

Patch age since disturbance drives patch dynamics for flycatchers breeding in both reservoir and riverine habitat

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Abstract. Species dependent upon early-successional landscapes often occupy patches at different stages of recovery after disturbance. The demographic processes that drive patch dynamics in these systems have rarely been described but are important for developing effective conservation and management plans, especially when humans have modified the timing and intensity of disturbances that drive regeneration. In riparian systems, disturbance by floods historically initiated plant regeneration, but many rivers are now regulated and stream flows disrupted by dams and reservoirs. We studied the demography and patch dynamics of an endangered, neotropical migrant bird dependent on remnant riparian patches for breeding, the southwestern willow flycatcher (*Empidonax trailli extimus*), over 9 yr at both a riverine and reservoir site in central Arizona. We found that at both sites, number of territories/ha within patches increased for 2–4 yr after colonization and then declined, with several patches abandoned after 6–10 yr. Age of birds increased with patch age, with younger birds in colonizing patches and older, site-faithful birds in older patches, while mean per capita reproductive success did not differ with patch age. Natal dispersal and breeding dispersal were primarily from intermediate-aged patches into either younger or other intermediate-aged patches. At both riverine and reservoir sites, both the number of patches and the number of territorial birds increased over time, with the percentage of territories shifting into younger and younger patches. The type of disturbance driving patch regeneration differed between riverine and reservoir sites (seasonal flooding vs. falling lake levels due to drought), but the demographic patterns did not, indicating that reservoirs can generate patch dynamics similar to those on rivers. Managing stream flows and reservoir levels to maintain disturbance cycles sufficient to generate riparian patches at different stages of regeneration through time would benefit succession-dependent species like the endangered flycatcher we studied, whether those disturbances arise from natural flooding events along free-flowing rivers or through changes in reservoir levels.

Key words: demography; disturbance; flooding; patch dynamics; reservoir; riparian; stand age.

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INTRODUCTION

Natural disturbances like fires and floods are key ecological drivers that maintain landscape heterogeneity in both time and space by creating patches at different stages of recovery after

disturbance (Brawn et al. 2001). Animals inhabiting these dynamic landscapes often exist as spatially structured populations that are themselves dynamic, with animals colonizing newly created patches and abandoning others (Pickett and White 1985, Wu and Loucks 1995). For animals

dependent on specific successional stages, the availability of suitable patches will depend both on the rate of disturbance and on the length of time patches remain in a suitable state. Spatially structured population models that incorporated the effects of patch age have shown that this parameter can have important implications for overall population persistence (Amarasekare and Possingham 2001, Hastings 2003, Wilcox et al. 2006), but for most species, we have little empirical data on demographic responses to patch age or estimates of the length of time patches remain suitable (but see Probst and Hayes 1987, Akresh et al. 2015).

Riparian areas are a classic example of disturbance-driven landscapes, and floodplains have been argued to represent a shifting mosaic (Bormann and Likens 1979) of patches at different stages of regeneration (Arscott et al. 2002, Ward et al. 2002, Hohensinner et al. 2005, Latterell et al. 2006). Flooding in riparian systems destroys or modifies existing vegetation and opens new areas for plant establishment, thereby altering both the structure and composition of riparian vegetation (Junk et al. 1989, Hupp and Osterkamp 1996). The scale and magnitude of vegetation change vary with flood intensity and frequency. Floods of high power and low frequency (100-yr events) can produce major geomorphic changes (Hauer and Lorang 2004), while less powerful, more frequent (1- to 5-yr return) floods scour smaller portions of the floodplain, while leaving larger areas intact. Many rivers are now dammed, and historical flood patterns along these rivers have been altered by reducing flood magnitude and periodicity (Poff et al. 1997). In addition, the area behind a dam within a reservoir's draw-down zone may experience a different pattern of disturbance as reservoir levels rise and fall (Ellis et al. 2009). Understanding the demographic consequences of these human-altered disturbance regimes for organisms adapted to dynamic riparian systems therefore has important implications for both conservation and management in these highly managed systems.

In the arid southwestern United States, riparian areas are biologically diverse, highly productive, and, although they occupy <1% of the land area, serve as critical habitat for many animal species (Skagen et al. 1998). Gallery riparian

forests of cottonwood (*Populus fremontii*) and Goodding's willow (*Salix gooddingii*) historically covered hundreds of kilometers along rivers of the southwestern United States (Stromberg 1993), but today these riparian forests are fragmented and reduced in area due to lowering water tables, altered flow regimes due to damming and irrigation, and conversion to agriculture (Stromberg 1993). The southwestern willow flycatcher (*Empidonax traillii extimus*) is one of several neotropical migrant birds that breed exclusively in these riparian areas (Unitt 1987, Marshall 2000), and the southwestern subspecies of the flycatcher was listed as federally endangered in 1995 (USFWS 1995), in part as a result of the loss and modification of riparian habitats on the breeding grounds (USFWS 1993, Marshall and Stoleson 2000). Monitoring of flycatchers by agencies throughout the southwestern United States between 1993 and 2001 indicated that the breeding population was widely dispersed across riparian fragments, with over half of all territorial birds occurring as small congregations of 5 or fewer territories, and only 2 of 221 sites having more than 50 territories (Sogge et al. 1993). Occupancy of those surveyed sites also varied through time, with territorial birds disappearing from some sites, and reappearing at the same or new sites years later (Sogge et al. 1993), suggesting a dynamic system in which abandonment, colonization, and recolonization of sites were common. Understanding how these dynamic demographic responses interact with patch age in both highly modified reservoir and relatively unmodified riverine landscapes has important implications for management and recovery of the subspecies.

Previous studies of early-successional species in shrub and forest systems allowed us to make several predictions about how flycatchers might respond to disturbance and patch recovery in a riparian system (Probst and Hayes 1987, Schlossberg and King 2009, Donner et al. 2010, Akresh et al. 2015). First, we predicted that flycatcher territory density (the number of territories/ha), like territory density in other early-successional species, would show a non-linear response to patch age over time, with density increasing after patch colonization to a peak and then declining as patches aged beyond their window of suitability (Schlossberg and King 2009, Donner et al.

2010, Akresh et al. 2015). Second, in many migratory passerines, natal dispersal (movement of birds from the area where they fledged to the area of first breeding) tends to be away from the natal patch, while older birds tend to be relatively site faithful, returning to the patch where they bred in previous years (Greenwood and Harvey 1982, Lehnert and Rodewald 2009). Therefore, we predicted that natal dispersal would contribute most to patch colonization, while breeding dispersal (the movement of adults from one breeding patch to another) would contribute less. The tendency of adults to return to a patch may depend upon previous breeding success, however, with adults that were unsuccessful breeders being more likely to move to new patches than birds that bred successfully (Haas 1998, Hoover 2003, Schlossberg 2009). Therefore, we predicted that breeding dispersal into new patches would be dominated by adults that had failed in their breeding attempts in other patches in previous years. Third, if colonization of newly developing patches was primarily by young birds in their first breeding season, as predicted above, while older patches were dominated by older, site-faithful adults, we predicted that mean age of flycatchers would be younger in newly colonized patches and would increase with patch age. Fourth, we predicted that reproductive success would increase with patch age, as older birds often have higher reproductive success than younger ones (Nolan 1978, Noll and Smith 1987). These predictions were tested at both a reservoir site where disturbance was limited to changes in water levels and a riverine site where seasonal flooding at the confluence of a free-flowing and regulated river was the main disturbance. We expected patch occupancy and territory density to eventually decline over time at the reservoir site as patches aged beyond their suitability and were not replaced by newly regenerating patches, while we expected territory density to be more constant through time at the riverine site due to the greater frequency and magnitude of disturbance due to flooding.

METHODS

Study site

We studied southwestern willow flycatchers at Roosevelt Reservoir (33°39' N, 110°58' W) and

along the San Pedro/Gila River confluence (32°59' N, 110°46' W), where we conducted demographic research in cooperation with Arizona Game and Fish Department (AGFD) from 1995 to 2004. In both areas, breeding habitat was a mosaic of discrete riparian forest patches of varying ages and vegetation composition separated by intervening non-riparian vegetation typical of Sonoran Desert Uplands or by agricultural lands. The dominant riparian trees in patches were native Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*) and exotic tamarisk (saltcedar; *Tamarix* spp.). Understorey vegetation included a variety of grasses, forbs, and shrubs, including mesquite (*Prosopis* spp.), coyote willow (*S. exigua*), baccharis (*Baccharis* spp.), and cocklebur (*Xanthium strumarium*). The Roosevelt Reservoir study site consisted of two sub-sites on opposite sides of the reservoir approximately 25 km apart at the inflows of the Salt River and Tonto Creek. The riverine study site included riparian patches along 101 km of river system, centered at the confluence of the free-flowing San Pedro River and the regulated Gila River, and extending upstream along the San Pedro River to San Manuel Crossing and downstream along the Gila River to Kelvin Bridge.

Both Roosevelt Reservoir and the San Pedro/Gila Rivers experienced changes in riparian habitat over the period of our study. In 1995, Roosevelt Reservoir was at full capacity, but long-term, persistent drought conditions between 1996 and 2002 resulted in reservoir levels dropping to a low of 10% capacity by 2002. As the reservoir level fell during that period, new areas of lakebed were exposed in successive years, allowing new riparian vegetation to establish that was subsequently colonized by breeding flycatchers. The San Pedro and Gila Rivers experienced an unusually large scouring flood in 1993 that removed much of the riparian vegetation along those rivers. The riparian patches we studied included some that survived that flood, and others that regenerated afterward.

Surveys, banding, and territories

Territories were identified by a combination of spatially mapping locations of singing territorial males and identifying pairs through behavioral observations, nest searching, and color band

re-sighting. We did not attempt to map territory boundaries and instead defined territories as locations with territorial birds. We classified birds as territorial if they were detected singing and/or displaying aggressive behavior toward conspecifics repeatedly at the same location. To census territorial birds, our study areas were surveyed 3 times each breeding season using standardized tape-playback protocols developed for surveying this endangered subspecies (Sogge et al. 1997). Wherever flycatchers were detected during one of those surveys, additional visits were made to verify territorial behavior, identify color-banded birds, and to capture and band unbanded birds. Any new birds or territories detected on these additional visits were also subsequently visited for re-sighting/banding. On average, each banded bird was re-sighted 7 times per year. With field crew sizes of 25–35 field technicians/yr, we believe we detected nearly 100% of all territorial birds within the study areas. Given the consistent effort across years and sites, as well as extensive nest searching and color band re-sighting, we believed any differences in detectability across years or among stands of different ages would be small relative to the patterns we documented.

A total of 1080 adults were banded at both sites from 1995 to 2004, while 498 nestlings were banded at Roosevelt Reservoir from 1995 to 2004 and at San Pedro from 1995 to 2000. Each adult was banded with a color-anodized, federal, numbered bird band and a second color band to create a unique color combination for each individual. Nestlings were banded at 7–10 d of age with a single colored-anodized, numbered federal bird band; banded nestlings detected and recaptured as adults in subsequent years were given an additional color band to produce a unique color combination to assist in re-sighting. A drop of blood was taken at the time of banding for genetic gender determination. To determine gender of adult flycatchers, we used a combination of physical characteristics (presence of a cloacal protuberance for males or brood patch for females), behavioral cues (copulation, lordosis), and genetic sexing methods (Paxton et al. 2002). Adult flycatchers were classified as known age if the individual was first banded as either a nestling or as a second-year (SY) bird based on retained secondary

feathers (Pyle 1998) and as an unknown-aged if those criteria were absent.

Patch colonization and dispersal

At Roosevelt Reservoir, new riparian vegetation established on bare soil exposed as reservoir levels receded between 1996 and 2004, giving us the ability to estimate age of riparian vegetation when first colonized by breeding flycatchers. To do so, we created GIS shapefiles of the boundaries of occupied patches in the year each patch had peak occupancy. We then overlaid those shapefiles onto successive years (1996–2004) of normalized difference vegetation index (NDVI) raster grids from LandSat TM images in ArcGIS 9.0 (ESRI, Redland, California, USA). The NDVI raster grids measure vegetation density, and we masked them for values below 0.33, a threshold value for riparian vegetation in our study area (Hatten et al. 2010). For a given patch, the first year that NDVI values >0.33 were detected was defined as the year riparian vegetation established in that patch. The number of years after that establishment year until the first flycatchers were detected in that patch was used as our estimate of the patch age at colonization. Riparian vegetation in patches at our riverine site, in contrast, was not entirely removed by the flood in 1993, creating a mosaic of varying amounts of newly established vegetation, regrowth from surviving rootstock, and retained vegetation in each patch. Given that we could not use time since vegetation regenerated as the age of patch at our riverine sites, we instead used the first year territorial flycatchers were detected in a patch as the initial year of patch age in our subsequent analyses at both sites.

We compared patterns of territory density and bird age and reproductive success as stands aged based on 11 riverine patches and 11 reservoir patches. We defined patches based on a combination of vegetation type, spatial discreteness, and age of vegetation. At Roosevelt Reservoir, where new riparian vegetation regenerated as lake levels fell in subsequent years, vegetation structure differed significantly between areas regenerating in one year compared to those regenerating in the following year. These areas of regenerating riparian vegetation (cottonwood, willow, and tamarisk) of differing ages were also separated in space, with younger areas nearer the falling

water line. Areas regenerating in the same year often arose as discrete patches separated by a minimum of 0.2 km of intervening non-riparian vegetation. These reservoir patches ranged in size from 3 to 43 ha and included three patches on the western side at the Tonto Creek inflow and eight on the Salt River inflow (Fig. 1). Along the San Pedro and Gila River, patches were designated based on spatial location and separation from other riparian stands by non-riparian vegetation or ribbons of riparian vegetation too narrow to support a flycatcher territory (Fig. 2B). The riverine patches ranged from 2 to 26 ha in size and were separated from the nearest other patch by a minimum of 0.2 km of either non-riparian vegetation or vegetation lacking the height, width, or structure necessary for flycatcher nesting as described in Sogge et al. (1997).

To determine how territory density and bird age varied with patch age, we compared territory density (the number of territories divided by patch size) and mean age of territorial birds (both males and females) in each patch in each year using repeated-measures ANOVA in SPSS, with time as the within-subject factor and riverine and reservoir as the between-subject factor. Given that we expected a non-linear response of territory density over time, but a linear response of bird age, we based interpretation of the territory density analysis on the strength of the quadratic model and interpreted the age analysis based on the linear model. All patches were not occupied at the outset of the study, so the number of years occupied patches were studied varied, with only two occupied patches at the reservoir site and 4 at the riverine site studied for over 8 yr. Therefore, we limited these analyses to patches that had a minimum of 4 yr of data but did not include data beyond 8 yr because of small sample size. Patch was the sampling unit, so we compared 11 reservoir patches to 11 riverine patches.

To compare reproductive success in patches of different ages, we limited our analysis to the number of fledglings produced by females, as we were less certain of male reproductive success because of the potential for polygyny and extra-pair offspring (Davidson and Allison 2003, Pearson et al. 2006). We then compared mean reproductive success in each of the 11 reservoir and 11 riverine

sites using repeated-measures ANOVA with time as the within-subject factor and riverine and reservoir as the between-subject factor.

To investigate patterns of philopatry and natal and breeding dispersal, we compared three time periods: the year of patch colonization (colonization stage), a year estimated as the midpoint of patch age (3–5 yr after colonization, typically when territory density peaked, hereafter referred to as peak stage patches), and the last two years before a patch was abandoned (typically 6–10 yr after colonization, hereafter referred to as decline stage patches). We combined two years of data for the latter stage because number of territories was typically very low in the last year before the site was entirely abandoned. For patches that were not abandoned before the end of our study, we used the 4th year after colonization to represent the peak. For patches that were occupied when our study began but were abandoned before it ended, we used the 4th year before abandonment as the intermediate stage year. We compared these three stages for these analyses rather than analyzing data as continuous variables across all years because we felt the stage approach represented more clearly the distinction between early, mid-, and end point patch dynamics. This approach resulted in a total sample of 791 flycatchers, with 247 in patches at the colonization stage, 449 in patches at the peak stage, and 95 in patches at the decline stage.

To compare demographics of birds present in each of those three stand stages, we used chi-square contingency table analysis to test for relative differences in the number of birds that were (SY) immigrants, after second-year (ASY) immigrants that were successful breeders in their previous year, ASY immigrants that were unsuccessful breeders in the previous year, and ASY birds that returned to the same patch as the previous year (site-faithful birds). To describe patterns of natal and breeding dispersal, we tallied movements by 321 birds banded as nestlings, and 142 movements by territorial adults, to determine net movements into and out of patches at different stand stages. We defined natal dispersal as movement from the natal patch to the patch where the bird was first detected exhibiting territorial behavior as an adult, and we defined breeding dispersal as movement from the patch where the bird was territorial in

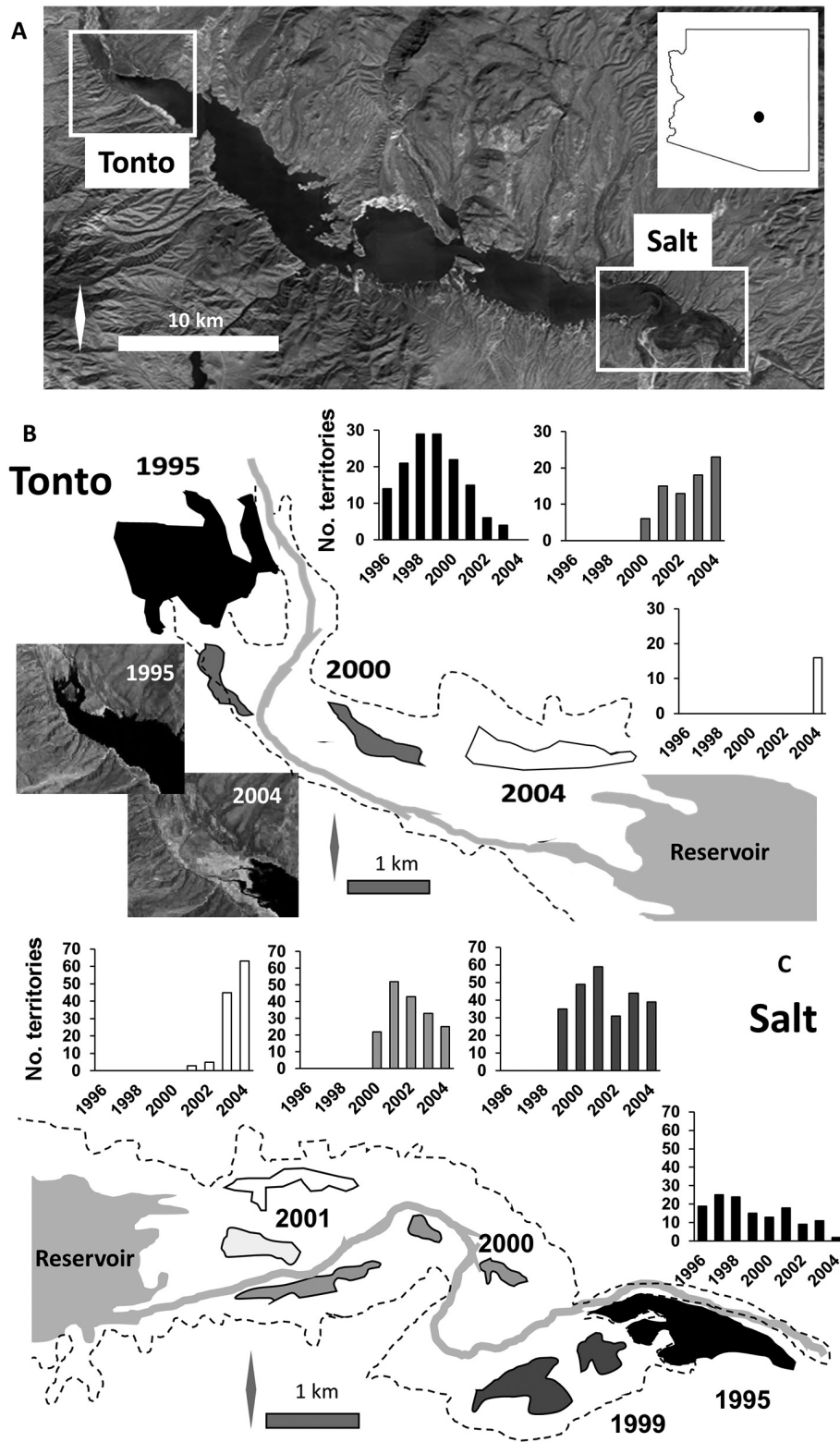


Fig. 1. (A) Aerial view of Roosevelt Reservoir, Arizona, USA, showing the Tonto Creek and Salt River inflows

(Fig. 1. *Continued*)

where southwestern willow flycatchers (*Empidonax traillii extimus*) were studied from 1995 to 2004. (B) The number of territorial male flycatchers through time in patches at the Tonto Creek inflow that were present in 1995 (black bars and polygon), and in new patches colonized by flycatchers in 2000 (gray bars and polygons) and in 2004 (white bars and polygons). Dashed line represents the reservoir water level in 1995, and light gray shaded area represents reservoir water levels in 2004. Inset is an aerial photograph of Tonto Creek that shows inflow in 1995 and 2004. (C) The number of territorial male flycatchers through time in patches at the Salt River inflow that were present in 1995 (black bars and polygon), and in new patches colonized by flycatchers in 1999 (dark gray bars and polygons), in 2000 (light gray bars and polygons), and in 2001 (white bars and polygons). Dashed line represents the reservoir water level in 1995, and light gray shaded area represents reservoir water levels in 2004.

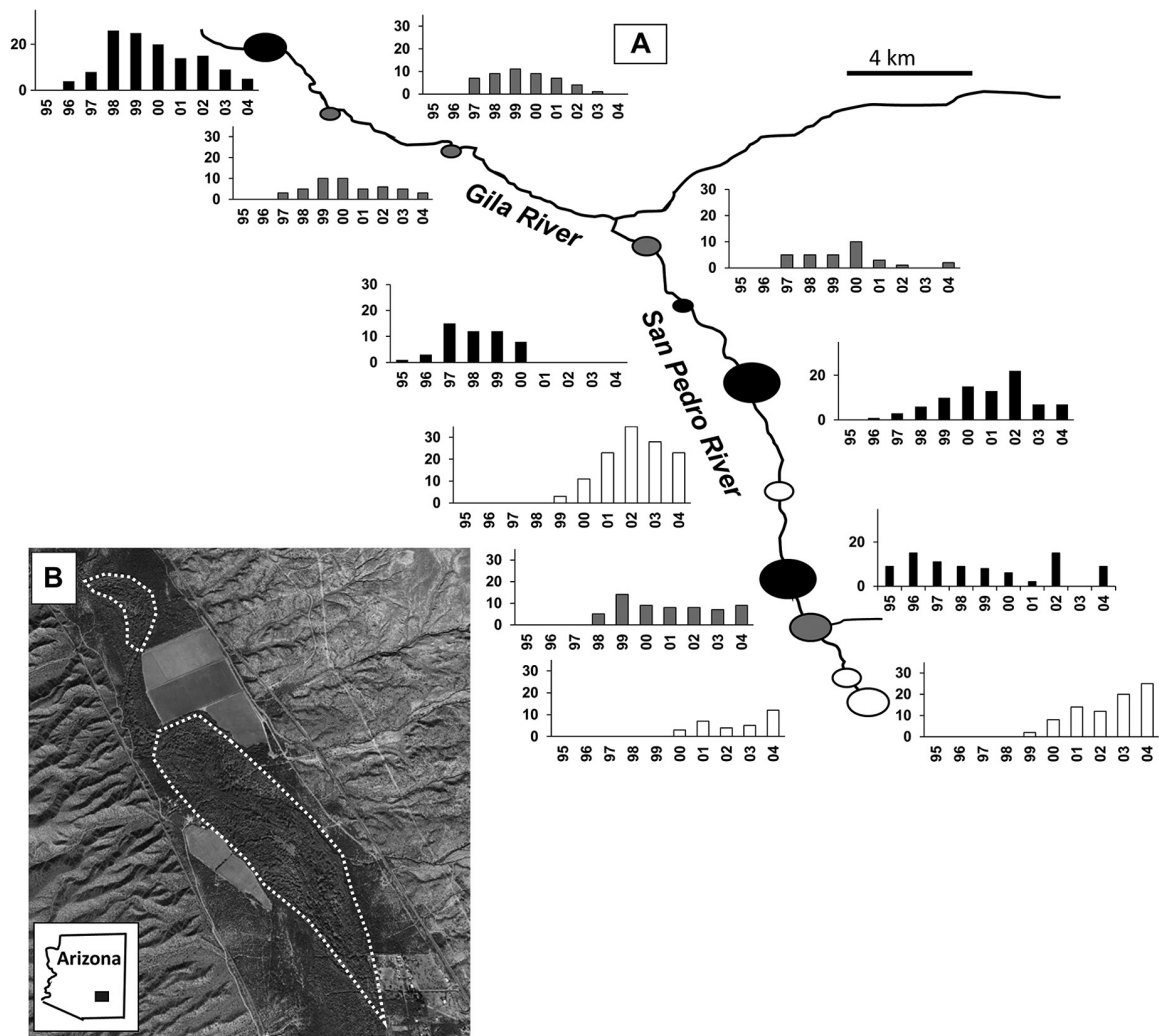


Fig. 2. (A) The number of territorial male flycatchers through time in patches along the Gila and San Pedro Rivers, Arizona, USA, between 1995 and 2004. Black bars and black circles represent patches occupied in breeding seasons of 1995 and 1996, gray bars and gray circles represent patches colonized in 1997 and 1998, and white bars and white circles represent patches colonized in 1999 and 2000. Size of circles reflects relative size of patch in one of 4 size categories: 1–4 ha (smallest circles), 5–8 ha, 12–15 ha, and 20–26 ha (largest circles). (B) Aerial view of the southernmost two patches (outlined with white dotted line) along the San Pedro Rivers, Arizona, USA.

one year to a territory in a different patch in a subsequent year.

Finally, to assess general patterns of patch occupancy through time, we graphed the total number of territories and the total number of occupied patches within the riverine and reservoir sites in each year. Within each year, we then calculated the percentage of territories that were in patches present at the outset of the study and in patches that recruited in subsequent years.

RESULTS

Spatially shifting patch occupancy

The number of patches occupied by territorial flycatchers, and the density of flycatcher territories within those patches, changed through time at both the riverine and reservoir sites. At Roosevelt Reservoir, drought caused water levels to fall farther and farther away from the two patches that were occupied at the outset of the study, while the soil exposed by the falling water provided regeneration sites for woody riparian trees like willows, cottonwood, and tamarisk along the retreating water line. The first of these new patches were colonized in 1999 (two patches on the Salt River inflow site), five new patches were colonized in 2000, two in 2001, and two in 2004 (Fig. 1). At the riverine site, two patches on the San Pedro River were occupied at the outset of the study, and new patches were colonized in each year from 1996 to 2000 (Fig. 2). All patches that were subsequently colonized at both the reservoir site and the San Pedro River portion of the riverine site were within 5 km of patches occupied at the outset of the study, while patches along the Gila River were from 8 to 20 km from the nearest patch occupied at the outset of the study. Thus, all of our patches were within the mean natal dispersal distance (20 km) (Paxton et al. 2007), and the great majority within the mean breeding dispersal distance (10 km) (Paxton et al. 2007), of an occupied patch, and distances to occupied patches decreased with time as more patches were colonized. Based on analysis of NDVI values at newly established patches at the reservoir site, we estimated new riparian habitat was first colonized by breeding flycatchers at the reservoir site when riparian vegetation was approximately 3 yr old (95% CI = 2.5–3.5). The smallest patch (2 ha) was

occupied for 6 yr, and the largest patch (43 ha) was still occupied after 9 yr but dwindled to only 2 territories by the end of our study.

Changes in territory density, age structure, and reproductive performance as stands aged

At both riverine and reservoir sites, mean territory density increased for 3–4 yr after patches were colonized and then decreased (within-subjects factor (time) $F = 7.4$; $df = 1, 10$; $P = 0.03$ for the quadratic model; between-subjects factor (site) $F = 0.961$; $df = 1$; $P = 0.37$; Figs. 1, 2, 3A).

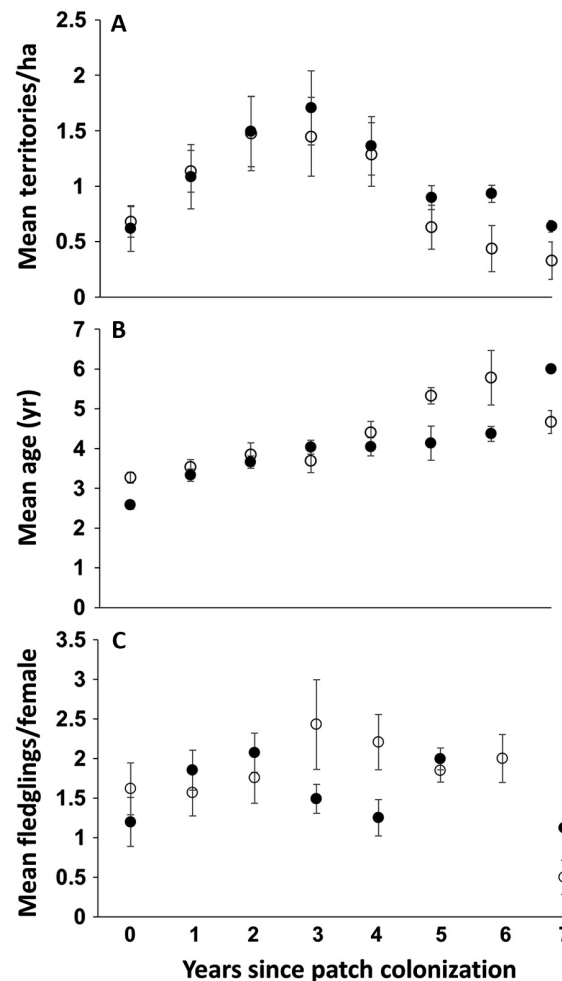


Fig. 3. (A) Mean (+SE) territory density, (B) bird age, and (C) number of fledglings/female vs. years since patch colonization for southwestern willow flycatchers based on 11 patches at a reservoir site (solid circles) and 11 patches at a riverine site (white circles) in central Arizona, USA, between 1995 and 2004.

At the reservoir site, territory density in the two patches occupied at the outset of the study initially increased and then declined, with one abandoned 8 yr after the study began and the other with 2 territories in the final year of the study. At the riverine site, one patch showed the full cycle from colonization to abandonment, with birds occupying the patch for 7 yr, while the other patches showed a general trend of increase in territory density after colonization followed by decrease (Figs. 2, 3A). As a result of this temporal change in territory density through time, although the maximum number of territories ever recorded in a patch across all years was positively related to patch size (simple linear regression $F = 18.3$; $df = 1, 20$; $P = 0.001$, $r^2 = 0.48$), by 2004, in the final year of the study, the number of territories was not significantly associated with patch size (2004: $F = 2.1$; $df = 1, 20$; $P = 0.16$, $r^2 = 0.07$), because many of the large patches occupied at the outset of the study contained few or no territories by the study's end.

As patches aged, mean age of territorial birds increased linearly, with no difference between riverine and reservoir sites (within-subjects factor [time] $F = 18.1$; $df = 1, 10$, $P = 0.07$; between-subjects factor [site] $F = 0.22$; $df = 1$; $P = 0.72$; Fig. 3B). Mean number of fledglings/female showed no significant relationship with patch age at either the riverine or reservoir site, and riverine and reservoir sites did not differ (within-subjects factor [time] $F = 1.0$; $df = 1, 10$; $P = 0.45$; between-subjects factor [site] $F = 0.95$; $df = 1$; $P = 0.43$; Fig. 3C).

Changing patterns of dispersal and philopatry

Based on the subset of birds in patches at the colonizing, peak and declining stages, the relative proportions of birds that settled through natal dispersal, breeding dispersal, or philopatry varied significantly across patch stages ($\chi^2 = 37.5$, $P < 0.001$; Fig. 4). Considering those birds of known age for which breeding history from the previous year was known, 46% of flycatchers in patches during the colonization stage were second-year (SY) birds in their first year of breeding (natal dispersers) and 53% were older birds that had bred previously at other locations (breeding dispersers). Of those breeding dispersers, birds that had previously bred

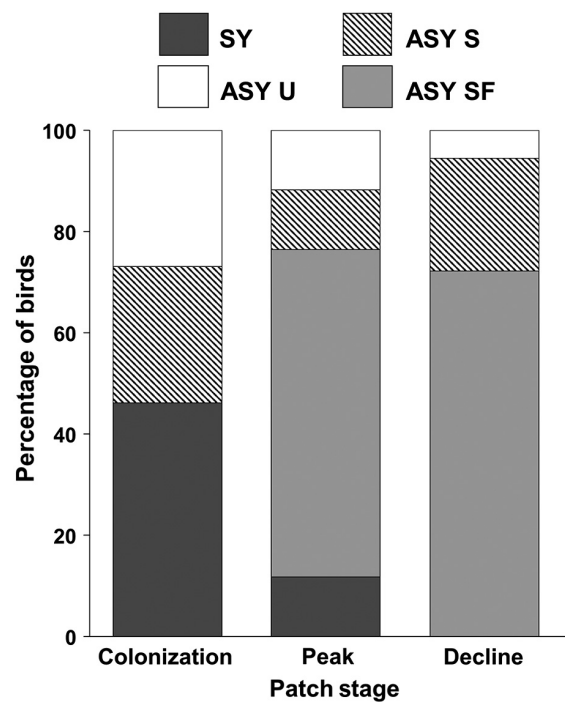


Fig. 4. The percentage of 791 southwestern willow flycatchers of known age and breeding history that were second-year (SY) immigrants (dark gray), after second-year (ASY) immigrants that were successful breeders in their previous year (ASY S, hatched), ASY immigrants that were unsuccessful breeders in the previous year (ASY U, white), and ASY, site-faithful birds that returned to the same patch as the previous year (ASY SF gray) in colonizing, peak, and declining stages of riparian stand development.

successfully and those that had not were roughly equally represented, in spite of the fact that 67% of birds that were successful in one year returned to breed in the same patch the next year, while only 27% of unsuccessful birds did so. The similar percentages of successful and unsuccessful breeding dispersers were due to the fact that previously successful breeders were two times more common in our sample, so that although a lower percentage of successful breeders dispersed in subsequent years than unsuccessful breeders, the overall number dispersing was similar. Most birds in patches at the intermediate and decline stages were site-faithful, philopatric, older adults that had returned to the same patch to breed after breeding there the previous year (65% and 71%, respectively).

Of the 321 nestlings we banded, 54 (17%) were banded in patches at the colonization stage, 226 (70%) in patches at the peak stage, and 41 (13%) in patches at the decline stage. Sixty-eight of those 321 banded nestlings were re-sighted on territories the following year as second-year birds, and 93% of those had originated in peak stage patches. As a result, the bulk of natal dispersal we documented was from peak stage patches, and 95% of those moved roughly equally into either colonizing or peak stage patches (Fig. 5B). Overall, the end point of natal dispersal was primarily into patches at either the colonizing stage (50%) or the peak stage (46%), with few (4%) dispersing into decline stage patches.

As with natal dispersal, peak stage patches contributed the most breeding dispersers into other patches, with most breeding dispersal into

other peak stage patches (Fig. 5C). Of the 142 adult flycatchers that were territorial in one patch in one year and were subsequently territorial in another patch in the following year, 104 (70%) originated in patches at the peak stage, while the remainder were roughly evenly divided between colonizing and decline stage patches (18 and 12%, respectively). Regardless of origin, most breeding dispersal (68%) was into patches at peak stages, while 21% was into patches at the colonizing stage and 11% into decline stage patches.

Shifting patch occupancy and population growth

When all 22 patches were considered, the number of flycatcher territories increased eight-fold at the reservoir site and 20-fold at the riverine sites during the course of the study (Fig. 6A).

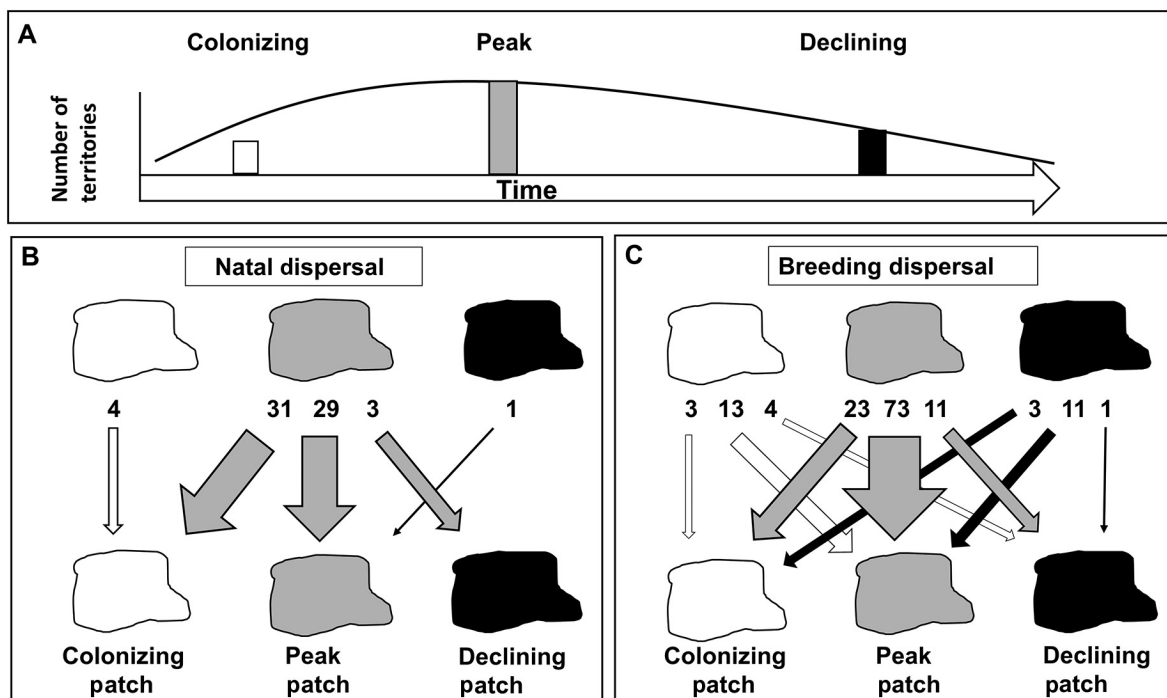


Fig. 5. (A) Conceptual model of how patches pass from an initial colonization stage (white bar) with relatively few southwestern willow flycatcher territories to a peak stage when the number of territories reaches a maximum (gray bar) and then a declining stage in the years before the patch is abandoned. (B) Natal dispersal was primarily from the peak stage into patches at the colonizing or peak stage (gray patches and arrows), while patches at the colonizing (white patches and arrows) and declining stage (black patches and arrows) contributed little. (C) Breeding dispersal was primarily from patches at peak stages to other patches at peak stage, with fewer to colonizing or declining stage patches. In both (B and C), arrows are scaled in size to reflect the relative number of birds and numerals above arrows are the number of birds moving from patches at each stage into patches at each stage.

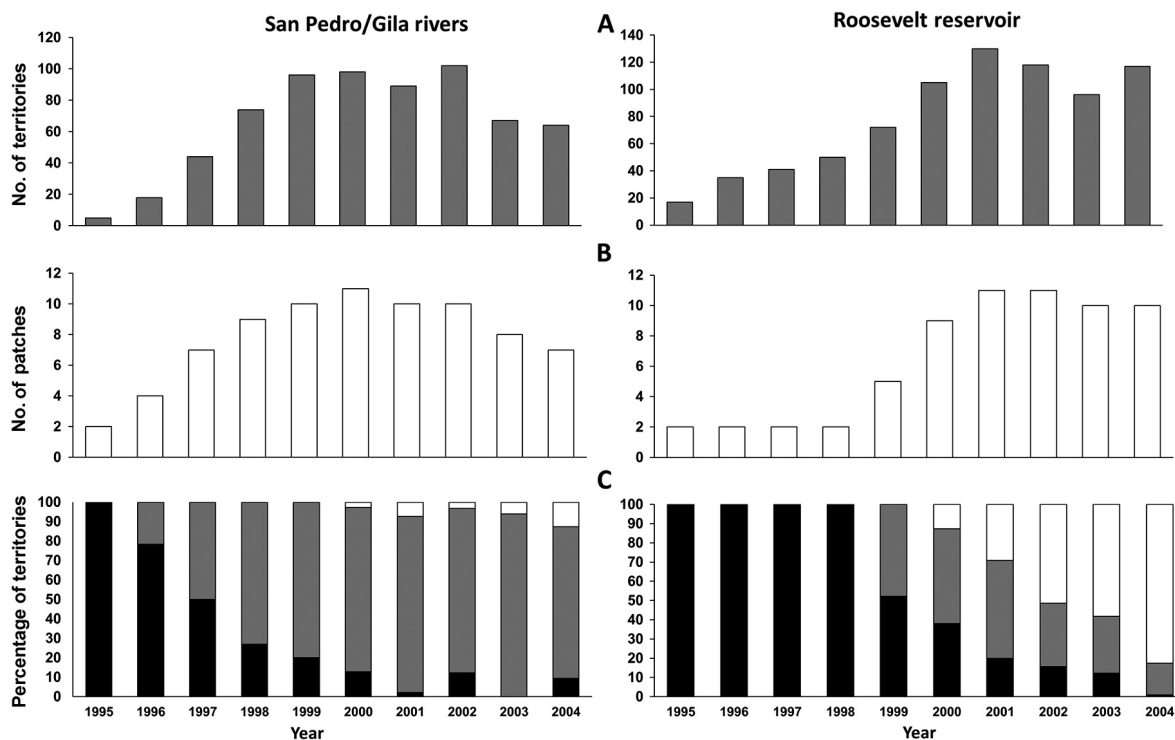


Fig. 6. (A) The number of southwestern willow flycatcher territories in 11 patches studied along the San Pedro and Gila Rivers and in 11 patches at Roosevelt Reservoir in central Arizona, USA, between 1995 and 2004. (B) The increasing number of occupied patches along the San Pedro and Gila Rivers and at Roosevelt Reservoir in each year (patch area showed a similar pattern). (C) The percentage of territories in patches that were occupied at the outset of the study in 1995 (black) or were colonized between 1996 and 1999 (gray) or were colonized between 2000 and 2004 (white), illustrating how the percentage of territories shifted from older patches to younger patches.

This increase in territories was associated with an increase in the number and total area of patches (Fig. 6B). Along the San Pedro and Gila Rivers, only two of the 11 patches were occupied in 1995, containing a total of 5 territories, but by 2002, 10 patches were occupied containing 102 territories. Likewise, in 1995 only two patches were occupied at Roosevelt Reservoir with a total of 17 territories while by 2001, all 11 patches were occupied with 130 territories. At both our reservoir and riverine sites, the percentage of territories in patches of differing age shifted over time, with a net movement of territories away from older patches to younger patches (Fig. 6C).

DISCUSSION

Patch dynamics are driven both by changes in the number of suitable patches through time and

by changes in productivity of occupied patches. For species dependent on early-successional habitats, large-scale disturbances, like floods and fires, are important for patch creation and loss, while patch productivity within patches may change as succession proceeds after disturbance. Early-successional species in shrubland and forest systems show demographic responses to patch age after disturbance similar to that we documented, with territory density increasing after patch colonization to a peak followed by a decline, consistent with the hypothesis that patch quality rises and falls over the life of a patch (Probst 1986, Probst and Weinrich 1993, Schlossberg and King 2009, Donner et al. 2010, Akresh et al. 2015). The related prediction that per capita reproductive success would also change over time was not evident in our study in terms of number of young fledged, similar to patterns

found in studies of other early-successional species recovering after disturbance (Holt and Martin 1997, Akresh et al. 2015). This finding would be consistent with an ideal-free model of habitat selection (Fretwell and Lucas 1970), in which reproductive success depends on territory density and individuals settle in patches of differing quality at densities that allow individuals to achieve similar reproductive success across patches. In this case, differences in number of territories between patches, rather than differences in per capita reproductive success between patches, drive differences in patch productivity. The larger reproductive output of peak patches in our study was due to the higher territory density in those patches. Patches at the peak stage contributed the bulk of both natal and breeding dispersers that made up the majority of colonizers, making patches at peak stages important drivers of patch dynamics.

Although our study focused on patch age as a driver of patch dynamics, other factors, like patch isolation and patch size, likely interact with patch age, but we did not explicitly test for these effects. Classical metapopulation theory emphasized the importance of patch isolation in determining rates of colonization and patch size in determining the rates of patch extinction (Hanski 1999). Although patch size was positively correlated with the maximum number of territories recorded in a patch, smaller patches at the peak stage often held more territories than larger patches in colonizing or declining stages. In studies of other successional species, patch size was positively correlated with the length of time a patch was occupied (patch lifetime) (Donner et al. 2010), and larger patches in our study appeared to last longer than smaller ones. Long-term studies of flycatchers at other sites have documented continuous patch occupancy for much longer periods than the 6–10 yr of patch life indicated by our study (Kus and Whitfield 2005). We suggest several, non-exclusive hypotheses to explain long-term occupancy of patches by flycatchers in these other sites. First, abandonment of old patches could be due to relative rather than absolute changes in suitability. Old riparian patches would in this case represent lower quality habitat that would continue to support fewer numbers of flycatchers indefinitely but would not be abandoned unless younger patches

became available, as was the case for Kirtland warblers in the absence of disturbance (Donner et al. 2010). Alternatively, older patches could experience spatially restricted or low-level disturbance that creates areas where regeneration of riparian habitat occurs, creating a mosaic of old and new habitat that maintains habitat suitability through time. This small-scale, within-patch disturbance could potentially explain why some patches in our riverine system showed a resurgence in the number of territories after an initial decline over time. Finally, variation between patches in hydrology, physiography, microclimate, and soil likely influences tree growth rates, stand structure, and prey availability in ways that contribute to variation in patch lifetimes.

We hypothesize that flycatchers were responding to age of patches in part due to the structural changes that accompanied patch regeneration and in part due to changes in abundance of their insect prey. Willow flycatcher nests are associated with dense foliage at and below nest height (Sedgwick and Knopf 1992, Allison et al. 2003), a patch structure more typical of young- and intermediate-aged riparian patches than older patches. Likewise, flooding and other disturbances can create bottom-up, trophic cascades driven by increases in herbivorous insects feeding on the vigorously growing, more nutritious leaves of younger, regenerating plants (Nakamura et al. 2005, Kersch-Becker and Lewinsohn 2012). Flycatchers are generalist insectivores (Durst et al. 2008) and so could potentially exploit increases in overall insect abundance associated with early and intermediate stages of patch regeneration.

Patch colonization and abandonment are key processes in patch dynamics, but relatively few studies have documented the age structure of individuals at these stages. Roughly half of the birds of known age that colonized the riparian patches we studied were young adults in their second year (SY), and roughly half of the natal dispersal events we documented were into patches at the colonizing stage, indicating birds in their first year of breeding play an important role as patch colonizers. In one of the few other studies that documented age of colonizers in early-successional species, 81% of colonizing male prairie warblers were also SY birds (Akresh et al. 2015). At our sites, the remaining birds in patches at the colonization stage were adults,

with roughly half of those having failed in their previous breeding attempt and the other half having bred successfully. Studies in which reproductive success has been manipulated experimentally have generally indicated that birds that failed to successfully breed in one year are more likely to disperse in subsequent years (Haas 1998, Hoover 2003, Schlossberg 2009), sometimes referred to as a win-stay, lose-switch strategy (Switzer 1993). This was the case in our study as well, with 67% of birds that were successful in the previous year returning to the same patch in the following year while only 35% of unsuccessful birds did so. Site fidelity by birds that were successful in an initial breeding attempt has been argued to depend upon how predictable reproductive success is from one year to the next (Switzer 1993). Early-successional species that live in dynamic and rapidly changing habitats would be predicted to have lower site fidelity because dynamic habitats would make breeding success at any one location less predictable from year to year. In spite of this, site fidelity in some early-successional shrubland birds has been shown to be relatively strong (Schlossberg 2009). Clearly many adults at our sites were strongly philopatric; as patches aged, the mean age of birds increased and most birds in both peak and declining stages were individuals that had repeatedly returned to the same site, with some 8- or 9-yr-old birds in declining patches having bred in that same patch throughout their lives. Abandonment of patches over time appeared to be largely driven by the disappearance of these older, long-time residents, presumably due to death, although low levels of emigration also contributed to patch decline. Similar patterns of patch abandonment through attrition and emigration have been proposed to explain the decline in density of prairie warblers as patches age (Akresh et al. 2015).

Our results should be interpreted within the context of an expanding population during a time of increasing habitat availability. Spatially structured population models that have incorporated patch age effects have demonstrated that declining populations react differently to habitat dynamics than expanding populations (Amarasekare and Possingham 2001, Wilcox et al. 2006). In both the riverine and reservoir systems we studied, the number of patches was increasing during

much of our study period. Although the patches we studied along the San Pedro and Gila Rivers experienced a scouring flood in 1993 that changed channel morphology more than any flood since 1905 (Huckleberry 1994), regeneration after that flood was variable. Some patches lost all riparian vegetation, while others retained some older vegetation, so that regeneration in patches was asynchronous, with different patches following different temporal trajectories. Rates of patch regeneration also differed due to idiosyncratic local characteristics, with some patches fenced from livestock grazing and therefore able to recruit riparian vegetation more rapidly, while others had additional sources of water from seeps, springs, or agricultural runoff that enhanced and maintained riparian vegetation recovery. At Roosevelt Reservoir, patches followed a more regular pattern of regeneration as successive annual decreases in water levels exposed new areas for plant colonization. In spite of these differing dynamics, the total number of patches increased two- to fourfold at both the riverine and reservoir sites. Concomitant with that increase in the number of patches was an increase in flycatcher population size. In a period of increasing population size paired with increasing habitat availability, colonization of new patches can be rapid and patch lifetimes shorter, as older, less suitable habitat is abandoned more rapidly (Donner et al. 2008, 2010). A key question remains of whether the pattern of patch dynamics we documented was a cause or a consequence of increasing population size. If the shift to younger patches was the driver of population increase, then increasing the number of patches in peak stages could increase population size of this endangered bird.

One of the most important findings of our study from a management perspective was that the demographic patterns at a highly modified reservoir site did not differ from those at a riverine site. At the reservoir site, the temporal and spatial pattern in the availability of newly regenerating patches was due to falling water levels during drought, and had reservoir levels instead remained constant, no new patches would have regenerated at that site. The dynamics we documented along the San Pedro and Gila Rivers were more typical of that experienced on unregulated rivers in the past, but those, too, could represent an unusual period of dynamism following

a large-scale, scouring flood, combined with subsequent drought conditions. In spite of these caveats, our study indicates that reservoirs can support populations with patch dynamics similar to those of more natural riparian areas and can therefore serve as important components in managing populations of riparian species dependent on early stages of riparian vegetation regeneration.

For species dependent on early stages of succession, the same disturbances that destroy patches are also vital for ultimately creating the most productive habitats (Stelter et al. 1997, Donner et al. 2010, King and Schlossberg 2014, Akresh et al. 2015). This is particularly true of riparian systems, but today few free-flowing rivers remain, and most are managed somewhere along their length by dams that alter both upstream and downstream flows (Molles et al. 1998). Our study demonstrates the potential for regulation of rivers to benefit animals adapted to these dynamic riparian systems, even in the reservoir systems where natural flows are most extremely altered. River regulation and reservoir habitat management that mimics the historical levels of disturbance necessary to create a temporal and spatial mosaic of patches at different stages of regeneration (Rood et al. 1998, Richter and Thomas 2007, Beechie et al. 2010), including the asynchrony in those disturbances necessary to maintain a diversity of successional stages through time (Johst and Drechsler 2003), will allow populations of early-successional species like the flycatchers we studied to persist and expand. Landscape-level management of successional habitats has been successful in maintaining and recovering endangered species associated with other successional habitats, like the Kirtland's warbler (Probst and Weinrich 1993, Donner et al. 2010), and we suggest a similar strategy could be used in riparian areas by coordinating changes in reservoir levels and downstream flows to maintain the dynamic, disturbance-driven changes in stand age necessary for long-term persistence of early-successional species through time.

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