Extreme drought alters frequency and reproductive success of floaters in Willow Flycatchers

Authors: Theimer, Tad C., Sogge, Mark K., Cardinal, Suzanne N., Durst, Scott L., and Paxton, E. H.

Source: The Auk, 135(3) : 647-656

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-17-206.1

The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 135, 2018, pp. 647–656
DOI: 10.1642/AUK-17-206.1

RESEARCH ARTICLE

Extreme drought alters frequency and reproductive success of floaters in Willow Flycatchers

Tad C. Theimer,[1]* Mark K. Sogge,[2] Suzanne N. Cardinal,[1] Scott L. Durst,[3] and E. H. Paxton[4]

[1] Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona, USA
[2] U.S. Geological Survey, Sacramento, California, USA
[3] U.S. Fish and Wildlife Service, New Mexico Ecological Services Office, Albuquerque, New Mexico, USA
[4] U.S. Geological Survey, Pacific Islands Ecological Research Station, Hawaii Volcanoes National Park, Hawaii, USA
* Corresponding author: Tad.Theimer@nau.edu

Submitted October 22, 2017; Accepted March 6, 2018; Published May 23, 2018

ABSTRACT

Changes in habitat quality, including those caused by extreme events like droughts and floods, could alter costs and benefits of territoriality and thereby the prevalence and reproductive consequences for individuals capable of breeding that do not do so (floaters). We studied floating behavior in a population of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) in central Arizona during one year of extreme drought, one year of lake inundation, and three years of near average precipitation. In all years, most floaters were second year (SY) males, and most subsequently settled outside of the patch where they were detected in the floating year, suggesting that floaters did not "queue" at high-quality territories in order to achieve higher reproductive success in subsequent years. Instead, cohorts that floated in non-drought years had lower apparent survival and lower reproductive success compared to territorial birds. In the extreme drought year, however, the number of floaters was 1.5 times greater than in all other years combined, more females floated, and apparent survival and mean annual productivity in subsequent years was higher for males that floated in that year than for those that were territorial. Inundation of habitat due to rising reservoir levels did not result in an increase in floaters because many birds nested in inundated areas where trees projected above the water so that the relative amount of available habitat was not reduced to the extent habitat models predicted. Overall, our results indicate that the prevalence and reproductive and demographic consequences of floating can change under extreme climatic events like severe drought.

Keywords: drought, *Empidonax*, floater, flycatcher, non-territorial, territoriality

La sequía extrema altera la frecuencia y el éxito reproductivo de los flotadores en *Empidonax traillii*

RESUMEN

Los cambios en la calidad del hábitat, incluyendo aquellos causados por eventos extremos como las sequías y las inundaciones, podrían alterar los costos y beneficios de la territorialidad y de ese modo la prevalencia y las consecuencias reproductivas para los individuos capaces de reproducirse que no lo hacen (flotadores). Estudiamos el comportamiento flotador en una población de *Empidonax traillii extimus* en el centro de Arizona durante un año de extrema sequía, un año de inundación del lago y tres años de precipitación casi promedio. En todos los años, la mayoría de los flotadores fueron machos del segundo año, y la mayoría se estableció subsecuentemente afuera del parche donde fueron detectados en el año flotador, sugiriendo que los flotadores no hicieron "cola" en territorios de alta calidad para lograr alcanzar un éxito reproductivo mayor en los años subsecuentes. En cambio, las cohortes que flotaron en años no secos tuvieron menor supervivencia aparente y menor éxito reproductivo comparadas con las aves territoriales. En el año de la sequía extrema, sin embargo, el número de flotadores fue 1.5 veces más grande que en todos los otros años combinados, más hembras flotaron y la supervivencia aparente y la productividad media anual en los años subsecuentes fue más alta para los machos que flotaron en ese año que para aquellos que fueron territoriales. La inundación del hábitat debido al aumento de los niveles del embalse no resultó en un aumento de flotadores debido a que muchas aves anidaron en áreas inundadas donde los árboles emergieron por arriba del agua, por lo que la cantidad relativa de hábitat disponible no se redujo al grado en que lo predijeron los modelos de hábitat. En conjunto, nuestros resultados indican que la prevalencia y las consecuencias reproductivas y demográficas de la flotación pueden cambiar ante eventos climáticos extremos como la sequía severa.

Palabras clave: atrapamoscas, *Empidonax*, flotador, no-territorial, sequía, territorialidad

INTRODUCTION

Among many territorial animals, some individuals capable of breeding and potentially holding a territory do not do so. In passerine birds, these non-territorial individuals may be difficult to detect, as they do not exhibit many of the behaviors that are used to census bird populations, such as singing and other territorial displays. Early studies initially identified these non-territorial birds when territory holders were naturally or experimentally removed and then quickly replaced by other birds from a surplus, "floating" population of unmated individuals (Stewart and Aldrich 1951).

Floating behavior can be viewed in 2 ways, either as a consequence of subordinate individuals being prevented from breeding due to competition with dominant conspecifics for limited territories (Newton 1992), or as a strategy in which individuals forego breeding in one year to maximize the potential for higher reproductive success in future years (Smith and Arcese 1989, Zack and Stutchbury 1992, Ens et al. 1995). In the latter case, floaters are argued to forego breeding but remain in the vicinity of high-quality territories to establish site dominance, thereby increasing the probability of acquiring a high-quality territory in subsequent years (Zack and Stutchbury 1992, Ens et al. 1995, Bruinzeel and van de Pol 2004), a behavior sometimes described as "queueing" (Ens et al. 1995) or "footholding" (Piper et al. 2015). In this case, floaters would be expected to ultimately obtain territories in the area where they concentrated activity and established site dominance in the floating year. Although floaters are most often young males (Newton 1998, Lenda et al. 2012), females could also forego breeding during a floater year and nest in subsequent years in one of the high-quality territories around which they concentrated activity in the floating year. Floating would be advantageous in these situations only to the extent that territories differ in quality and that quality is predictable from year to year (Zack and Stutchbury 1992). Ultimately, it is the relative lifetime reproductive success (LRS) that floaters achieve relative to territorial birds that determines whether floating is an equal or superior alternate strategy or simply the result of subordinate individuals "making the best of a bad job" (Newton 1992). An important caveat in estimating LRS in floaters is that floaters may gain reproductive success in years they are non-territorial by engaging in extra-pair copulations (Kempenaers et al. 2001, Pearson et al. 2006, Sardell et al. 2010, Brekke et al. 2013, 2015) or, in the case of female floaters, laying eggs in the nest of a territorial pair (Shugart et al. 1987).

Large-scale changes in habitat quality could affect floating either due to direct effects on habitat quality and availability, or through indirect effects via changes in population size driven by changes in habitat quality (Rohner 1996, Brown and Sherry 2008). Anthropogenic factors or extreme events, like droughts and floods, could change population density, habitat availability, or the relative costs and benefits of territoriality, and thereby alter the prevalence and consequences of floating, but the effects of these changes have rarely been examined. Floods remove habitat over wide areas, but strong site tenacity may cause birds to remain in the area and attempt to breed, at least in the initial year of flooding (Knopf and Sedgwick 1987). As a result, competition for the reduced number of high-quality territories during floods could potentially increase the prevalence of floating. In contrast, droughts would have a less dramatic effect on habitat quantity and a greater impact on habitat quality, lowering territory quality overall and potentially increasing the costs of territoriality relative to benefits. In some cases, adults may forego breeding during extreme drought conditions (Reichert et al. 2012) and potentially increase the floater population. In both cases, the reproductive costs of floating during extreme events could be lower if overall nest success of territorial birds is low in those years (George et al. 1992, Bolger et al. 2005). Finally, by acting as a surplus of potential breeders, floaters may buffer populations from environmental extremes like droughts and floods that result in loss of territorial breeders (Ferrer et al. 2004, Grimm et al. 2005). In spite of the potential for disturbances like these to alter the prevalence and consequences of floating, we know of no studies that have examined the relationship between floating prevalence, reproductive success, and extreme weather events.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a small, insectivorous, migratory passerine that is considered to be territorial on the breeding grounds (Sedgwick 2000). These flycatchers typically establish territories and nest in relatively dense riparian vegetation where surface water is present or soil moisture is high (Sogge 2000). Male flycatchers arrive on breeding grounds before females, and old males typically arrive and establish territories earlier than young males (Paxton et al. 2007). Willow Flycatchers exhibit strong site fidelity and low natal philopatry (Sedgwick 2004) typical of many migratory passerine birds (Greenwood 1980, Greenwood and Harvey 1982). Adult movement to new breeding patches between years is more common in areas where new habitat is developing or where habitat patches are clustered (Paxton et al. 2007). Despite substantial research on this species, there is limited information about the nature and prevalence of floaters during the breeding season (Stafford 1986, Pearson et al. 2006).

We used data obtained during a 5-yr demographic study of Willow Flycatchers at a site in central Arizona to investigate floating in this population before, during, and after an extreme drought that dramatically reduced arthropod prey abundance and flycatcher breeding success

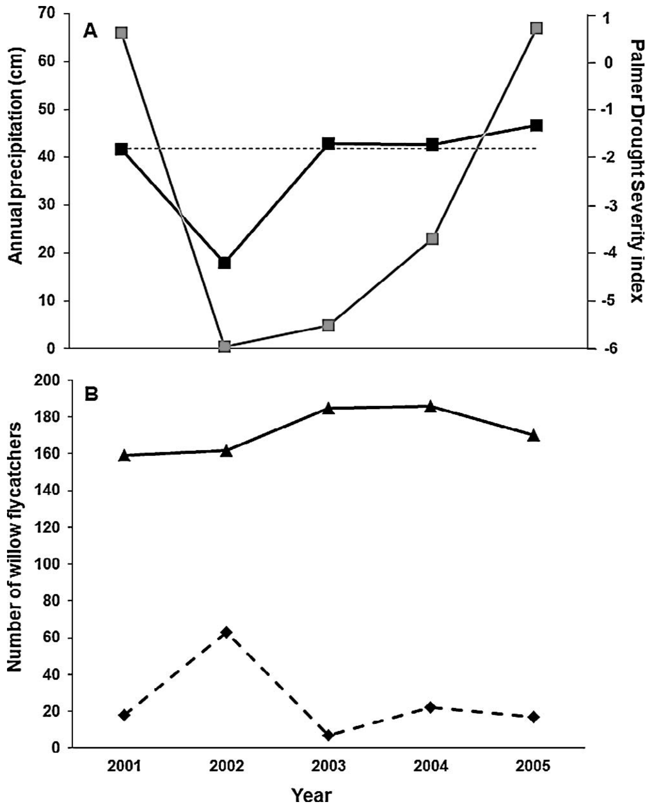

FIGURE 1. (**A**) Annual precipitation (cm) (solid line, black squares), 50-yr mean annual precipitation (dashed line), and mean of January–December monthly values of the Palmer Drought Severity Index (gray line, gray squares) at Roosevelt Reservoir, Arizona, USA, from 2001 to 2005. (**B**) Number of territorial (solid line, black triangles) and floater (dashed line, black diamonds) Southwestern Willow Flycatchers (*Empidonax traillii extimus*) at Roosevelt Reservoir 2001–2005.

(Durst et al. 2008) and, in the last year of the study, when lake levels rose and inundated much of the available habitat (Ellis et al. 2009). Based on Willow Flycatcher natural history and behavior, and previous studies of floating behavior in other species, we made 4 predictions about how drought and flooding would impact floaters in this system. First, we predicted that floaters would move widely in search of territories, as in other migratory species (e.g., Tanferna et al. 2013), rather than queueing at high-quality territories, and subsequently settling near those (Newton 1998, Lenda et al. 2012). This prediction was based on the fact that flycatchers breed in riparian habitats that are dynamic, with winter floods often altering habitat structure between breeding seasons, thereby leading to a lack of predictability of high-quality territories from year to year, a precondition for queueing to be advantageous (Zack and Stutchbury 1992). Second, we predicted that both in the drought year, when insect biomass fell to 20% of that of the following year (Durst et al. 2008), and in the inundation year, when lake levels rose to flood much of the habitat, the number of floaters would increase because of increased competition for fewer suitable territories, and because some birds would forego territory establishment and breeding due to lack of resources. Third, given the low reproductive success of territorial birds during the drought (Paxton et al. 2007, Durst et al. 2008), we predicted floating in an extreme drought year would be less costly for floaters relative to territorial birds in terms of annual reproductive success and that birds that floated in that year would contribute more offspring to the population than those that floated in other years. Fourth, we predicted that floating in a drought year, when the costs of maintaining a territory and breeding could be higher, would result in higher subsequent survival for floaters than for territorial birds that did not avoid those costs.

METHODS

Study Area

We studied Willow Flycatchers at Roosevelt Lake (33°39′N, 110°58′W), a site with one of the largest known breeding populations of this subspecies during our study period (Durst et al. 2006). Flycatcher breeding habitat at Roosevelt Lake was limited to the floodplain inflows of the Salt River and Tonto Creek at opposite sides of the reservoir and consisted of a heterogeneous mosaic of riparian forest patches of varying ages and vegetation composition, ranging from 0.2 to 43 ha in size (Paxton et al. 2007). Native habitat patches were characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix* spp.).

A long-term drought between 1996 and 2004 resulted in Roosevelt Reservoir water levels dropping to a low of 10% capacity in 2002. Lowering of lake levels resulted in an overall increase in habitat for flycatchers because it allowed young, vigorously growing riparian vegetation to establish on the exposed lakeshore (Hatten et al. 2010), and birds continued to colonize these new patches through 2004 (Paxton et al. 2007). In 2002, the year we define as an extreme drought year, rainfall at our study site was 50% lower than the annual average, and the Palmer Drought Severity Index (mean of January–December monthly values for the county) was –6.1 (Figure 1A). Although 2001, 2003, and 2004 also had low Palmer Drought Severity indices, annual rainfall in those years at our study site was near normal (Figure 1A). Aerial arthropod biomass in 2002 was 20% of that in 2003 (Durst et al. 2008), and seasonal fecundity of flycatchers was 6% of the mean over the other 9 yr (Paxton et al. 2007). In 2005, following unusually high winter precipitation and associated runoff, Roosevelt Lake filled to near capacity, inundating much of the breeding habitat that was occupied in 2004 (Ellis et al. 2009).

Aging, Sexing, and Assessing Reproductive Success

From 1996 to 2005 we captured adult Willow Flycatchers via both target-netting within known territories and passive netting in suitable habitat, and banded some nestlings at nests. We banded flycatchers with a color-anodized federal band and a second color band of solid, half-, or triple-split colors to create a unique color combination for each individual (Koronkiewicz et al. 2005). Willow Flycatchers are not sexually dimorphic in plumage. Therefore, sex was determined either based on physical characteristics (presence of a cloacal protuberance for males or brood patch for females), or genetically from blood samples taken from adults or nestlings at the time of banding.

Adult flycatchers were aged as "known" if the bird was first banded as either a nestling or could be aged based on retained secondaries as a bird entering its second year (SY) (Pyle 1998); otherwise, they were considered after-hatch-year (AHY). As AHY birds were captured in succeeding years, they were classed as after-second-year (ASY), after-third-year (ATY), etc. When the distributions of age at last detection were compared between 317 known-aged birds (first aged as SY) and 932 birds of estimated age (first aged as AHY), the relative proportions were not significantly different, suggesting most, if not all, AHY birds were SY when first captured (Paxton et al. 2007). Given that pattern, combined with the fact that an average of 74% of all detected adult flycatchers were banded in any one year (range: 68–88%), we felt justified in assuming AHY birds were SY birds.

We classified birds as territorial if they were repeatedly detected singing and/or displaying aggressive behavior toward conspecifics. We classified birds as floaters if they were detected via color band resights and/or recapture multiple times in a given year, but were never observed engaging in territorial behaviors such as singing, territory defense, nesting, or feeding young. Although birds that we never recorded exhibiting territorial behavior in any year could arguably have been territory holders, we feel this is unlikely given the intensity and spatial extent of surveys. To census territorial and non-territorial birds, the entire study area was surveyed 3 times each breeding season. Wherever flycatchers were detected during one of those surveys, additional visits were made to identify color-banded birds and to capture and band non-banded birds. Any new birds or territories detected on these additional visits were also subsequently visited for resighting/banding. On average, each banded bird was resighted 7 times per year. With field crew sizes of 25–35 technicians per year, we believe we detected nearly 100% of all territorial birds within the study area, which was geographically isolated from other known breeding sites. In addition to territorial birds captured through target netting on territories, birds were also captured in mist nets placed randomly in suitable habitat throughout the study area. Many of the non-territorial birds we recorded as floaters were captured during these passive netting attempts.

Reproductive success was determined by searching for nests within each territory and then visiting each nest every 2–4 days after incubation was confirmed until the nest successfully fledged or failed. If nests failed, territories were monitored through repeated visits to discover any new nesting efforts, and to resight birds to confirm that the same pair was present or to identify new individuals. Nests were considered successful if (1) fledglings were observed within 10 m of or leaving the nest, (2) adults were observed feeding fledglings, or (3) nestlings were present in the nest within 2 days of the estimated fledge date. We did not systematically collect blood from nestlings and adults, so we could not genetically assess parentage of nestlings. In the absence of those genetic data, we attributed the offspring from the nests within a territory to the male and female associated with that territory, and assumed floaters had no reproductive success in the year they floated.

Testing Predictions

We tested the prediction that floaters would not queue for high-quality territories by comparing the number of floaters that subsequently settled in (1) the same patch—if floaters established territories in the year subsequent to floating in the same patch where they had been detected as floaters, (2) a nearby patch—if subsequent territories were in patches within 5 km of the patch where initially detected as a floater, (3) cross-lake—if territories were on the opposite end of the lake (30 km) from floater detections, and (4) out of basin—if subsequent territories were established beyond the Roosevelt Reservoir basin (>50 km distant). If floaters were queueing at high-quality territories during the floater year, we expected most birds to fall into the first category.

To test our prediction that floaters would be more prevalent in the year of severe drought and inundation, we tabulated the total number of both male and female floaters and territorial birds in each year. We then used a chi-square contingency test to test whether the relative number of floater and territorial birds differed across years.

To test our prediction that floating in a drought year would be less costly for floaters relative to territorial birds in terms of annual reproductive success, we examined reproductive success of SY males that floated versus those that were territorial within each annual cohort from 2001 to 2004. We limited our analysis to SY birds because most floaters fell within this age category. We examined birds as cohorts to control for effects of year and age on reproductive success. Because the number of years we documented subsequent reproductive success differed for each cohort, we could not estimate lifetime reproductive success (LRS). Instead, we used mean annual reproductive success so that we could compare the same metric across all cohorts. Within each cohort, we estimated mean annual reproductive success as the mean of total number of fledglings attributed to a bird each year over all years a bird was subsequently encountered. Thus, reproductive success for a male that was SY in 2001 (the 2001 cohort) that survived until 2005 was the mean of fledglings produced each year averaged across 5 yr, while reproductive success for a male in that cohort that did not return in 2002 would be the number of fledglings produced in 2001. We compared males in 4 cohorts (2001, 2002, 2003, 2004) but analyzed only the 2002 cohort of females because sample sizes of floater females were too low in other years. For each cohort, we then used Mann–Whitney U tests to determine whether the distributions of mean annual success for floaters and territorial categories were the same within each cohort. We used this nonparametric approach because it is robust for data that are non-normally distributed, as reproductive success in short-lived passerines like those we studied is typically skewed toward zeros. We were not concerned about effects of spatial autocorrelation in these data because the riparian habitat these birds nested in was dynamic, with new habitat available in each year as new riparian vegetation established, resulting in 66% of birds reestablishing territories in new areas in subsequent years (Paxton et al. 2007).

To test the hypothesis that birds that floated in the severe drought year had higher apparent survival over time than birds that were territorial in that year, we used Kaplan–Meier survival analysis in SPSS to compare floater and territorial survival for the cohort in the extreme drought year (2002) through 2004. We did not include apparent survival to 2005 as the inundation in that year may have biased our survival estimates. We analyzed apparent survival of males and females separately as costs of territoriality during drought could differ between the sexes. We report values for both the rank sum and Gehan–Breslow–Wilcoxon estimator, as the latter is influenced more by survival early in the period of interest and we expected drought to have the greatest effect on survival immediately after the drought rather than in later years.

RESULTS

Out of the 127 floaters that we documented across all years, only one bird (1%) floated in more than one year. Most floaters were young, SY males ($n = 96$, 76%), while the majority (70%) of territorial birds in all years were TY or older (Table 1). Only 19 floaters were female, with 15 of those females floating in the drought year of 2001 (Table 1).

Our prediction that floaters would not subsequently settle in the patch in which they were detected during the floating year was generally supported. We were able to follow a total of 46 floaters from the year they were first detected to the following year when they established territories. Of these birds, 11 (24%) settled in the same habitat patch where they were first detected, 27 (59%) settled in a different habitat patch but within 5 km of the patch where they were first detected, and 6 (13%) settled in patches at the opposite side of the lake (approximately 30 km away). A separate study of flycatcher demographics was being conducted along the San Pedro and Gila Rivers approximately 100 km south of our study site, and 2 additional birds that were floaters at our site subsequently settled there. Given that that study site was only one of several other breeding areas in our region, our estimate of the number of floaters subsequently settling outside our study area was an underestimate.

Our prediction that severe drought and inundation would increase the number of floaters relative to the number of territorial birds was supported for the drought year but not for the inundation year. The number of territorial Willow Flycatchers of both sexes was lowest (Table 1) and the percentage of floaters was highest in the year of severe drought (Figure 1B). Our contingency table analysis indicated that the relative number of territorial and floater birds varied significantly across years ($\chi^2 = 98.6$, df $= 4$, $P < 0.001$) with the drought year contributing 78% of the total chi-square value. Contrary to our prediction that inundation would result in a larger than expected number of floaters, in 2005 we documented a total of only 17 floaters at a frequency similar to that in other years (Figure 1B). Across years, the total number of birds estimated at our sites was relatively constant (Table 1, Figure 1B), indicating that changes in floating behavior were not driven by large changes in overall population size.

Our prediction that the loss of reproduction in the year of floating would result in lower mean annual reproductive success for a cohort that floated in most years, but not for a cohort that floated in an extreme drought year, was supported for males but could be only partially tested in females. For all 3 SY male cohorts experiencing non-extreme drought in their initial year (2001, 2003, and 2004), floaters had lower mean annual reproductive success than birds that were territorial in their first year and the distributions in the 2 groups differed significantly (2001: Mann–Whitney $U = 341$, $n_1 = 23$, $n_2 = 16$, $P = 0.012$; 2003: Mann–Whitney $U = 367$, $n_1 = 6$, $n_2 = 7$, $P = 0.008$; 2004: Mann–Whitney $U = 413$, $n_1 = 29$, $n_2 = 21$, $P = 0.001$; Figure 2). This pattern was reversed in the extreme drought year of 2002, as SY males that initially floated in this cohort averaged more fledglings per year than birds that were territorial in the year of the drought (Mann–Whitney $U = 290$, $n_1 = 17$, $n_2 = 44$, $P = 0.048$; Figure 2). In contrast, mean number of fledglings per year for SY females that floated in 2002 (mean $= 0.74$) and those that

TABLE 1. Number of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) that were SY males, TY or older males, SY females, TY or older females, and total of all ages and both sexes that were either territorial or floaters in 2001 through 2005 at Roosevelt Reservoir in central Arizona, USA. In 2002, an extreme drought caused nearly complete reproductive failure. In 2005, reservoir levels had risen and much previously occupied habitat was inundated.

	2001		2002		2003		2004		2005	
	Territorial	Floater	Territorial	Floater	Territorial	Floater	Territorial	Floater	Territorial	Floater
SY M	23	16	17	44	6	7	29	21	13	8
≥TY M	45	0	48	4	78	0	54	0	74	8
SY F	40	2	15	12	33	0	34	0	22	1
≥TY F	33	0	19	3	61	0	47	1	44	0
Total	141	18	99	63	178	7	164	22	153	17

were territorial in that year (mean = 0.72) were similar and distributions in the 2 groups did not differ significantly (Mann–Whitney $U = 99.5$, $n_1 = 15$, $n_2 = 22$, $P = 0.83$). We could not compare reproductive success of floater versus territorial females in years that did not experience an extreme drought because there were too few female floaters in those years.

Overall, birds that floated during the extreme drought contributed more breeders and more offspring in the subsequent year than birds that floated in other years. In 2003, the year following the extreme drought, 19 of 84 (23%) of all territorial males were birds that had floated in 2002, and these males were associated with 38 of 184 (21%) of all fledglings produced in 2003. For territorial females in 2003, 8 of 94 (9%) had floated the year before and these females contributed 25 of 184 (14%) of all fledges attributed to females in 2003. In contrast, in 2002, 2004, and 2005, floaters from the previous year made up 2–8% of all territorial males and 0–3% of all territorial females and contributed 0–3% of the fledglings produced in any of those years.

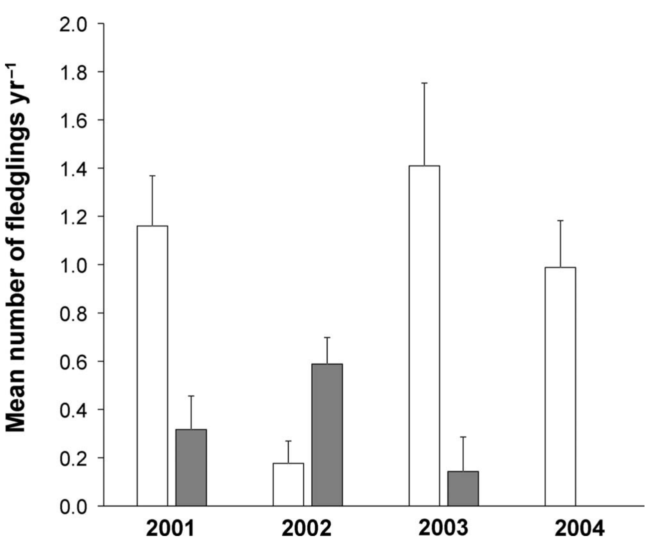

FIGURE 2. Mean ± SE number of fledglings produced per year by male Southwestern Willow Flycatchers (*Empidonax traillii extimus*) that were either territorial (open bars) or floaters (gray bars) as SY birds in 2001, 2002, 2003, or 2004 at the Roosevelt Reservoir study site in central Arizona, USA.

Our prediction that floating during an extreme drought would increase subsequent survival was supported for males but not females (Figure 3). Based on Kaplan–Meier survival analysis, SY males that floated in 2002, the year of extreme drought, had significantly higher survival to 2004 than males that were territorial in that year (log-rank $\chi^2 = 3.6$, df = 1, $P = 0.05$, Gehan–Breslow–Wilcoxon $\chi^2 = 4.8$, df = 1, $P = 0.03$). In contrast, the survival of 2002 SY females that floated during the extreme drought was not different from that of females that were territorial in that year (log-rank $\chi^2 = 0.007$, df = 1, $P = 0.93$, Gehan–Breslow–Wilcoxon $\chi^2 = 0.033$, df = 1, $P = 0.86$).

DISCUSSION

To be advantageous, a floater strategy of queueing (Ens et al. 1995) or footholding (Piper et al. 2015) requires that territory quality be predictable through time, so that floaters can establish site dominance in the floating year that will increase the probability of gaining a territory in that area in subsequent years (Zack and Stutchbury 1992). The flycatchers we studied did not follow this strategy and we hypothesize this was in part due to the lack of predictability of territory quality through time. Predictability of territory quality is likely low for flycatchers because of the dynamic nature of the riparian habitat caused by frequent low-intensity, and occasional high-intensity, floods that remove or alter habitat from year to year, and to rapidly growing riparian vegetation that can change dramatically in height and structure across years. Instead, in most years, floaters in our system appeared to float due to competition for limited territories, and the result was lower survival and lower reproductive success of floaters compared to territorial birds similar to that documented in other studies (Smith and Arcese 1989, Rohner 1997, Cam et al. 1998, VanderWerf 2008).

Extreme events that dramatically alter habitat quality over large areas could change this dynamic. In years of

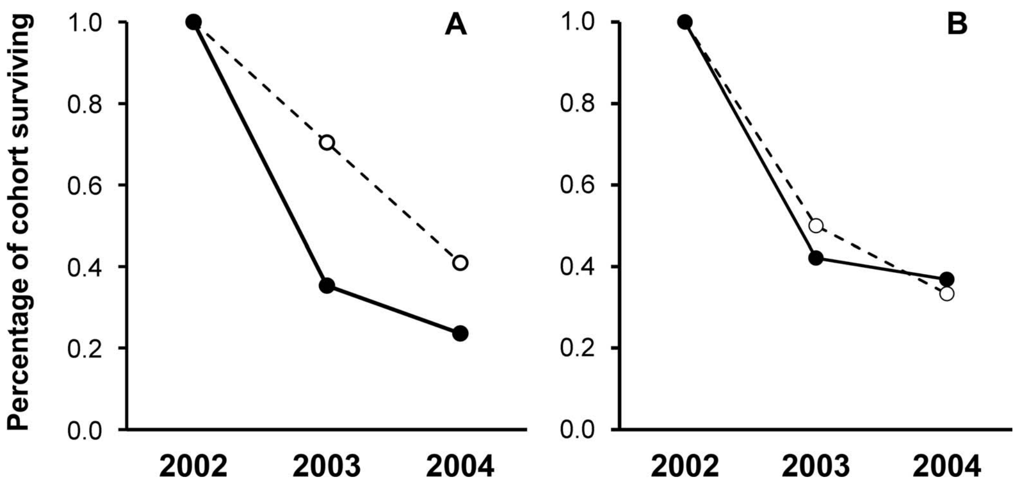

FIGURE 3. The percentage of the 2002 cohort of SY male (**A**) and SY female (**B**) Southwestern Willow Flycatchers (*Empidonax traillii extimus*) at the Roosevelt Reservoir study site in central Arizona, USA, that survived in 2003 and 2004 that either floated in their initial year (open circles, dashed lines) or were territorial in their initial year (solid circles, solid line).

extreme drought, when overall habitat quality is low, most territories would be of such low quality that the probability that higher quality territories would be available in the following year would be high, and foregoing breeding in a drought year could increase lifetime reproductive success. Consistent with this hypothesis, males that floated in the extreme drought year had higher apparent survival than males that were territorial and achieved higher mean annual reproductive success. Part of the difference in reproductive success among males during the severe drought was due to the fact that territorial birds in the drought year produced no young, thereby negating any reproductive benefit of territoriality in their first year. Overall, these results demonstrate that the advantages of floating switch under changing environmental conditions. Floating behavior that resulted in negative reproductive and survival consequences when exhibited in most years became advantageous in the year of extreme drought.

In contrast to the drought of 2002, inundation of habitat caused by rising reservoir levels in 2005 did not result in a change in the frequency of floaters. Habitat modeling indicated that suitable breeding habitat at Roosevelt Lake increased from 1996 to 2004 and then fell by 90% in 2005 during the year of inundation caused by rising lake levels (Hatten et al. 2010), but the number of flycatcher territories did not show a similar decline, nor did the number of floaters increase relative to other years. This was due in part to the fact that flycatchers continued to nest in inundated areas where treetops remained above water level and moved to areas that had previously been too far from water to be considered suitable. Similarly, Knopf and Sedgwick (1987) found that Brown Thrasher (*Toxostoma rufum*) and Spotted Towhee (*Pipilo maculatus*) densities did not decline in the year their study area along the Platte River in Colorado was entirely submerged under floodwaters, but rather was delayed until the next year, suggesting strong site tenacity by the breeding birds in the initial year of flooding. Consistent with this, some older birds of both sexes were identified as floaters in 2005 at our site, suggesting that some site-faithful adults remained in the area but may have been unable to reoccupy territories that were completely submerged. Perhaps most importantly, unlike in the year of extreme drought, when a dramatic decline in insect prey was documented at our site (Durst et al. 2008), we lack data on insect abundance in the year of inundation. Given that flycatchers rely on aerial insects as their major prey, inundation may not have had the same negative effect on overall habitat quality in terms of food abundance that the extreme drought did, and therefore the prevalence of floating did not differ from that in non-flood years.

The number of floaters in 2003 was the lowest we recorded, and this followed a year of widespread reproductive failure for flycatchers at our study site, and for other bird species in the southwestern United States (Bolger et al. 2005). Natal philopatry is generally low in migratory birds (Weatherhead and Forbes 1994), and nestlings banded at our site rarely returned to their natal patch, instead moving on average 20 km, and occasionally moving between drainage basins (Paxton et al. 2007). Even so, the low reproductive success at our site in 2002 was likely experienced across much of the southwestern United States, resulting in overall lower numbers of SY birds searching for territories in the following year. As a result, SY males in the year following the drought would have faced lower competition and had greater opportunity to obtain territories, and young birds that would have potentially been floaters in other years were recruited into the breeding population. Floaters represent a surplus of potential breeders, and have been hypothesized to potentially buffer populations from perturbations by quickly replacing breeders when they are lost (Walters et al. 2002, Grimm et al. 2005, Penteriani et al. 2011, Lenda et al. 2012). Likewise, demographic models have suggested that delayed breeding associated with floating can increase population viability by reducing the magnitude of population fluctuations that can sometimes drive small populations to extinction (Ferrer et al. 2004). Although these effects may be most relevant for long-lived birds (Sergio et al. 2009, Tanferna et al. 2013) or when nonbreeders make up a large part of the population (Tella et al. 2013), the birds that floated in the year of extreme drought in our study contributed significantly to the breeding population in the following year, and for following years thereafter, thereby increasing the rate of population recovery after an extreme climatic event.

A major caveat of our study was that our estimates of reproductive success for floaters did not include the potential for floaters to produce young through extra-pair matings. Several studies have confirmed that male floaters contribute genetically to populations during the years they float through extra-pair copulations (Ewen et al. 1999, Kempenaers et al. 2001, Sardell et al. 2010, Brekke et al. 2013, 2015). Territorial males can also benefit from extra-pair copulations, however, and in some studies, territorial males still have overall reproductive success greater than that of floaters when both pair and extra-pair young are included (Brekke at al. 2013, 2015). In the only study that quantified extra-pair paternity in Willow Flycatchers (Pearson et al. 2006), 6 of 16 extra-pair offspring were sired by non-territorial males and 10 by territorial males, suggesting that territorial and floater Willow Flycatchers achieve roughly equal success through extra-pair matings. Still, given this limited data set, the contribution of extra-pair offspring to lifetime reproductive success of floaters in this species remains an open question.

Overall, our study highlights that the role of floaters in populations may change under extreme climatic events, and therefore could become more important as those events become more likely under climate change (Frich et al. 2002), especially for small populations of conservation concern (Penteriani et al. 2011, Brekke et al. 2015). An important caveat of our study is that we lack replication of the severe drought year in which floating behavior differed. Rare events are difficult to replicate, but it is these rare, but extreme, events that may have long-term repercussions for population demography (e.g., Pardo et al. 2017). As a result, documenting the effects of individual events like the one we describe is an important step in eventually understanding the general response of populations to extreme events (Altwegg et al. 2017).

ACKNOWLEDGMENTS

We appreciate the coordination, sharing of information, and/or land access permission from the Arizona Game and Fish Department (AGFD), EcoPlan Associates, Inc., the USFS Tonto Ranger District, Salt River Project (SRP), SWCA Environmental Consultants, Inc., and Westland Resources, Inc., which was critical for this research. We especially thank S. Sferra and H. Messing (BOR), and G. Smith, C. Woods, and H. Plank (USFS), and the outstanding USGS banding crews 1996–2005. T. Arundel, G. Beatty, L. Ellis, B. Kus, J. Lovich, T. Koronkiewicz, H. Messing, K. Paxton, S. Sferra, S. Stoleson, C. van Riper, and M. Whitfield reviewed earlier drafts of this manuscript.

Funding statement: This research was funded by the Bureau of Reclamation, Phoenix Area Office, with support from the USGS Southwest Biological Science Center and Northern Arizona University. Funders had no input into the content and did not require approval of the manuscript before submission.

Ethics statement: This research was conducted in compliance with the *Guidelines to the Use of Wild Birds in Research* using protocols approved by the Northern Arizona University IACUC and under all relevant state and federal permits.

Author contributions: EHP, MKS, TCT conceived the idea and design; EHP, SNC, and SLD collected field data; TCT, EHP, SLD, and SNC analyzed the data; TCT, EHP, MKS, and SLD wrote the paper.

LITERATURE CITED

Altwegg, R., V. Visser, L. D. Bailey, and B. Erni (2017). Learning from single extreme events. Philosophical Transactions of the Royal Society B 372:20160141.

Bolger, D. T., M. A. Patten, and D. C. Bostock (2005). Avian reproductive failure in response to an extreme climatic event. Oecologia 142:398–406.

Brekke, P., P. Cassey, C. Ariani, and J. G. Ewen (2013). Evolution of extreme-mating behaviour: Patterns of extrapair paternity in a species with forced extrapair copulation. Behavioral Ecology and Sociobiology 67:963–972.

Brekke, P., J. G. Ewen, G. Clucas, and A. W. Santure (2015). Determinants of male floating behaviour and floater reproduction in a threatened population of the hihi (*Notiomystis cincta*). Evolutionary Applications 8:796–806.

Brown, D. R., and T. W. Sherry (2008). Alternative strategies of space use and response to resource change in a wintering migrant songbird. Behavioral Ecology 19:1314–1325.

Bruinzeel, L. W., and M. van de Pol (2004). Site attachment of floaters predicts success of territory acquisition. Behavioral Ecology 15:290–296.

Cam, E., J. E. Hines, J. Y. Monnat, J. D. Nichols, and E. Danchin (1998). Are adult nonbreeders prudent parents? The kittiwake model. Ecology 79:2917–2930.

Durst, S. L., M. K. Sogge, H. English, S. O. Williams, B. E. Kus, and S. J. Sferra (2006). Southwestern Willow Flycatcher breeding site and territory summary—2005. U.S. Geological Survey Report to the Bureau of Reclamation, Phoenix, AZ, USA.

Durst, S. L., T. C Theimer, E. H. Paxton, and M. K. Sogge (2008). Age, habitat, and yearly variation in the diet of a generalist insectivore, the Southwestern Willow Flycatcher. The Condor 110:514–525.

Ellis, L. A., S. D. Stump, and D. M. Weddle (2009). Southwestern Willow Flycatcher population and habitat response to reservoir inundation. Journal of Wildlife Management 73: 946–954.

Ens, B. J., F. J. Weissing, and R. H. Drent (1995). The despotic distribution and deferred maturity: Two sides of the same coin. American Naturalist 146:625–650.

Ewen, J. G., D. P. Armstrong, and D. M. Lambert (1999). Floater males gain reproductive success through extrapair fertilizations in the stitchbird. Animal Behaviour 58:321–328.

Ferrer, M., F. Otalora, and J. M. García-Ruiz (2004). Density dependent age of first reproduction as a buffer mechanism affecting persistence of small populations. Ecological Applications 14:616–624.

Frich, P., L. V. Alexander, P. M. Della-Marta, B. Gleason, M. Haylock, A. K. Tank, and T. Peterson (2002). Observed coherent changes in climatic extremes during the second half of the twentieth century. Climate Research 19:193–212.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen (1992). Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Greenwood, P. J., and P. H. Harvey (1982). The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Grimm, V., E. Revilla, J. Groeneveld, S. Kramer-Schadt, M. Schwager, J. Tews, M. Wichmann, and F. Jeltsch (2005). Importance of buffer mechanisms for population viability analysis. Conservation Biology 19:578–580.

Hatten, J. R, E. H. Paxton, and M. K. Sogge (2010). Modeling the dynamic habitat and breeding population of Southwestern Willow Flycatcher. Ecological Modelling 221:1674–1686.

Kempenaers, B., S. Everding, C. Bishop, P. Boag, and R. J. Robertson (2001). Extra-pair paternity and the reproductive role of male floaters in the Tree Swallow (*Tachycineta bicolor*). Behavioral Ecology and Sociobiology 49:251–259.

Knopf, F. L., and J. A. Sedgwick (1987). Latent population responses of summer birds to a catastrophic, climatologic event. The Condor 89:869–873.

Koronkiewicz, T. J., E. H. Paxton, and M. K. Sogge (2005). A technique to produce aluminum color bands for avian research. Journal of Field Ornithology 76:94–97.

Lenda, M., B. Maciusik, and P. Skorka (2012). The evolutionary, ecological and behavioural consequences of the presence of floaters in bird populations. North-Western Journal of Zoology 8:394–408.

Newton, I. (1992). Experiments on limitation of bird numbers by territorial behaviour. Biological Reviews 67:129–173.

Newton, I. (1998). Population Limitation in Birds. Academic Press, San Diego, CA, USA.

Pardo, D., S. Jenouvrier, H. Weimerskirch, and C. Barbraud (2017). Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. Philosophical Transactions of the Royal Society B 372: 20160143.

Paxton, E. H., M. K. Sogge, S. L. Durst, T. C. Theimer, and J. Hatten (2007). The Ecology of the Southwestern Willow Flycatcher in Central Arizona–A 10-year Synthesis Report. USGS Open-File Report 2007–1381. http://pubs.usgs.gov/of/2007/1381.

Paxton, E. H., M. K. Sogge, T. D. McCarthey, and P. Keim (2002). Nestling sex ratio in the Southwestern Willow Flycatcher. The Condor 104:877–881.

Pearson, T., M. J. Whitfield, T. C. Theimer, and P. Keim (2006). Polygyny and extra-pair paternity in a population of Southwestern Willow Flycatchers. The Condor 108:571–578.

Penteriani, V., M. Ferrer, and M. D. M. Delgado (2011). Floater strategies and dynamics in birds, and their importance in conservation biology: Towards an understanding of nonbreeders in avian populations. Animal Conservation 14:233–241.

Piper, W. H., J. N. Mager, C. Walcott, L. Furey, N. Banfield, A. Reinke, F. Spilker, and J. A. Flory (2015). Territory settlement in common loons: No footholds but age and assessment are important. Animal Behaviour 104:155–163.

Pyle, P. (1998). Eccentric first-year molt patterns in certain tyrannid flycatchers. Western Birds 29:29–35.

Reichert, B. E., C. E. Cattau, R. J. Fletcher, W. L. Kendall, and W. M. Kitchens (2012). Extreme weather and experience influence reproduction in an endangered bird. Ecology 93:2580–2589.

Rohner, C. (1996). The numerical response of great horned owls to the snowshoe hare cycle: Consequences of non-territorial 'floaters' on demography. Journal of Animal Ecology 65:359–370.

Rohner, C. (1997). Non-territorial "floaters" in great horned owls: Space use during a cyclic peak of snowshoe hares. Animal Behaviour 53:901–912.

Sardell, R. J., L. F. Keller, P. Arcese, T. Bucher, and J. M. Reid (2010). Comprehensive paternity assignment: Genotype, spatial location and social status in Song Sparrows *Melospiza melodia*. Molecular Ecology 19:4352–4364.

Sedgwick, J. A. (2000). Willow Flycatcher (*Empidonax traillii*). In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.533

Sedgwick, J. A. (2004). Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). The Auk 121:1103–1121.

Sergio, F., J. Blas, and F. Hiraldo (2009). Predictors of floater status in a long-lived bird: A cross-sectional and longitudinal test of hypotheses. Journal of Animal Ecology 78:109–118.

Shugart, G. W., M. A. Fitch, and G. A. Fox (1987). Female floaters and nonbreeding secondary females in Herring Gulls. The Condor 89:902–906.

Smith, J. N., and P. Arcese (1989). How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. The American Naturalist 133:830–845.

Smith, S. M. (1978). The "underworld" in a territorial sparrow: Adaptive strategy for floaters. The American Naturalist 112: 571–582.

Sogge, M. K. (2000). Breeding season ecology. In Status, Ecology and Conservation of the Southwestern Willow Flycatcher (D. M. Finch and S. H. Stoleson, Editors). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-60.

Stafford, M. D. (1986). Supernumerary adults feeding Willow Flycatcher fledglings. The Wilson Bulletin 98:311–312.

Stewart, R. E., and J. W. Aldrich (1951). Removal and repopulation of breeding birds in a spruce-fir forest community. The Auk 68:471–482.

Stutchbury, B. J. (1991). Floater behaviour and territory acquisition in male purple martins. Animal Behaviour 42: 435–443.

Tanferna, A., L. Lopez-Jimenez, J. Blas, F. Hiraldo, and F. Sergio (2013). Habitat selection by black kite breeders and floaters: Implications for conservation management of raptor floaters. Biological Conservation 160:1–9.

Tella, J. L., A. Rojas, M. Carrete, and F. Hiraldo (2013). Simple assessments of age and spatial population structure can aid conservation of poorly known species. Biological Conservation 167:425–434.

Vanderwerf, E. A. (2008). Sources of variation in survival, recruitment, and natal dispersal of the Hawai'i 'Elepaio. The Condor 110:241–250.

Walters, J. R., L. B. Crowder, and J. A. Priddy (2002). Population viability analysis for red-cockaded woodpeckers using an individual-based model. Ecological Applications 12:249–260.

Weatherhead, P. J., and M. R. Forbes (1994). Natal philopatry in passerine birds: Genetic or ecological influences? Behavioral Ecology 5:426–433.

Zack, S., and B. J. Stutchbury (1992). Delayed breeding in avian social systems: The role of territory quality and “floater” tactics. Behaviour 123:194–219.