fig. 2) is not surprising given the greater availability of food (Fig. 4); indeed, there are many empirical studies demonstrating the ability of birds to track food availability (Morris et al. 1958; Hildén 1965; MacArthur & Pianka 1966; Zach & Falls 1976; Hutto 1980, 1981, 1985b; Yard et al. 2004). Surprisingly, experimental tests of the importance of food availability in stopover decisions have failed to find a causal relationship (e.g. Hutto 1990); however, our data suggest an important distinction. Previous experiments altered food availability without changing the proximate cues birds rely upon to select appropriate habitats (Hutto 1990). Here we directly manipulated one settlement cue, flower phenology, and show migrants prefer honey mesquite trees with more flowers independent of other vegetative cues (Fig. 5) or actual food availability. Alternatively, by manipulating flower abundance, we may have inadvertently reduced arthropod abundance, leading to changes in migrant habitat preferences based on food availability and not flower phenology; however, this is unlikely. First, although flower availability likely influences the distribution of pollinating arthropods, a minor component of migrant diet, herbivorous arthropod are more dependent on leaf phenology (e.g. Murakami et al. 2007), which was unchanged (Fig. 5a). Second, migrants primarily persist on small cryptic arthropods, thus even if we did alter food availability, it is unlikely that birds could directly assess differences before visiting each tree. Indeed, the failure of previous studies to affect migrant habitat preferences by altering food availability (e.g. Hutto 1990) may reflect the importance of arthropod behaviours in determining which cues birds use to select stopover locations. Still, any accidental change to arthropod abundance may have been advertised via public information (e.g. Doligez et al. 2004), but given that migrants tended to arrive and forage alone suggests otherwise, and highlights the potential importance of vegetative cues in selecting foraging locations.

Conclusion

In the western USA, Neotropical migrants and their riparian migratory corridors are topics of conservation concern (Heglund & Skagen 2005; van Andel & Aronson 2006); yet little is known about the factors limiting migratory bird populations, particularly as it pertains to the ecology of migration. Given the strong correlation between honey mesquite flowering phenology and migrant populations at the macro-habitat level, as well as experimental and observational evidence of preference for flowering honey mesquite at the micro-habitat level, it appears that the flowering phenology of honey mesquite is an important settlement cue for Neotropical migrant birds. That the flowering phenology of honey mesquite is a reliable indicator of food availability indicates the importance of this cue for migrant populations, at least along the Colorado River. It remains unclear how the phenology of honey mesquite or other tree species may influence migratory behaviours along other important migratory corridors that differ geographically, have different migratory peaks, and support different population and species assemblages (Skagen et al. 2005; Paxton et al. 2007). Furthermore, preferences based on proximate vegetative cues that likely...
respond independently from ultimate selective pressures acting on migratory timing or food availability, highlight the potential for this system to transform into an ecological trap (Robertson & Hutto 2006). Future research should focus on the generality of flowering phenology as a settlement cue and how anthropogenic change, such as climate change and invasion by exotic tree species, may alter flower cues, migrant preference, and food availability independently to impact migrant populations.

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References


Bell, G.W., Hejl, S.J. & Verner, J. (1990). Proportional use of substrates by preference, and food availability independently to impact how anthropogenic change, such as climate change and invasion by exotic tree species, may alter flower cues, migrant preference, and food availability independently to impact migrant populations.


Skagen, S.K., Kelly, J.F., van Riper, C., Hutto, R.L., Finch, D.M., Cruse,

Sturman, W.A. (1968). The foraging ecology of *Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons with other species of *Parus*. *Condor, 70*, 309–322.


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