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Survivorship and Breeding Dispersal Patterns of a Migratory, Socially Monogamous Passerine; the Scissor-tailed Flycatcher (*Tyrannus forficatus*)

By

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ABSTRACT

Survivorship (the likelihood of survival from one year to the next) and breeding dispersal (movement between breeding seasons) exhibit considerable variability at both the inter- and intraspecific levels. Using eight years of data (2008-2015), from my study site in southwest Oklahoma, I characterized survivorship and breeding dispersal of the Scissor-tailed Flycatcher (*Tyrannus forficatus*) in a mixed-grass prairie ecoregion. My results suggest that estimated survivorship of Scissor-tailed Flycatchers is low, especially to the congeneric Eastern Kingbird (*T. tyrannus*), and was likely underestimated due to the tendency of Scissor-tailed Flycatchers to disperse long distances.

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SURVIVORSHIP OF A MIGRATORY, SOCIALLY MONOGAMOUS, GRASSLAND PASSERINE; THE SCISSOR-TAILED FLYCATCHER (*TYRANNUS FORFICATUS*)

Adam J. Becker

ABSTRACT— Estimates of apparent survival (ϕ) have been shown to exhibit considerable variability in both inter- and intraspecific levels. Interspecific ϕ has been shown to vary with body mass, latitude, phylogeny, mating system, and parental investment, while intraspecific ϕ may vary between the sexes, with age, by varying body mass, or in temporal relation to the surrounding environment. I used data from a 7-yr period to characterize ϕ of Scissor-tailed Flycatchers (*Tyrannus forficatus*; STFL) interspecifically, in relation to its congener the Eastern Kingbird (*T.tyrannus*), and intraspecifically, among individuals at my study sites in the southern Great Plains near Lawton, Oklahoma. I found adult ϕ of STFLs (0.45) to be much lower than that of Eastern Kingbirds (0.65). STFL ϕ was expected to be higher due to a lower breeding latitude, shorter migration distances, delayed migration, and possible pre-migratory molt; I found the opposite to be true. One possible explanation for low apparent survival is that STFLs, which lay more eggs than Eastern Kingbirds, is that their greater investment in reproduction comes at a cost of reduced survival. The more likely alternative explanation is that lower apparent survivorship is an artifact of more extensive dispersal behavior in STFLs, which leads to more permanent emigration and thus failure to detect surviving individuals. Intraspecifically, I found slightly higher ϕ at one of my sites, Wichita Mountain Wildlife Refuge, and a likely linear temporal trend among years, but no variation in apparent survival associated with an individual's sex, age, or body size (i.e., mass).

KEY WORDS: *Survivorship, annual survival, Program MARK, detection probability,* Tyrannus forficatus, *sex, age, mass, sexual dimorphism,* Tyrannus

INTRODUCTION

Mortality and length of life differ greatly among species; it is this variation that gives rise presumably to the tremendous diversity of animal life histories. Annual survival rates scale with body size (Brawn et al. 1995, McCarthy et al. 2008) and the mechanism is suggested to be the ¾ scaling of metabolism with body mass (Calder 1984, Savage et al. 2004); larger species with lower mass-specific metabolic rates, on average, live longer. However, much diversity exists in survival rates of vertebrates that can be traced to phylogeny, ecology, and behavior. For instance, annual survival rates and life spans of birds exceed those of mammals of similar body size (Pomeroy 1990), the probable reason being the advantages conferred by flight. Likewise, phylogeny accounts for a portion of variability in average survival rates of birds at the level of order (Bennett and Owens 2002) but less so at the level of family and especially genus (Brawn et al. 1995, Bennet and Owens 2002). Ecological factors associated with geographic location generate additional variability. Although still debated and in need of much further work, average annual survival rate of bird species from north temperate regions appear to be less than that of species breeding in the tropics and south temperate latitudes (Faaborg and Arendt 1995, Johnston et al. 1997, Møller 2006, Lloyd et al. 2014), possibly because of greater seasonal variation of climate and resources in the north.

Differences in survival can also be linked to behavior. Brawn et al. (1995) showed that annual survival rates of forest dwelling Panamanian birds was associated with foraging guild (but not phylogeny), while those of migrant birds appeared to exceed those of residents breeding in similar temperate-zone locations (Greenberg 1980, Møller 2006). Reproduction is generally considered costly and trade-offs between reproduction and survival are seen as pivotal in life history theory (Williams 1966, Stearns 1976, 1989). Variation in reproductive investment among closely related species may thus manifest itself as differences in adult survival, and indeed, Martin (1995) suggested that the inverse relationship seen between annual fecundity and annual survival among North American breeding passerines and woodpeckers was driven by costs of reproduction (see also Bennett and Owen 2002). Ekman and Askenmo (1986) similarly showed that for two sympatrically breeding European tit species (*Parus* spp.), adult survival was lower in the species laying the larger clutch, a difference that disappeared when nonbreeding adults were compared.

Two facets of reproduction, mate attraction and parental care, have the potential to generate interspecific and intrapopulation differences in survival. Social monogamy and biparental care is the norm for most bird species (Cockburn 2006), but polygyny is common in some families. Males of polygynous species largely forego parental care and instead invest heavily in mate attraction and harem defense. Body size and ornamentation of males of polygynous species typically exceeds that of females, and in blackbirds (Icteridae), the degree of sexual size dimorphism is directly related to harem size (Webster 1992) and to progressively lower survival of males relative to females (Searcy and Yasukawa 1983). Sexual signals can be costly even among monogamous species, as shown by studies of European barn swallows (*Hirundo* *rustica*). Males have significantly longer tails than females, a difference driven by female preference. Experimental elongation of tails enhances a male's immediate reproductive success, but carries with it the cost of reduced survival over the ensuing winter, in keeping with the general notion that long tails are a handicap (Zahavi 1975).

The effort expended in reproduction by socially monogamous species is presumably more nearly equal than in polygynous species. Males exert more effort at mate attraction, but this may be countered by greater female parental effort. Brighter plumaged males may face greater risk of predation (Slagsvold et al. 1995), while direct reproductive costs may hit females harder because they lay eggs, and in many passerine species, build nests and incubate eggs without male assistance. Egg-laying, perhaps not surprisingly, can be costly (Monaghan et al. 1998, Nager et al. 2001, Bowers et al. 2012), but even increased incubation effort carries potential long-term costs (Heaney and Monaghan 1996, Hanssen et al. 2005), and numerous studies have demonstrated that feeding young often takes a toll on parents (Maigret and Murphy 1997, Murphy 2000). Males and females contribute, on average, equal effort at feeding young in most socially monogamous passerine species (Woodard and Murphy 1999 and associated erratum 1999), but Breitwisch (1989) showed that an excess of males exists in many populations of passerines. This suggests that prospects of survival for females may be less than that of males (Breitwisch 1989), a portion of which may be attributed to greater exposure of females to predators as they incubate eggs and brood young (e.g., Arlt et al. 2008) or cumulative costs of breeding that are paid for in the nonbreeding season (e.g., Murphy 2000).

Annual survival is arguably the life history trait that drives variation in other traits (e.g., clutch or litter size, age at first reproduction, etc.), but knowledge of interspecific differences in survival lags far behind that of virtually all other fitness-related traits. The reason is simple, but the solution is not. Measuring survival rate for any species is often physically demanding, time intensive, and statistically difficult. Sandercock et al. (2000) described the various shortcomings of different approaches used to estimate annual survival and concluded that capture-mark-release-resight/recapture methods, when combined with appropriate statistical analyses, generate the most robust estimates of survival. Assuming sufficient numbers of animals can be captured, marked and released, the next most fundamental problem is accounting for the various reasons for failure to resight individuals after release. Possibilities may include (1) death, (2) temporary emigration, (3) permanent emigration, or (4) failure to detect a marked individual that was present. Return rate (number returned/number marked) fails to account for all but death, but Cormack-Jolly-Seber (CJS) methods of analysis (Lebreton et al. 1992, White and Burnham 1999) account for all except permanent emigration because an estimate of “detectability” (p) is produced that can be used to correct for temporary emigration and failure to resight marked individuals. The CJS estimate of survival, referred to as “apparent survival” (and symbolized by ϕ) is a vast improvement over return rate (except when p is very high), but still fails to separate true mortality from permanent emigration (Lebreton et al. 1992).

The genus *Tyrannus* includes 13 species that breed across nearly the entirety of South, Central, and North America (south of 54° N latitude), but an estimate of apparent survival exist for only one species. Roughly two-thirds of Eastern Kingbirds (*T. tyrannus*; EAKI) in New York (Murphy 1996, 2000) and Oregon (Redmond and Murphy 2012) survive annually, a figure that matches nearly exactly that predicted on the basis of body mass (McCarthy et al. 2008). All kingbirds (*Tyrannus* spp.) are socially monogamous, but migratory behavior varies from resident to long-distance migrant (Jahn et al. 2004, 2013). Males and females have nearly identical plumages in all species except the North American breeding Scissor-tailed Flycatcher (*T. forficatus*; STFL) and Central and South American breeding Fork-tailed Flycatcher (*T. savana*). As the names suggest, tail length of the two latter species are especially long in both sexes, but nearly twice as long in males as females. In both species, birds of both sexes in their first potential breeding season have shorter tails than same-sex older birds (Pyle 1997). Of North American breeding species, reproductive rates of EAKIs are among the lowest, while those of STFLs are the highest of all *Tyrannus* (Murphy 1989, unpubl. data).

STFLs thus stand out among kingbirds in exhibiting sexual plumage dimorphism and age-based differences in plumage (Regosin and Pruett-Jones 2001), the largest clutch size (Murphy 1989), and—among migratory North American species—a delayed start to fall migration and possible completion of annual molt on the breeding grounds prior to migration (Jahn et al. 2013). The potential implications of these characters for adult survival are substantial. For instance, increased sexual selection for longer tail length in males may reduce their flight efficiency and compromise survival. On the other hand, the roughly equal contribution of males and females to parental care (Woodard and Murphy 1999, M. Husak, unpubl. data) argues for equivalent rates of annual survival. The existence of identifiable age classes also permits us to ask whether adult survival differs between young and older adults, as younger birds might invest less in their first breeding attempt and accrue lower energetic costs from parental investment (Curio 1983). Younger birds also have shorter tails and may avoid extraneous costs if the longer tails of STFLs come at an energetic cost. On an interspecific level, relatively low annual survival would be predicted given that Scissor-tailed Flycatchers raise the largest broods of all kingbirds (Murphy 1989) and occasionally raise two broods/season (Regosin and Pruett-Jones 1995). However, delaying departure after breeding until molt is completed might mitigate the stress accumulated during breeding and enhance prospects of survival.

I used Cormack-Jolly-Seber methods to model survival of STFLs in Program MARK (White and Burnham 1999) using live-encounter data for a demographically open population breeding at two sites in southwest Oklahoma. I tested whether survival differed between (1) sexes, (2) age classes, (3) by individual body mass (expecting larger birds to be more likely to survive), (4) varied annually among years of my study, or (5) differed from its similar-sized congener the EAKI.

METHODS

Study Site.—I collected data from two contiguous study sites in Comanche County, Oklahoma; the west artillery range of Fort Sill Military Reservation (Fort Sill; 34°39'33.3" N 98°30'11.0" W) managed by the US Department of Defense, and the Wichita Mountains Wildlife Refuge (the Refuge; 34°43'28.1" N 98°40'15.7" W) managed by the US Fish and Wildlife Service. They share a border at the southeastern end of the Refuge and are within the mixed-grass prairie ecoregion characterized by oak (*Quercus*) or mesquite (*Prosopis juliflora*) savannah. The Refuge is comprised of prairie stretches broken by low mountains, small man-made lakes, and riparian forests of mainly oak, predominantly blackjack oak (*Q. marilandica*) and post oak (*Q. stellata*). Fort Sill is primarily mesquite savannah dominated by little bluestem (*Andropogon scoparius*) and Johnsongrass (*Sorghum halepense*), and other species of trees including hackberry (*Celtis reiculata*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*). Although my study sites are contiguous, suitable STFL habitat is patchy, and between sites, a distance of 7.2 km separated the nearest known nests at the two sites because the majority of this gap is unsuitable habitat for STFLs. In addition to the habitat differences, the government agencies managing the sites have different ecological practices that greatly influence the landscape. Fort Sill is an active artillery and training range that is susceptible to much greater anthropomorphic disruption than the nearby Refuge, which is highly regulated and managed strictly for conservation purposes. Also, as long as fires do not threaten human lives or structures, fires are allowed to burn at Fort Sill, whereas policy at the Refuge is to actively extinguish fires.

Suitable habitat for STFLs is patchy, but in areas of high nest density the same territories are consistently occupied from year to year. At Fort Sill, I regularly surveyed an area of suitable habitat on the southern edge of Fort Sill that encompassed ≈ 30 km^2, while STFLs at the Refuge were regularly found in an area of suitable habitat that encompassed ≈ 34 km^2. Other areas of habitat that may have been suitable or STFLs were sighted in were also searched throughout the field season, but nests were rarely found. Fort Sill's southern edge represents the northern boundary of the city of Lawton, Oklahoma, which covers 194.6 km^2 and contains a population of 96,867 (2010 census).

Data Collection.—Beginning in late April of each year I searched suitable habitat for STFL nests and returning banded adults. When detected, their location was recorded with a Global Positioning System (GPS) satellite receiver (Garmin CSX). Areas deemed as unsuitable habitat were also searched throughout the field season, but nests and adults were rarely found. During nest searching and resighting efforts, adult STFLs seen carrying nesting material or food were followed in order to locate nests, and visits to nests were made every 2-3 days during the nesting cycle until a nest was either successful (when one or more nestlings fledged) or failed. Nest frequently fail and attempts were made to relocate and determine fates of replacement nests.

All captured adults were uniquely banded with one numbered metal Federal band and three colored Darvic leg bands (2 per leg). After banding efforts were concluded at a nest, banded adults were monitored within a day or two of banding in order to confirm the association of color-banded birds with their presumed nest. Nestlings also were banded prior to fledging; however, because return rates of young were so low, survival rates were only estimated for adults. Body mass, wing chord, tarsometatarsus, and tail lengths were measured on captured birds, and a blood sample taken for use in a companion study of extra-pair paternity. Sex was determined using both morphological and molecular methods (see Roeder et al. in press, for methods); molecular assignments of sex were given priority if a discrepancy existed between assignments by the two methods.

Data Summary and Analysis. —I used capture and resighting data from seven breeding seasons (2008-2014) to model survivorship. My analysis was restricted to individuals of breeding age, for which I recognized two age classes; second-year (SY, ~11 months old), and older after-second-year (ASY, at least 23 months old) birds. Annual sampling effort varied due to variation in number of personnel and resources. Partly as a consequence, resighting rates were variable across years, but generally low in all (Table 1.1).

In Program MARK (White and Burnham 1999) I used Cormack-Jolly-Seber models to characterize live-encounter data, estimating apparent annual survival (ϕ) and detectability (p) at my two sites. Banding and resighting data were analyzed with individuals being classified into two groups by site (Fort Sill or the Refuge) for my global model. Individuals were grouped into these categories because of possible differences between sites in dispersal (Chapter 2), which is closely linked to p, and possibly ϕ. I also included three covariates; sex, age category, and body mass (as z-scores) at capture. I used z-scores for body mass because male STFLs are significantly heavier than females (D. Roeder and M. S. Husak unpubl. data). All further references to body mass are for z-scores but I will simply refer to them as "mass".

My global model design matrix in MARK included a constant intercept term, a group effect (site), and a group by time interaction for both ϕ and p. The global model was denoted as {ϕ (group * time) p (group * time)} (White and Burnham 1999). I used Program RELEASE GOF (Dinsmore et al. 2003) and Bootstrap GOF within MARK to calculate goodness of fit for my global model. In Program RELEASE GOF, my estimate of $\hat{c}$, the variance inflation factor (pooling results of tests 2 and 3) was < 1, and the $\hat{c}$ estimate from Bootstrap GOF was 1.436 (calculated as global model deviance/ mean deviance from bootstrap simulations) and showed some concern for over dispersion but was within acceptable limits (deviance = 32.503, rank 88 of 100 simulations, $P = 0.12$). I therefore did not adjust $\hat{c}$ within MARK (Rotella et al. 2009).

Further over dispersion is possible when covariates are added into relatively small datasets, therefore I constrained my model and did not include time interactions with my covariates. My starting, most complex, model was denoted as {ϕ (site + linear + quadratic + sex + age + mass) p (site + linear + quadratic + sex + age + mass)}. I included quadratic effects of time (year) to account for potential temporal trends that were non-linear (Dinsmore 2008). After running the above model (my most complex), all possible combinations of model variables were run through MARK that included either no time trend, a linear time trend, or a quadratic time trend; for a total of 1280 models.

I used Akaike's Information Criterion adjusted for small sample size (AIC_C) to rank the 1280 models, and selected the most competitive models (ΔAIC_C values ≤ 2). To account for model selection uncertainty, I present model averaged estimates (± SE) of ϕ and *p* (Burnham and Anderson 2002) for each variable and used Akaike weights (w_i) to determine relative support for each model. Model averaged estimates for mass were calculated for three groupings in my continuous scale that represented heavy, average, and light birds. Heavy birds had a z-score of + 2 (2 standard deviations above the mean value, ≈ 95th percentile), average birds had a z-score of zero, and light birds had a z-score of – 2 (2 standard deviations below average, ≈ 95th percentile). Beta (β_x) estimates are given for parameters in the top model and those in which the confidence interval did not include zero.

RESULTS

Model selection results.— I captured, uniquely banded, and released 229 adult STFLs between 2008 and 2014 and had a raw return rate of 27.8% (Table 1.1). From the full model set, 13 received sufficient support to be considered competitive ($\Delta AIC_C \leq 2$; Table 1.2). The global model, by contrast, received little support ($\Delta AIC_C = 15.537$, $w_i < 0.001$). Model weights were all relatively low, even for the top model, indicating that model uncertainty was high and that no single variable exhibited an especially strong relationship with ϕ. In fact model selection (Table 1.2) showed that, for both ϕ and *p*, all of the parameters were included in at least one of the top 13 models but the number of times they appeared differed greatly. With respect to ϕ, a temporal component always existed, most often as a linear (10/13) rather than a quadratic (3/13) trend with year. Age (4/13), site (3/13), body mass (2/13), and sex (1/13) were also present in our top models. However, most parameter estimates from the models of ϕ included zero within the 95% confidence interval, the only exceptions being a site effect (model #3 = -1.222 ± 0.550, model #6 = -1.418 ± 0.599), with STFLs at Fort Sill tending to exhibit higher ϕ than individuals from the Refuge, and a linear effect of time (once; model 10 = -1.516 ± 0.627).

Analyses of detectability (*p*) suggested that the probability of resighting a bird was affected by different sets of variables. Body mass appeared as a contributor to variation in *p* in all 13 models (Table 1.2). *p* also varied over time, usually as a quadratic (10/13) rather than as a linear term (3/13), and between sites (4/13). Sex (3/13) and especially age (1/13) were increasingly less important sources of variation in *p* (Table 1.2). 95% confidence intervals around parameter estimates for mass did not include zero in 10 of 13 models. The same was true for site in 3 of 4 cases, while the time component did so only once. Thus, *p* varied consistently with body mass (higher in heavier individuals), and tended to be higher at the Refuge than at Fort Sill.

On the basis of the model averaged parameter estimates, ϕ was similar for the first four years and then increased slightly in the final two years (Table 1.3), but averaged 0.45 (± 0.14) over the duration of the study. ϕ was slightly but not significantly higher at Fort Sill (0.48 ± 0.14) than at the Refuge (0.42 ± 0.14; Table 1.4), while *p* at the Refuge (0.46 ± 0.19) was slightly higher than at Fort Sill (0.38 ± 0.16). Between the sexes I found similar model averages of mean ϕ and *p* for males (0.45 ± 0.14 and 0.41 ± 0.18, respectively) and females (0.45 ± 0.14 and 0.43 ± 0.19, respectively; Table 1.5). Model averaged estimates of ϕ and *p* for SY (0.44 ± 0.15 and = 0.41 ± 0.18, respectively) and older birds (0.46 ± 0.14 and 0.42 ± 0.18, respectively; Table 1.6) were similar. The same was true for model averaged ϕ of heavy birds (0.44 ± 0.14) and light individuals (0.46 ± 0.15) but *p* was much greater for heavy birds (0.65 ± 0.19) than lighter (0.22 ± 0.16; Table 1.7).

DISCUSSION

One of the most frequently and predictably asked questions of wildlife biologists is “how long do they live.” It is a simple question for which there are no simple answers because probability of survival from one year to the next often differs with age, sex, reproductive state, and a host of other variables. Even more to the point is that measuring survival and lifespan is one of the most difficult challenges faced by wildlife or population ecologists because the absence of an individual in a year after it was first captured, marked, and released, may be because it died, but it is also possible that it survived and the researcher missed it, the animal temporarily left the study area, or it permanently emigrated (Lebreton et al. 1992). The usual answer given to the question of “how long does it live,” even for common and abundant species, is “well, I don’t know for this species, but other similar species about this size typically live X years.”

The STFL is the poster-child for the common, visible, charismatic, and abundant species for which we lack this most basic yet essential biological trait. They are abundant throughout the southcentral Great Plains and are highly visible because of their use of open habitats where their extremely elongated tail enhances their conspicuousness. I attempted to measure annual probability of survival of STFLs and evaluate potential sources of variation in this demographic trait. STFLs possess the longest tail of any North American breeding bird relative to body size, and long tails are considered a handicap (sensu Zahavi 1975) that, while presumably being favored by sexual selection (e.g., Pryke et al. 2001), produce less efficient flight (Evans and Thomas

1992) that carries a survival cost (Møller and de Lope 1994). That some species of long-tailed birds molt into shorter tails at the end of the breeding season (e.g., the Strange-tailed Tyrant [*Alectrurus risora*] and Long-tailed Widowbird [*Euplectes progne*]) is *prima facie* evidence that long tails are a hindrance in flight. Evidence, albeit limited, suggests that male Strange-tailed Tyrants have lower annual survival than females (Di Giacomo et al. 2011). The existence of sexual size dimorphism in STFLs for both body mass and especially tail length (males > females in both cases) and greater tail length in ASY birds of both sexes leads to a prediction of higher survivorship of females and possibly SY birds.

On the other hand, annual reproductive output and survival are inversely related in birds (Martin 1995, Bennett and Owens 2002), and the equal commitment of both parents to rearing what are the largest broods (5 nestlings) of all 13 species of *Tyrannus* (Murphy 1989) would presumably exact an equal cost on both sexes of STFLs. Experimental evidence from the congeneric EAKI, which usually lays a 3-egg clutch, showed that females given enlarged broods exhibited lower return rates and reduced fecundity in the year following brood enlargement (Murphy 2000), confirming that reproduction is costly. The high apparent commitment to reproduction by STFLs also predicted lower survivorship than found in EAKIs.

My estimates of apparent annual adult survival of STFLs (0.45 ± 0.14) were much lower than that of the EAKI in both New York (0.60 to 0.70; Murphy 2000) and Oregon (0.65; Redmond and Murphy 2012). Survival was slightly higher at Fort Sill (~0.48) than at the Refuge (~0.42), but the differences did not approach significance. Likewise, apparent annual survival showed no tendency to differ between the sexes, age classes, or in relation to an individual's size as measured by body mass. Thus, the elongated tails of males and older birds either seemingly carried no cost, or those individuals are of higher quality and tail length is an honest signal that prevents less fit individuals from cheating the system by displaying them (handicap principle; Zahavi 1975); consequently, only those individuals capable of bearing the cost exhibit the exaggerated trait.

Possibly the most noteworthy finding, therefore, is the much poorer apparent survival of STFLS in comparison to EAKIs. STFLs and EAKIs are of roughly equal size (37.5 g vs. 40.0 g, respectively), and based on allometric scaling of passerine survival rates (McCarthy et al. 2008), the median predicted annual survival rate for STFLs and EAKIs are 0.65 and 0.66, respectively. The match between observed and predicted for EAKIs is striking, as is the equally strong mismatch of the STFL. The 95% credibility interval bounding McCarthy et al.'s (2008) prediction line is wide and STFLs fall within the bounds. STFLs are thus not atypical passerines, but that still does not explain why their annual survival falls far short of the EAKI's.

While costs of survival associated with the higher annual reproductive output of STFLs might explain some of the difference, I must consider the possibility that I underestimated apparent annual survival. Factors that have the possibility of reducing detectability (*p*; which then leads to an underestimate of survival) include weak sampling effort and frequent dispersal behavior. *p* did not differ between sex or age classes of STFLs and thus the conclusion that survivorship was independent of both variables appears secure. On the other hand, of the six years when it was possible to resight individuals, *p* was low in the first four, but then increased greatly in the last two. This rise was likely related to an increased resighting effort during those years, when the number of field researchers increased. Although the difference was not significant, *p* was slightly higher at the Refuge than at Fort Sill probably because the Refuge is patchier habitat and relatively easy to thoroughly search compared to the larger continuous habitat at Fort Sill. Restricted access due to military training exercises at Fort Sill also prevented the research team from surveying sites at Fort Sill for extended periods in some years, thus increasing the probability of missing banded birds that returned for at least brief periods. The especially low return rate (Table 1.1) and low *p* (Table 1.3) prior to 2012-2013 are probably not to be trusted, and therefore the survival estimates from the last two years of the study likely better reflect true survivorship.

However, annual adult survival of 0.5 seems too low to sustain stable population numbers. For example, rearranging the basic population growth equation ($\lambda = S_A + [F*NS*S_J]$) to solve for F ($F = [\lambda - S_A]/[NS*S_J]$) where F = number of female young per successful nest, λ = growth rate, S_A = annual adult survival, NS = average nest success, and S_J = survival of fledglings to the next breeding season, provides insight as to minimum F needed to maintain population numbers. Assuming population stability ($\lambda = 1$), S_A of 0.5, S_J equal to that of EAKIs (0.30; Redmond and Murphy 2012), and NS of 75%, then each successful nests must fledge nearly 2.25 female young. This is more than can be expected, as it means that most females must breed successfully and experience no partial clutch or brood loss. Reducing NS to 50%, closer to a more realistic expectation, raises F to 3.33 female young per year. Assuming a 50:50 sex ratio of nestlings, this translates to 6.66 young per successful nest, an impossibly high figure.

The irrefutable conclusion is that 0.5 underestimates true survival, and the likely explanation is low detectability associated with dispersal behavior. Breeding dispersal, the movement of adults to different locations in consecutive years, occurs more commonly in STFLs than EAKIs (Chapter 2). At least 50% of STFLs at Fort Sill changed breeding locations among years. In EAKIs this figure averages ≤ 20% of returning birds (Murphy 1996, unpubl. data). Dispersal distances of up to 16 km were documented for non-territory holding SY STFL males showing that individuals disperse long distances. Breeding distance dispersal in studies of other migratory species that were designed to detect long distance dispersers have been documented to exceed 200 km (Southwestern Willow Flycatcher [*Empidonax traillii eximus*]; Paxton et al. 2007) and nearly 300 km (Tree Swallow [*Tachycineta bicolor*]; Winkler et al. 2004). Frequent dispersal will not only reduce *p*, but long distance dispersal results in permanent emigration that then becomes inseparable from death. Interestingly, body mass of STFLs was included in all top 13 models as a predictor of *p*. The greater *p* of heavier birds may reflect the ability of large birds to outcompete other birds for territories in high quality areas that would likely have higher densities of STFLs, and that, as a consequence, would be more heavily surveyed by researchers who would then detect the heavy birds.

However, another nonmutually exclusive interpretation exists. I found that heavier birds, especially males, were more likely to disperse the greatest distances (Chapter 2). Dispersal distance appears to exhibit an exponential decline with a long right skewed tail to the distribution (Chapter 2). However, it might be that this is due to few records of a second group of dispersers, the truly long distance dispersers that were only weakly sampled because of declining detection with increasing distance. True dispersal might appear as a bimodal distribution with short-dispersers being the group that I sampled well, and a group of long-dispersers that I sampled very poorly (Fig. 1). If dispersal behavior is truly bimodal, and the heaviest (and thus most competitive) long-distance dispersers settled in the first available high quality territories beginning at a dispersal distance of 2 km to 3 km, this might also explain why long distance dispersal was associated with heavy birds. A bimodal pattern of dispersal would also result in the movement of many birds outside the range of detection to produce the low apparent annual survival rate of 0.5.

CONCLUSIONS

The return rate and estimate of apparent annual survival of STFL near Lawton, Oklahoma, at the geographic center of the species breeding distribution, were both surprisingly low. Annual survival was well below that predicted for a passerine bird of this size, and in comparison to the congeneric EAKI. Like EAKIs, however, survival did not differ between the sexes, and as in the few passerine species in which it has been measured (e.g., Sillett and Holmes 2002), survival did not differ between younger and older birds. Detectability, a measure of the probability of detecting a bird that was present, was low. Low detectability might arise for several reasons, but weak sampling effort and frequent dispersal by the study species are two of the more important contributors. I conclude that weak sampling effort in some years of the study contributed to a moderate underestimate of true survival, but the major reason for the low apparent annual survival of STFLs is frequent dispersal and a predilection for long distance dispersal that resulted in permanent emigration from the study area. Higher annual reproductive output of STFLs might account for some of the difference in annual survival of STFLs and EAKIs, but the most parsimonious explanation for the dissimilarity of annual survival is substantial differences in dispersal behavior of the two species.

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TABLES AND FIGURES

TABLE 1.1 Number of adult Scissor-tailed Flycatchers banded each year and the number that were resighted the following year. Banding and observations made near Lawton, OK, 2008-2014. F =first time banded and R = returning birds. For instance, of the 9 birds banded in 2008, only 1 was resighted in 2009.

	Females		Males	
Year	F	R	F	R
2008	5	--	4	--
2009	14	0	14	1
2010	9	2	12	3
2011	22	2	23	2
2012	13	5	28	2
2013	34	6	51	10
2014	--	17	--	25
Total	97	32	132	43

TABLE 1.2 Competing models from CJS modeling in Program MARK used to estimate apparent survival (ϕ) and detection probability (*p*) for Scissor-tailed Flycatchers near Lawton, OK, 2008-2014. These are the top models (ΔAIC ≤ 2) from my all subsets model set run in MARK. I allowed ϕ or *p* of my models to vary across years in either a linear or quadratic manner. Models could also carry a dummy variable for each of my two sites (group) and were allowed to include or exclude my three covariates (sex, age, and mass). Bold and italicized parameters indicate betas that did not include zero for that model.

	Model Structure		Model Statistics			
#	ϕ	*p*	ΔAIC_C	w_i	K	Deviance
1	linear	quadtratic + ***mass***	0.000	0.14	6	367.08
2	linear + age	***quadtratic*** + ***mass***	0.651	0.12	7	365.62
3	quadtratic +***group***	linear + ***group*** + mass	0.725	0.10	8	363.57
4	linear	quadtratic + sex + ***mass***	0.860	0.09	7	365.83
5	linear + mass	quadtratic + ***mass***	1.169	0.08	7	366.14
6	quadtratic + ***group*** + age	linear + ***group*** + mass	1.433	0.07	9	362.13
7	linear + age	quadtratic + sex + ***mass***	1.557	0.06	8	364.40
8	quadtratic	quadtratic +***mass***	1.588	0.06	7	366.56
9	linear	quadtratic + age + ***mass***	1.594	0.06	7	366.57
10	***linear*** + group	linear + ***group*** + ***mass***	1.630	0.06	7	366.60
11	linear + age + mass	quadtratic + ***mass***	1.817	0.06	8	364.66
12	linear	quadtratic + group + ***mass***	1.932	0.05	7	366.91
13	linear + sex	quadtratic + sex + mass	1.991	0.05	8	364.84
14	group*time	group*time	15.537	< 0.001	24	341.89

AIC_C and deviance of top model were 379.414 and 367.085, respectively

TABLE 1.3 Model averaged estimates of annual apparent survival (ϕ) and detection probability (*p*) for Scissor-tailed Flycatchers near Lawton, OK, 2008-2014.

	ϕ		*p*	
Year	Estimate	SE	Estimate	SE
2008-2009	0.43	0.20	0.39	0.27
2009-2010	0.42	0.14	0.26	0.16
2010-2011	0.43	0.11	0.24	0.14
2011-2012	0.44	0.09	0.31	0.12
2012-2013	0.48	0.11	0.52	0.14
2013-2014	0.52	0.19	0.78	0.23
Mean	0.45	0.14	0.42	0.18

TABLE 1.4 Model averaged estimates at both of my sites, FSMR and WMWR, of annual apparent survival (ϕ) and detection probability (*p*) for Scissor-tailed Flycatchers near Lawton, OK, 2008-2014.

	ϕ				*p*			
	FSMR		WMWR		FSMR		WMWR	
Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
2008-2009	0.46	0.19	0.40	0.21	0.35	0.26	0.43	0.28
2009-2010	0.45	0.12	0.39	0.16	0.22	0.11	0.30	0.21
2010-2011	0.45	0.08	0.40	0.13	0.20	0.09	0.28	0.20
2011-2012	0.48	0.09	0.41	0.10	0.27	0.08	0.35	0.17
2012-2013	0.51	0.15	0.45	0.07	0.48	0.16	0.56	0.13
2013-2014	0.53	0.21	0.50	0.16	0.74	0.28	0.82	0.18
Mean	0.48	0.14	0.42	0.14	0.38	0.16	0.46	0.19

TABLE 1.5 Model averaged estimates for male and female birds of annual apparent survival (ϕ) and detection probability (*p*) for Scissor-tailed Flycatchers near Lawton, OK, 2008-2014.

	ϕ				*p*			
	Male		Female		Male		Female	
Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
2008-2009	0.43	0.20	0.43	0.20	0.38	0.26	0.41	0.28
2009-2010	0.42	0.14	0.42	0.14	0.25	0.16	0.28	0.17
2010-2011	0.43	0.11	0.42	0.11	0.23	0.15	0.26	0.15
2011-2012	0.45	0.09	0.44	0.09	0.30	0.13	0.33	0.14
2012-2013	0.48	0.11	0.48	0.11	0.50	0.14	0.54	0.16
2013-2014	0.52	0.19	0.51	0.19	0.77	0.23	0.78	0.23
Mean	0.45	0.14	0.45	0.14	0.41	0.18	0.43	0.19

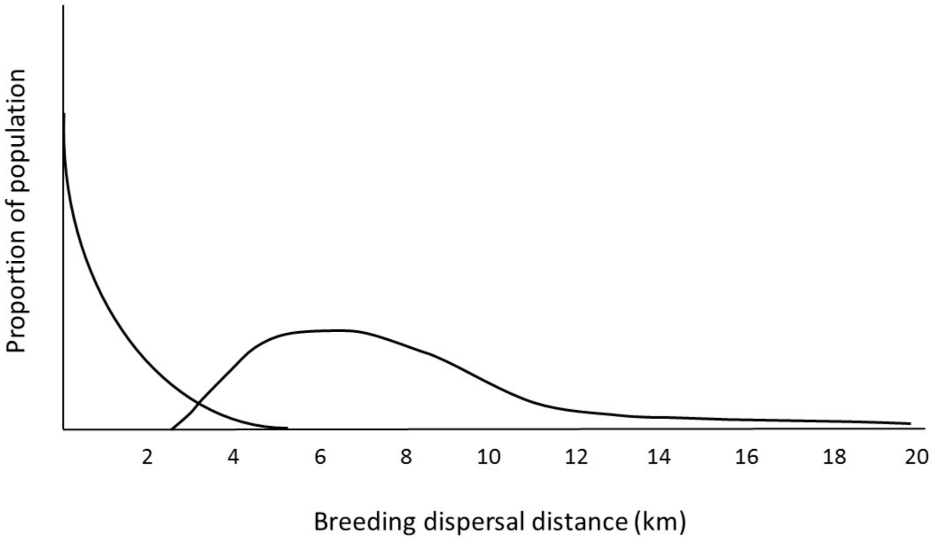
Table 1.6 Model averaged estimates for SY and ASY birds of annual apparent survival (ϕ) and detection probability (*p*) for Scissor-tailed Flycatchers near Lawton, OK, 2008-2014.

	ϕ				*p*			
	SY		ASY		SY		ASY	
Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
2008-2009	0.41	0.20	0.44	0.20	0.39	0.27	0.39	0.27
2009-2010	0.40	0.15	0.43	0.14	0.26	0.16	0.26	0.16
2010-2011	0.41	0.12	0.44	0.11	0.24	0.15	0.24	0.14
2011-2012	0.43	0.10	0.46	0.09	0.31	0.13	0.31	0.12
2012-2013	0.46	0.12	0.49	0.11	0.51	0.15	0.52	0.14
2013-2014	0.50	0.19	0.53	0.19	0.77	0.23	0.78	0.23
Mean	0.44	0.15	0.46	0.14	0.41	0.18	0.42	0.18

TABLE 1.7 Model averaged estimates for small (normalized mass - 2), average (mean mass), and large (normalized mass + 2) birds of annual apparent survival (ϕ) and detection probability (*p*) for Scissor-tailed Flycatchers near Lawton, OK, 2008-2014.

	ϕ						*p*					
	Light		Average		Heavy		Light		Average		Heavy	
Year	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
2008-2009	0.44	0.21	0.43	0.20	0.42	0.20	0.17	0.19	0.39	0.27	0.67	0.26
2009-2010	0.43	0.15	0.42	0.14	0.41	0.14	0.12	0.13	0.26	0.16	0.53	0.19
2010-2011	0.44	0.12	0.43	0.11	0.42	0.11	0.11	0.12	0.24	0.14	0.49	0.17
2011-2012	0.46	0.10	0.44	0.09	0.43	0.10	0.13	0.12	0.31	0.12	0.59	0.17
2012-2013	0.49	0.12	0.48	0.11	0.47	0.12	0.25	0.12	0.52	0.14	0.77	0.18
2013-2014	0.53	0.19	0.52	0.19	0.51	0.19	0.57	0.27	0.78	0.23	0.88	0.18
Mean	0.46	0.15	0.45	0.14	0.44	0.14	0.22	0.16	0.42	0.18	0.65	0.19

Fig. 1.1 Depiction of the hypothesis that individuals can be categorized into short- (declining exponential curve between 0 and 5 km) and long-distance dispersers (humped curved between ~2 km and 20 km). The short-dispersers are the typical set sampled in most field studies including Scissor-tailed Flycatchers. The long-distance dispersers can only be detected in studies specifically designed for that purpose. Failure to measure long-distance dispersal in species with high site fidelity will have little influence on estimates of annual survival, but in species with low site fidelity and the propensity to move widely across the landscape, failure to detect long-distance dispersal will lead to underestimates of annual survival in direct relation to the proportion of dispersers move long distances.



BREEDING DISPERSAL OF A MIGRATORY, SOCIALLY MONOGAMOUS, GRASSLAND PASSERINE; THE SCISSOR-TAILED FLYCATCHER (*TYRANNUS FORFICATUS*)

Adam J. Becker

ABSTRACT— Breeding dispersal (i.e., movement between breeding locations in successive years) in birds exhibits considerable interspecific variability, but the generally expected patterns are for dispersal to be more common in younger birds, females, after reproductive failure, or when habitat/territory quality is low. I used resightings of banded birds made over a 7-yr period (2009 to 2015) to describe breeding dispersal of Scissor-tailed Flycatchers (*Tyrannus forficatus*; STFL) to test whether the aforementioned factors, along with body size (mass), were associated with territory fidelity and breeding dispersal distance (BDD). Return rates of banded birds from my two sites near Lawton, OK (Fort Sill Military Reserve [Fort Sill] and Wichita Mountain Wildlife Refuge [the Refuge]) were low (31.2%) and did not differ between sites or years. Territory fidelity of the 76 resighted birds was lower at Fort Sill than at the Refuge. Average BDD was 600 m (range = 1 m to 6.3 km), but was greater at Fort Sill (870 m) than at the Refuge (268 m). Territory fidelity and BDD were unrelated to a bird's sex, while territory fidelity was also unrelated to nest success in the previous year. Younger (second year [SY]) birds were more likely to change territories at Fort Sill. Analysis of BDD from both sites using generalized linear models in an information theoretic framework indicated that age, prior nest success, and their interaction were most influential; BDD was greatest in SY birds and in birds with prior nest failure. BDD was also greater at Fort Sill and in heavy birds, the latter being opposite of that predicted by the hypothesis that large socially dominant individuals take the best and closest territories. Variation of BDD with age and prior reproductive success thus conform to typical patterns for birds, but the absence of an association with sex is unusual and in STFLs appears related to frequent male dispersal. Habitat disturbance is more common at Fort Sill and this possibly explains why dispersal is more common at that site. I propose that year-to-year stability of habitat is low, and that larger birds, which are likely the first to arrive on the breeding grounds following spring migration, have the most time to search the landscape for the best territories. As a consequence, the greatest dispersal distances are seen among larger birds.

KEY WORDS: *Breeding dispersal; site fidelity, territory fidelity,* Tyrannus forficatus*, divorce, mate fidelity*

INTRODUCTION

Migratory and seasonally breeding organisms must, between reproductive events, regularly choose to either return to their former breeding location (i.e., territory fidelity), or disperse to a new location (Harvey et. al. 1979, Greenwood and Harvey 1982). This decision is based presumably on the costs and benefits to the individual, such that fitness will be enhanced. However, the proximate basis for territory fidelity or dispersal is often not obvious, especially in migratory species that may be influenced by carryover effects from wintering areas (Marra et al. 1998). The benefits of territory fidelity include familiarity with food sources and refuges from predators (Greenwood and Harvey 1982, Piper 2011), and possibly familiarity with neighbors (Lovell 2004). Familiarity with local resources and dangers maximizes food intake, minimizes risk of predation, correlates with earlier nesting dates, and minimizes the risk of territorial intrusion by conspecifics (Greenwood and Harvey 1982, Murphy 1996, Yoder and Swanson 2004, Saunders et al. 2012). Ultimately, either alone or in combination, the above elements may lead to increased survival and/or reproductive success of individuals exhibiting territory fidelity.

By contrast, territory fidelity can also be costly if it prevents an individual from moving to higher quality territories when the opportunity arises. If predators learn nest locations and return to check those territories, faithful birds may face an increased likelihood of future predation at a previously depredated nest (Sonerud and Fjeld 1987). However, on the basis of current research, it appears that individuals of many species have low rates of breeding dispersal (Harvey et al. 1984, Bollinger and Gavin 1989, Murphy 1996, Bernard et al. 2011), possibly because of the uncertainty over whether an open and suitable territory can be found or that it will lead to an improvement of reproductive success (Belichon et al. 1996, Bernard et al. 2011). The implications of dispersal or territory fidelity run deep and have the potential to affect population dynamics, gene flow, the stability of social relationships, and may be vital in the conservation of endangered species.

Dispersal decisions can influence both fecundity and survival of individuals, and numerous studies have attempted to identify predictors of dispersal. Below I review the factors that have repeatedly emerged as strong correlates of variation in the probability of dispersal in terrestrial birds

Sex— Sex-specific differences in territory fidelity are common. With the exception of Anatidae, the typical pattern in birds is greater frequency and distance of dispersal in females (Greenwood and Harvey 1982, Clarke et. al. 1997). These patterns may be associated with two factors. First, because a male bird's ability to acquire a mate depends on his possession of a territory, a male's first priority is the acquisition and retention of a physical space. Territory familiarity likely enhances an individual's ability to retain a territory, and reduces time and energy expended in possibly fruitlessly searching for a new territory. Individuals in possession of a territory may also have the advantage in territorial disputes (Krebs 1982, Jakobsson 1988, Cooper et al. 2009a). By contrast, females are not constrained by the need to hold a territory and it may be to their advantage to seek better opportunities, either with a different male or at a new territory. The potential for a female to find a new territory with an unpaired male, especially if she is an older experienced breeder, is likely greater than that of a male finding an uninhabited suitable territory because older females often return from migration before younger females (Francis and Cooke 1986, Cooper et al. 2009b, Maggini and Bairlein 2012).

Age, size, and social dominance.—Older birds tend to be more territory faithful than younger birds, possibly because experienced birds are socially dominant and better able to compete for breeding opportunities, already occupy superior territories, and/or more effectively defend them. Older birds often exhibit higher nest success than younger breeders, thus, another possible explanation for the higher territory fidelity of older birds is that they more often breed successfully (Greenwood and Harvey 1982, Saether 1990, Forslund and Part 1995, Bradley and Safran 2014).

Like age, larger size and good body condition are sometimes associated with social dominance (Lange and Leimar 2003). A larger, higher quality individual may be better able to compete with conspecifics, and consequently, be more likely to return and retain a former territory than if it was small and/or in poor condition. Body condition is difficult to assess, but sexually dimorphic traits may be good indicators of the quality of individuals, especially in the sex in which selection is stronger. Thus, a reasonable expectation is that the probability of dispersal, and distance moved between years, is inversely related to competitive ability (social dominance hypothesis; Gowaty 1993) where size (body mass) is a surrogate for competitive ability.

Personal and conspecific reproductive success.—Correlational studies have shown that an important "decision rule" influencing dispersal for many species may be their past reproductive success at a territory; succeed and stay, fail and move (Greenwood and Harvey 1982, Switzer 1997, Murphy 1996, Hoover 2003, Pearson and Colwell 2014). However, the effectiveness of such decision rules for guiding dispersal based on past reproductive success is only viable if territory-based success is temporally correlated (Blancher and Robertson 1985). Nest predation is far and away the most important cause of nest failure in most passerine bird species (Martin 1993a, 1993b, 1995), and, as noted above, dispersal is generally more common after reproductive failure (Murphy 1996, Haas 1998, Hoover 2003, Winkler et al. 2004, Fisher and Wiebe 2006, Jiménez-Franco et al. 2013). It is not unreasonable to expect that predators are likely to occupy the same territories, certainly within a breeding season, but also between years. A simple decision rule might therefore work well in environments where conditions for success are relatively predictable within and/or between years, and dispersal may lead to increased success (Forero et al. 1999).

Aside from predators, the likelihood of major disturbance (e.g., fire, flooding, and wind storms) to habitat also may affect evolved proclivities towards dispersal. Different strategies may be more advantageous in a highly predictable environment where conditions are similar from year to year than in unpredictable environments where it is difficult to ascertain habitat quality based on previous experience (Switzer 1993, Boulinier and Danchin 1997). Dispersal following failure appears to be a "reasonable move", but few studies have explored the possibility of whether birds are more likely to disperse from habitats where large scale disturbance, of either natural or human origin, occur more commonly.

Assessing habitat quality on the basis of personal experience and observation is also time intensive, energetically costly, and may expose individuals to higher rates of predation. A possible alternative means of evaluating the potential quality of a habitat is by using conspecifics cues. Using social cues such as density of conspecific adults and fledglings may be valuable in evaluating nearby territory quality (Boulinier and Danchin 1997, Doligez et. al. 1999, 2002, 2003, Betts et al. 2008, Redmond et al. 2009). Such information may even trump primary indicators of habitat quality such as vegetation structure (Betts et al. 2008; but see Cornell and Donovan 2010); for instance, if birds in highly seasonal environments make choices of where to settle prior to the full development of vegetation (e.g., Arlt and Pärt 2008) the only possible cue for naïve new breeders may be the presence of conspecifics.

Habitat quality.—If an individual can obtain a higher quality territory by dispersing, and this is likely to improve reproductive success, then dispersal is favored despite the potential costs (Brooke 1978, Greenwood and Harvey 1982, Newton and Marquiss 1982, Part and Gustafsson 1989). The converse is also true, and Bernard et al. (2011) reported that return rates of Ovenbirds (*Seiurus aurocapill*) to former territories were similar for both successful and unsuccessful breeders presumably because of uniformly high territory quality within their study area. However, species may respond differently even when studied under identical conditions. For instance, Fajardo et al. (2009) showed that Bobolinks (*Dolichonyx oryzivorus*) nesting in the same fields as Savannah Sparrows (*Passerculus sandwichensis*) were more likely to disperse to higher quality habitats than were the highly site faithful sparrows.

Re-establishment of pair bonds.—Among socially monogamous species, especially if long-lived, selection favoring the re-establishment of pair bonds may lead to increased territory fidelity (Harvey et al. 1984, Payne and Payne 1993, Black 2001). Re-establishment of pair bonds carries the potential advantage of reducing the energy and time spent searching for and becoming accustomed to a new mate, which may allow for earlier breeding and better coordination in raising young. Murphy (1996) found that Eastern Kingbird (*Tyrannus tyrannus*) males were extremely territory faithful regardless of previous nest success, and although females were more likely to disperse after nest failure, most (72.5%) returned to former territories. In addition, most pair bonds between surviving partners were reestablished, and reunited birds tended to breed earlier than new pairs, suggesting an advantage of maintaining long-term pair bonds. Later, however, Woodard and Murphy (1999) detected no advantage of breeding with the same mate, and that the apparent advantage of reforming pair bonds was an outcome of increasing age of the birds, strong site fidelity, and associated improved reproductive success of experienced breeders. Apparent advantages of mate fidelity may thus appear to exist because of the existence of strong site fidelity. The extent to which this applies to other species remains to be determined.

The Scissor-tailed Flycatcher (*Tyrannus forficatus*; STFL), is a Neotropical migrant passerine that breeds in the southern Great Plains and overwinters in southern Central America (Jahn et al. 2013). They are socially monogamous, modal clutch size is five eggs, and most pairs raise only one, or rarely two, broods per season (Murphy 1988, Regosin and Pruett-Jones 1995). STFLs, along with Fork-tailed Flycatchers (*T. savanna*) show strong sexual dimorphism in tail length (Regosin and Pruett-Jones 2001), which is unique among *Tyrannus spp*. STFLs are birds of savannah-like habitats, and although a wide range of habitats may be occupied, STFL nests are typically found in an isolated tree or isolated small group of trees surrounded by a sea of grass.

STFL's experience frequent nest failure (M. Husak, pers. comm.) and are therefore regularly faced with decisions to remain faithful to a territory or strike out for better prospects. I chose to examine patterns of breeding dispersal in STFLs in relation to a set of variables identified in other species as important drivers of dispersal behavior. On the basis of past research (see above), I predicted that (a) breeding dispersal would be common, (b) males would disperse shorter distances and less often than females, (c) individuals that successfully fledged young from a previous nest would disperse shorter distances and less often than those that failed, (d) older after-second-year (ASY) birds would disperse shorter distances and less often than younger second-year (SY) birds, and (e) heavier (i.e. dominant) birds would disperse shorter distances and less often than light individuals. My research was conducted at two study sites (see below) characterized by different levels of disturbance. I thus also predicted (f) that dispersal would occur more commonly at the site experiencing more frequent habitat disturbance. Lastly, I also was able to investigate the association between re-establishment of pair-bonds and breeding dispersal distance (BDD), and expected pairs that reunited to disperse shorter distances and less often than those that divorced.

METHODS

Study Site.—Data were collected from April to August of 2008-2015 at two contiguous study sites in Comanche County, Oklahoma; the west artillery range of Fort Sill Military Reservation (Fort Sill; 34°39'33.3", N 98°30'11.0"W) managed by the US Department of Defense, and the Wichita Mountains Wildlife Refuge (the Refuge; 34°43'28.1", N 98°40'15.7"W) managed by the US Fish and Wildlife Service. My study sites are part of the mixed-grass prairie ecoregion that are characterized by oak (*Quercus*) or mesquite (*Prosopis juliflora*) savannah.

The Refuge and Fort Sill share a border at the southeastern end of the Refuge. The Refuge is characterized by prairie stretches broken by low mountains, small man-made lakes, and riparian forests of predominantly blackjack (*Q. marilandica*) and post oak (*Q. stellata*). Fort Sill is primarily mesquite savannah dominated by little bluestem (*Andropogon scoparius*) and Johnsongrass (*Sorghum halepense*), and other species of trees including hackberry (*Celtis reiculata*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*) (Regosin 1998). Although the study sites are contiguous, areas of occupied habitat are not, with the nearest Fort Sill monitored nest being 7.2 km from that of a Refuge nest. The majority of this gap is unsuitable habitat for STFLs (low, rocky, mountains and thick oak forest). In addition to the habitat differences, the Refuge and Fort Sill are managed differently. FMSR, being an active artillery and training range, is susceptible to much greater disruption than the nearby the Refuge, which is highly managed for conservation purposes. Also, Fort Sill allows fires to burn, unless threatening to humans or structures, but the Refuge actively fights and extinguishes fires. Free-ranging herds of bison (*Bison bison*) and longhorn cattle (*Bos primigenius*) keep grasslands at the Refuge closely cropped.

Suitable habitat for STFLs is relatively patchy, but the same territories are frequently occupied from year to year. At Fort Sill, I worked a single large patch on the southern border with the city of Lawton, OK (≈ 30 km^2), but at the Refuge I focused my efforts on several medium sized patches (totaling ≈ 34 km^2). The populations are open and STFLs bred breed commonly in unsurveyed habitats surrounding both sites.

Data Collection.—I searched suitable habitat for nests and banded adults beginning in late April of each year, and locations of all resightings and nests were recorded using a Global Positioning System (GPS) satellite receiver (Garmin CSX). Sightings of STFLs carrying nesting material or food were often used to locate nests, but STFL nests are fairly conspicuous and relatively easily detected as they are often placed low in trees and towards the ends of horizontal branches (Fitch, 1950, Murphy 1983). To ensure appropriate coverage of all habitats, I also searched areas of seemingly unsuitable habitat regularly throughout the field season; nests and adults were rarely found in these areas. Visits to nests were made every 2-3 days during the nesting cycle until nest fate was known. If nests failed I attempted to located replacement nests and similarly record their fates.

Adults were captured and banded during the nestlings period beginning when young were 6 days old. The most effective banding efforts included opening mist nets before dawn along with presentation of an American Crow (*Corvus brachyrhynchos*) decoy with vocal playback. All captured adults were uniquely banded with a combination of one numbered metal Federal band and three colored Darvic leg bands (2 per leg). Nests of banded adults were monitored within a day or two to confirm the association of color-banded birds with their presumed nest. Morphological measurements and blood samples were taken from captured birds; adults were generally processed and released within 20 minutes.

Blood samples were collected by venipuncture of the brachial vein of the wing with a 22 gauge sterile, disposable needle for a concurrent study of extra-pair paternity in STFLs (Roeder at al. in press). Heparinized capillary tubes were used to draw 50 µL blood samples. Blood was transferred into microcentrifuge tubes containing 1.5 mL of Longmire's buffer and kept cool until processing in the laboratory. Sex was determined in the field using plumage characters, presence or absence of brood patch and cloacal protuberance (Pyle 1997), and DNA extracted from the sampled blood. If discrepancies existed in sex assignment occurred I assigned sex using genetic methods).

Statistical Analysis. —Nests that fledged at least one nestling were classified as successful, and all adults that were resighted were considered to have returned, regardless of whether they were associated with a nest in the subsequent years. Natal return rates were extremely low (11/205). I therefore focused on dispersal behavior of adult breeding birds, and used the distance between nests as a measure of breeding dispersal distance (BDD). The latter was calculated for all birds that were individually marked and resighted in consecutive years. If an individual had more than one breeding/nesting attempt in a single year nest success was based on the first attempt. BDD was calculated in ArcMap 10.1 (ESRI 2012) as the Euclidean distance between GPS coordinates of nests in year (x) and year (x + 1).

Nest success, resighting rates, probability of resighting were calculated with data from 2008-2014, unless otherwise stated. I omit data from 2015 because reduced number of personnel and flooding prevented thorough searches of most habitats. Nest success is reported only for birds included in my sample of captured adults and is uncorrected for exposure time (Mayfield 1961). I examined BDD as both a categorical and continuous variable. As a categorical variable, I classified individuals as using the same, adjacent, or distant territory in year (x+1) if BDD was ≤ 400 m, between 401 m and 600 m, or > 600 m. STFL territories average ≈ 400 m in diameter (D. V. Roeder and M. S. Husak unpubl. data), therefore, starting at the center of a bird's initial territory (year x), a move of 401 m would place a bird beyond the center of its previous territory (assuming territories are perfectly circular and the nest is placed in the center), while a move of > 600 m would be necessary to place a bird beyond the boundary of its previous territory and center of an adjacent territory (Fig. 1). I considered a bird to be territory faithful if it returned to use the same or adjacent territory. Distant territories were considered new. The two categories were meant to represent different levels of familiarity: high to intermediate (same or adjacent territory) and little to no familiarity (beyond the neighboring territory). I examined territory fidelity in relation to site, sex, age, and previous nest success using Fisher's exact test, and compared mass between territory faithful and dispersing birds using a Student's t-test (Welch's *t*-test when variances were unequal). Males and females were examined together in some analyses and therefore body mass was converted to z-scores (within each sex) in all analyses because of known sexual size dimorphism (Regosin and Pruett-Jones 2001).

I then used a Student's *t*-test to compare BDD between sites (Fort Sill and the Refuge), sexes (male and female), age (SY or ASY), and nests of different fates (successful or failed), and examined BDD in relation to mass using least-squares linear regression. BDD was strongly right-skewed (Fig. 2) and was $\log_{10}$ transformed for all statistical tests. I conducted all the aforementioned analyses by combining the two sites and then within each site separately.

Decisions to disperse are likely influenced by multiple factors acting simultaneously. I therefore also used an information theoretic approach to examine the simultaneous influence of all variables on BDD. My *a priori* predictions were that BDD would be greatest in SY birds, females, failed breeders, at the site of greater physical disturbance (Fort Sill), and in smaller (presumably) socially subordinate individuals (i.e., low body mass). In addition to these factors I included the following 2-way interactions: sex*previous success, sex*age, sex*site, and site*previous success. I treated sex, age, previous nest fate, and site, as dummy variables and assigned values of 1 (female, SY, failed, and Fort Sill, respectively) or 2 (male, ASY, successful, and the Refuge, respectively) to each. I then used generalized linear models (GLM) to examine all four variables plus body mass, with and without interactions, and then reduced the number of models by successively eliminating variables (and interactions) that led to reductions in AICc scores (corrected for small sample size). All models within 2 units of the top model (ΔAICc = 0.0) were considered competitive and used to compute model weights and model average parameter estimates (Burnham and Anderson 2000) to gauge the relative importance of the remaining variables to individual differences in BDD. Parameters were considered to have contributed to differences in BDD when the 85% confidence interval of model averaged parameter estimates did not include zero (Arnold 2010).

Analyses of mate fidelity were performed only on pairs in which both parents were known to be alive in consecutive years. These birds were classified as either reunited (i.e., paired together in consecutive years) or divorced (i.e., paired to a new individual). Reunited birds were treated as a single dispersal event in these calculations, while divorced pairs contributed two dispersal distances, one for each individual. One resighted male (band 230104790) was not associated with a nest in 2012. His mate from 2011 (previous year) nested in the same territory in 2012 (BDD = 229 m) but with a different male. I am certain that male 230104790 did not nest on either the original or adjacent territory as numerous visits were made to survey this area for banded birds. This individual was therefore given a conservative dispersal distance estimate of 601 m (or new territory) for purposes of analysis.

Analyses were done using Statistix (Analytical Software) and JMP® Pro 11.2.0 (SAS Institute 2013). Results are reported, unless otherwise stated, as statistically significant ($P \leq 0.05$), marginally significant ($0.05 \leq P \leq 0.10$) or not significant ($P > 0.10$; Murtaugh 2014). Statistics are reported as mean ± SE, N = sample size. I also report other results for which sample sizes were too small to make meaningful statistical comparisons.

RESULTS

Nest success of banded adults from 2008 to 2014 was 62.4% (N = 197; uncorrected for exposure time). 127 males and 96 females were banded, and 32.7% of individuals were resighted in a year after banding (2009 to 2014). Nest success did not differ between Fort Sill (59.7% successful [N = 139]) and the Refuge (68.1% successful [N = 110]; Fisher's Exact test [FET], *P* = 0.187), nor did probability of resighting (32.9% at Fort Sill [N = 143]; 30.5% at the Refuge [N = 82]; FET, *P* = 0.768). After excluding the first year (2008) because of small sample size (N = 9), the likelihood of resighting was the same for females (33.3% [N = 94]) and males (32.3% [N = 122]; FET, *P* = 0.885) and for individuals that bred successfully (37.8% [N = 127]) or failed to fledge young (31.7% [N= 60]) in the previous year (FET, *P* = 0.514). The probability of resighting SY birds (22.4% [N = 67]) was significantly lower than that of resighting ASY birds (36.1% [N = 172]; FET, *P* = 0.046), however, there were not significantly more SY birds between sites (Fort Sill = 29.2% [N = 40], the Refuge = 29.4% [N = 27]; FET, *P* = 1.000) or sexes (male = 33.1% [N = 44], female = 24.7% [N = 24]; FET, *P* = 0.190).

To be included in further analyses of territory fidelity and BDD an individual had to be associated with nests in consecutive years. I obtained 76 records for 69 individuals. Six of the 69 were resighted in three consecutive years while a seventh was resighted over four years. I compared BDD within individuals between successive years to evaluate whether they exhibited consistent differences in BDD that would indicate lack of statistical independence and preclude using all observations of each individual in my analyses. A sign test of BDD in consecutive years suggested that individuals tended to move shorter distances the second time they dispersed ($P = 0.062$), but a Spearman rank correlation did not suggest that distances moved in consecutive years were correlated ($r_s = -0.432$, N = 7, $P = 0.349$). Indeed, there was little similarity in movements between years as the difference in BDD between first and second dispersal events was ≥ ~500 m in 4 of 7 cases, and under 225 m only once. I therefore treated all 76 records of BDD as independent events.

Territory fidelity.–Resighted birds used the same territory (BDD ≤ 400 m) 64.5% of the time, while 7.9% and 27.6% used either an adjacent (401 m ≤ BDD < 600m) or distant territory, respectively. Differences existed between Fort Sill (N = 42) and the Refuge (N = 34; $X^2 = 7.08$, $P = 0.020$); at both sites most birds returned to the same territory (Fort Sill = 52.4%, the Refuge = 79.4%), but nearly four times as many settled at a distant territory at Fort Sill (40.5%) as at the Refuge (11.8%). Relatively few birds moved to an adjacent territory at either site (Fort Sill = 7.1%, the Refuge = 8.8%).

Given the small number of birds to disperse to adjacent territories I combined them with birds from the same territory (same + adjacent = same territory, and distant = new territory) for remaining analyses. Territory fidelity was equally common in males (66.7%, N = 42) and females (79.4%, N = 34; [FET], $P = 0.209$), a result mirrored by birds at both Fort Sill (FET, $P = 0.227$) and the Refuge (FET, $P = 0.397$). The combined sample from both sites suggested SY and ASY birds were equally likely to exhibit territory fidelity (62.5% [N = 16] and 77.2% [N = 57] respectively, FET, $P = 0.224$), but at Fort Sill, SY birds tended to be less territory faithful than ASY birds (33.3% [N = 9] *v*. 70.0% [N = 30], FET, *P* = 0.057). Territory fidelity was equally likely for birds that bred successfully or failed (70.8%, N = 48, *v*. 66.7%, N = 18; *P* = 0.482), a pattern detected at Fort Sill (FET, *P* = 0.264) and the Refuge (FET, *P* = 0.292).

Body mass of territory faithful (-0.057 ± 0.124, N = 54) and dispersing birds (0.250 ± 0.209, N = 21) did not differ significantly when sites were combined (*t* = 1.247, *P* = 0.216) or at either Fort Sill (territory faithful = -0.083 ± 0.209, N = 25; dispersers = 0.129 ± 0.253, N = 17; *t* = 0.644, *P* = 0.523) or the Refuge (territory faithful: -0.035 ± 0.157, N = 29; disperser: 0.766 ± 0.422, N = 3; *t* = 1.781, *P* = 0.085).

Dispersal distance.–BDD averaged 600 ± 124 m (N = 76), but as noted above, was strongly right-skewed (Fig. 2). Indeed, 17% of individuals dispersed more than 1.0 km and 5% of individuals dispersed over 2 km between successive years (range = 1 m to 6,293 m). These results do not include two non-nesting SY males that were caught and banded at the nest of another male in year (x), and then located in year (x + 1) 11 km and 14 km from where they were banded.

BDD did not differ among years, between the sexes, age classes, or with prior nest fate (Table 1). However, STFLs at Fort Sill dispersed, on average, more than three times the distance moved by STFLs at the Refuge (870 ± 209 m, N = 42 *v*. 268 ± 69 m, N = 34; *t* = 2.89, df = 74, *P* = 0.005). Given the site differences in BDD, I conducted additional within-site comparisons. At both sites BDD was unrelated to a bird's sex (Table 1). Birds that failed in the past year's breeding attempt moved greater distances than successful breeders at Fort Sill, but at the Refuge the BDD of failed and successful breeders was similar (Table 1).

BDD increased with body mass (β = 0.253 ± 0.112), and although little of the variation in BDD was accounted for ($r^2 = 0.065$), the relationship was statistically significant (df = 74, $P = 0.026$) and evident in both sexes (Fig. 3; analysis of covariance [ANCOVA]: difference in slopes between females [β = 0.176] and males [β = 0.309], $F = 0.81$, df = 1, 73, $P = 0.372$). The increase in BDD with body mass was mainly due to the stronger relationship at Fort Sill (β = 0.335 ± 0.127; $r^2 = 0.149$, df = 40, P = 0.012) than at the Refuge (β = 0.128 ± 0.187; $r^2 = 0.014$, df = 32, $P = 0.499$). At Fort Sill, BDD of both females (β = 0.406 ± 0.226, $P = 0.090$) and males (β = 0.295 ± 0.144, $P = 0.060$) increased with body mass (ANCOVA: $F = 0.18$, df = 1, 38, $P = 0.678$), but at the Refuge, the only indication that BDD increased with body mass was due to a weak trend in males (β = 0.282 ± 0.222, $P = 0.221$) but not females (β = 0.044 ± 0.327, $P = 0.894$).

Missing information for either previous nesting success or age reduced the sample available for analysis of BDD using model selection by GLM from 76 to 64. The criterion that all models within 2 AICc units of the top model (ΔAICc = 0.000) are competitive yielded four viable models (Table 2). Age, nest fate, and the interaction between age and nest fate appeared in all four models, while both body mass and site (Fort Sill or the Refuge) were present in three each. An interaction between site occupied and an individual's sex appeared in the top model, but not in the other three. The second ranked model, which did not include the sex by site interaction was nearly as likely as the top model (Table 2). Model averaging across the four top models indicated that all of the parameter estimates' confidence intervals excluded zero except for the sex by site interaction (Table 3). The inference, therefore, is that BDD of STFLs in southcentral Oklahoma were most strongly influenced by a bird's age and fate of its previous nest: the greatest BDDs were exhibited by SY birds that failed to breed successfully. The interaction between age and previous nest fate emerged as a consequence of the fact that, within SY birds, failed breeders dispersed the greatest distances of all birds, whereas in ASY birds, successful breeders tended to disperse farther than failed breeders (Fig. 4).

Divorce.–The 12 instances in which both partners from a nest in year (x) were resighted in year (x+1) (divorce or reunite) had a mean BDD of 360 (± 100 m, N = 15). The nine former mates that reunited (75%) had a mean BDD of 324 (± 140 m), which did not differ from the BDD of individuals that divorced (415 ± 147; $t = 0.435$, df =12.72, $P = 0.807$). Of the nine reunited mates, mean BDD for the six pairs that were successful in year x (295 ± 456 m) was statistically similar to that of the three pairs that were failed in year x (381 ± 245 m). Of the divorced pairs, the four individuals from the two successful nests (297 ± 278 m) had shorter BDDs than the two individuals from the single failed nest (651 ± 504 m). Among the divorced pairs, BDD of males (688 ± 166 m) was greater ($t = 2.057$, df = 4, $P = 0.109$) than that of females (142 ± 83 m) and the greatest female BDD (295 m) did not exceed that of the shortest male BDD (456 m).

DISCUSSION

Resighting (= return) rate of STFLs at both Fort Sill and the Refuge (~31%) was among the lowest reported for migratory, temperate-zone breeding tyrant flycatchers (see studies cited in Greenberg 1980; also: Sedgwick 2004, Murphy 1996, Beheler et al. 2003, Paxton et al. 2007, Redmond and Murphy 2012). The low return rate is especially pronounced given that my study was a focused attempt to resight targeted individuals rather than a passive netting effort that only captured a random sample of a marked population. Possible explanations for why resighting rate was low is treated in another paper hence will not be discussed here (Chapter 1). However, the open nature of my populations and the long dispersal distances exhibited by some individuals (Fig. 2) may have contributed to low resighting rates and low apparent annual survival (Chapter 1). Appreciation of this has bearing on my interpretation of territory fidelity and BDDs.

Territory fidelity.–Resighting rates of banded birds did not differ between the two study sites, sexes, or history of breeding success, but did differ between age classes. However, age ratio did not differ between sites or sexes and the difference in resighting rate between age classes is potentially due to a population of banded STFLs which were never associated with a nest. A large proportion of these “floaters” were SY individuals and were never seen again after their initial banding. Since this dispersal analysis did not include birds that were not associated with a nest, I suspect that my analyses of variation in territory fidelity and BDD were not biased by differences in return rate that had the potential to be associated with these factors. The exception to this is in the assessment of the degree of territory fidelity. My results showed that resighted birds were more likely to be territory faithful than to disperse. This was especially evident at the Refuge where only 12% of individuals dispersed more than 600 m. However, like other species (Winkler et al. 2004, Paxton et al. 2007), STFLs showed a right skewed BDD and resighting of individuals is never complete (Winkler et al. 2004) because an unknown proportion of individuals disperse long distances and go undetected (e.g., up to 214 km in Southwestern Willow Flycatcher [*Empidonax traillii extimus*]; Paxton et al. 2007). As a consequence, the proportion of birds that I documented using the identical territory in successive years (52% at Fort Sill and 79% at the Refuge) must be viewed as an overestimate of territory fidelity due to our inability to distinguish between long distance dispersal and death. The high nest success that I reported also argues for a lower true frequency of site fidelity because nest success was based mainly on only those pairs whose nests survived long enough for adults to be captured (nestling age of ~6 days); the sample of banded birds was thus biased towards the successful portion of the population, and this is the segment that would be most likely to exhibit territory fidelity. It is thus almost a certainty that the majority of STFLs at Fort Sill used different territories in successive years, especially given that when they dispersed they typically chose a distant rather than an adjacent territory. The same is likely to be true, albeit to a lesser degree, at the Refuge. STFLs thus differ considerably from Eastern Kingbirds (*T. tyrannus;* EAKI), their closest relative with similar data (Murphy 1996). EAKIs exhibit much higher return rate and territory fidelity, but also a sexual difference in territory fidelity (96% in males and 72.5% in females). Between year territory fidelity of Eastern Phoebes (*Sayornis phoebe*), another tyrannid, was also high (~75% [Beheler et al. 2003]), but in Willow Flycatchers (*E. traillii* [Sedwick 2004]), and especially the Southwestern Willow Flycatcher (Paxton et al. 2007), territory fidelity is generally below 50%.

Aside from the caveat that the potential true frequency of territory switching was underestimated, I did not find any difference in the tendency to change territories when comparisons were made between the sexes or with nest fate in the previous year. Territory fidelity was lower in female EAKIs (Murphy 1996) and Willow Flycatchers (Sedgwick 2004), in male Eastern Phoebes (Beheler et al. 2003), but no difference existed between the sexes in Southwestern Willow Flycatchers (Paxton et al. 2007). In all the aforementioned species, successful breeders were generally more site faithful, especially females. SY STFLs tended to be less site faithful at Fort Sill, but when combined with the Refuge, no difference existed between age classes. The much lower apparent territory fidelity at Fort Sill stands in sharp contrast to the either slight or nonexistent association of territory fidelity with other variables. That, and the greater dispersal tendencies of heavier birds, will be discussed below.

Breeding d*ispersal distance*.–BDD of STFLs averaged 600 m, but including nonterritory holding SY males, ranged up to 14 km. Comparisons to species from other studies is difficult because of different spatial scales on which each study was conducted. Paxton et al. (2007), for instance, reported mean BDDs of Southwestern Willow Flycatchers for within (0.3 km) and between suitable patches of habitat (9.2 km and 13.2 km), and between study sites (97 km and 120 km) that exemplify the problem. My study involved two sites separated by several kilometers of unsuitable habitat. Within each site I had the potential to document movements on the order of ≈ 15 km at Fort Sill and ≈ 26 km at the Refuge. The scale of my study probably fell between the within and between patch scales of Paxton et al. (2007) because of differences in the patchy nature of the riparian habitat used by Southwestern Willow Flycatchers and the more continuous distribution of suitable habitat used by STFLs in Oklahoma. Aside from the two nonterritory holding SY males, STFL BDD seems low compared to Southwestern Willow Flycatchers. The difference is at least in part likely attributable to differences in the landscape as Willow Flycatchers in riparian habitat in eastern Oregon dispersed over much shorter distances than their southwestern counterparts (Sedwick 2004). Most (~75%) Eastern Phoebes showed territory fidelity between years, but when they dispersed, males (mean = 1.5 km) and especially females (mean = 3.1 km) jumped many territories and moved long distances (Beheler et al. 2003).

The EAKI population studied by Murphy (1996; see also Woodard and Murphy 1999) was similar to the Oklahoma STFL population in that in both regions two study sites were located in suitable habitat that was patchily but continuously distributed over a moderately large landscape. Comparison between species (data for EAKI from Murphy 1996) of the number of dispersal events that males and females made that were under or over 1.0 km showed that female STFLs and EAKIs exhibited nearly identical behavior; 14.7% (N = 34) and 13.2% (N = 68) of STFLs and EAKIs dispersed > 1.0 km, respectively

(FET, *P* = 1.00). By contrast, BDD > 1.0 km were much less frequent in male EAKIs (2.8% [N = 71]) than in male STFLs (21.4% [N = 42]; FET, *P* = 0.002).

Intrapopulation analysis using univariate approaches gave only weak indications of the sources of variation in BDD. BDD was independent of sex, age, and prior nest success when sites were combined. Differences between Fort Sill and the Refuge were considerable, however, and when sites were analyzed separately, BDD varied with age and prior nest fate at Fort Sill. BDD also increased with body mass of both sexes at Fort Sill, but at the Refuge, a weak trend in the same direction existed only in males. Model selection results emerging from the simultaneous analysis of the influence of all variables provided a clearer picture of the factors underlying variation in BDD. The primary sources of variation of BDD were age and prior nest success, and an interaction between them. Thus, like most other species that have been studied (Pärt and Gustafsson 1989, Winkler et al. 2004, Bernard et al. 2011; but see Hoover 2003, Fisher and Wiebe 2006), younger individuals were more likely to disperse, and to disperse longer distances, than older individuals. This may not be a difference between just SY and ASY birds as my comparison of BDD of the same STFLs in consecutive pairs of years showed that, in 6 of 7 cases, BDD was shorter in the later year and 5 of 7 were ASY birds when first banded. The greater BDD following reproductive failure is likewise consistent with much previous research (Murphy 1996, Hoover 2003, Winkler et al. 2004, Fisher and Wiebe 2006, Jiménez-Franco et al. 2013). Collared Flycatchers (*Ficedula albicollis*) and STFLs were similar in that failed SY birds dispersed the greatest distances while successful SY birds and ASY individuals dispersed similar distances (Pärt and Gustafsson 1989).

Female biased BDD is one of the most well recognized contributors to variation in dispersal in birds (Greenwood 1980, Clarke et al. 1997). A recent phylogenetic analysis confirmed that female biased dispersal is an ancestral trait in birds, and that it is widespread (84% of 56 species included in the analysis; Mabry et al. 2013). Thus, the absence of a sex-based difference in STFLs was unexpected and, as described above, the absence of sex-biased dispersal was not because females were unlikely to disperse: rather, it was because males exhibited a much higher likelihood of dispersing. A variable rarely examined in avian dispersal studies as a possible factor influencing dispersal is body size. Pärt and Gustafsson 1989 failed to detect any association between dispersal behavior and body mass in Collared Flycatchers, but I found that larger STFLs of both sexes exhibited greater BDDs. However, the positive association was opposite of my prediction that larger individuals would be socially dominant and more likely to retain former territories.

I suggest that the heightened tendencies for male dispersal in STFLs, the positive association between body mass (i.e., dominance) and BDD, and site differences in BDD, are interrelated factors, and linked to the long period of time that STFLs spend on the breeding grounds just prior to and after nesting. In the southcentral Plains region, STFLs do not begin fall migration until nearly the end of October, almost three months after nesting has ended. Other *Tyrannus* spp. depart soon after breeding (Jahn et al. 2013).

STFLs also return from migration well before congeners (Jahn et al. 2013). First arriving STFLs may appear by the 1st of April at my study sites (M. S. Husak, pers. comm.), that is, approximately six weeks prior to the start of nesting (M. S. Husak, unpubl. data). STFLs thus have much time to assess prospective territories both before and after breeding (Reed et al. 1999) to assess the potential to "upgrade". EAKIs, in particular, do not have this luxury as they spend much less time on the breeding grounds.

In many migratory species, older and/or higher quality individuals are the first to arrive in spring (e.g., Marra et al. 1998, Rockwell et al. 2012); differences in individual arrival dates can exceed a month (Marra et al. 1998), as is the case in the EAKI (Cooper et al. 2009b). Cooper et al. (2009b) also showed that older male EAKIs were the first to return in spring. Assuming the same is true of STFLs, I propose that the oldest and highest quality STFL males are the first to arrive in spring, up to 6 weeks before nesting begins. They thus have time to move about, and possibly based on information learned in the previous fall, search for the best breeding sites. Lighter (subordinate) birds arrive later, have less time to prospect, and are more likely to go directly to known former breeding sites. Heavy birds are probably also better able to outcompete would be usurpers for quality sites.

However, dispersal is only favored if it enhances fitness. For instance, Bernard et al. (2011) showed that dispersal did not occur following nest failure in Ovenbirds (*Seiurus aurocapillus)* breeding in uniformly high quality habitat because prospects for improvement were negligible. Individuals almost certainly cannot predict success at a particular territory, but cues indicative of the likelihood of success within a locale appear possible (Doligez et al. 2002, 2003). As one example, dispersing EAKIs settled preferentially in areas where fledging success was high in the previous year (Redmond et al. 2009). Dispersal may also be motivated by the need to move because of change in habitat from previous conditions, and in the STFL system this may differ between sites. The propensity to disperse and the actual distance moved were both greater at Fort Sill than at the Refuge. Both sites are properties managed by Federal agencies but the approaches taken differ radically. Fort Sill is an active training facility for the armed forces, including artillery. Movement of heavy equipment and troops over the landscape creates disturbances that may reduce habitat quality by destroying foraging sites and trees used for nesting. Fires, once begun, are not extinguished unless they threaten humans or buildings. Lack of grazing, as is the case at Fort Sill, may lead to an increased fuel load and more severe fires. Management of the Refuge is for maintenance of the status quo and thus disturbance is minimized, including extinguishing fires. The relationships between BDD and age, prior nest success, and body mass, were mainly associated with birds from Fort Sill and I would hypothesize that the greater habitat disturbance characteristic of that site created substantial spatial variation in habitat quality that lead to greater dispersal by both sexes. Thus, the reason why male EAKIs and STFLs differed to such a degree, is that STFLs not only experienced more disturbance to nesting habitat (which may have forced dispersal), but that they also had more time to search over a large area for suitable sites (because they are on site well before breeding begins).

CONCLUSION

My study has shown that substantial differences in dispersal behavior can exist between individuals of one bird species located at different sites within close proximity. Ecological factors appear to have had a significant influence on STFL behavior. Apparent territory fidelity of STFLs at the Refuge was high, but at Fort Sill true territory fidelity would be below 50%. Dispersal distances at Fort Sill were also nearly four times those detected at the Refuge. Further analyses showed that the distances dispersed were mainly influenced by age (greater in young birds), prior nesting success (greater in failed breeders), but that the effect of nest failure was greater in younger than older birds. Dispersal distances were thus affected by a number of variables acting simultaneously, some of which were inherent to the individual (age and body mass) while others were not (prior nesting success and breeding site). Differences between sites were most likely related to differences in disturbance to the overall landscape that created greater temporal and spatial variability in breeding conditions at Fort Sill, the site of more frequent and greater dispersal distance. My results thus highlight the importance of conducting research at multiple sites that present a range of conditions, given that without that contrast, the range of potential responses exhibited by a species is likely to be underestimated.

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TABLES AND FIGURES

Table 2.1 Breeding dispersal distance (BDD; m) of Scissor-tailed Flycatchers in southcentral Oklahoma over the period 2008 to 2014. Comparisons were made between the sexes, age classes (second-year [SY] and after-second-year [ASY]) and between birds that successfully fledged young or failed in the year prior to measurement of BDD. Analyses were conducted for the two sites combined (Fort Sill Military Reservation [FSMR] and Wichita Mountain Wildlife Refuge [WMWR]) and then separately for each site.

		Sites combined		FSMR		WMWR	
Variable	Contrast	BDD (SE, N)	*t* (*P*)	BDD (SE, N)	*t* (*P*)	BDD (SE, N)	*t* (*P*)
Sex	Female	752 (257; 34)	0.85 (0.398)	1201 (433, 19)	0.05 (0.960)	185 (83, 15)	1.45 (0.157)
	Male	478 (82, 42)		597 (124, 23)		334 (104, 19)	
Age	SY	892 (304, 16)	0.92 (0.359)	1,473 (458, 9)	1.98 (0.055)	300 (84, 7)	0.81 (0.424)
	ASY	513 (140, 57)		705(252, 30)		145 (68, 27)	
Nest fate	Fail	681 (208, 18)	1.22 (0.228)	1006 (303, 11)	2.31 (0.027)[1]	170 (67, 7)	0.24 (0.813)
	Succeed	657 (177, 48)		879 (301, 27)		372 (103, 21)	

[1] *t* -test for unequal sample size

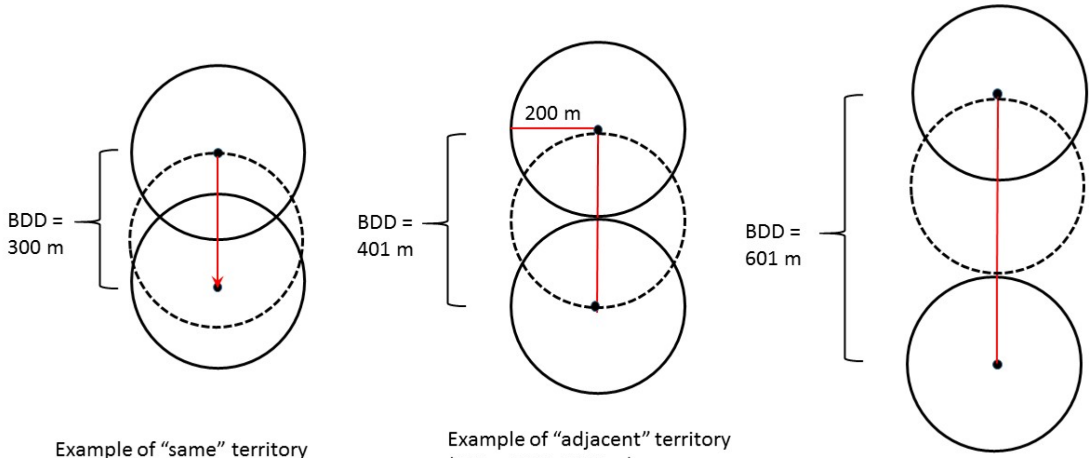
Table 2.2 Reduced model set used to examine variation in breeding dispersal distance for Scissor-tailed Flycatchers (N = 64) breeding near Lawton, OK, between 2008 and 2015. Model weights (w_i) computed only for models within 2 AIC_c of the top model that were used to compute model averaged parameter estimates. Number of parameters (k), AIC_C, difference in AICc (ΔAICc) between each model and the top model, model weights, model likelihood in relation to the top model are given.

Model	**k**	**AIC_C**	**ΔAIC_C**	**w_i**	**Model likelihood**
site + mass + age + nest fate + age*nest fate + sex*site	8	177.032	0.000	0.358	1.000
site + mass + age + nest fate + age*nest fate	7	177.512	0.480	0.281	1.271
mass + age + nest fate + age*nest fate	6	177.985	0.953	0.222	1.610
site + age + nest fate + age*nest fate	6	178.913	1.881	0.140	2.561
site + mass + age + nest fate + age*nest fate + sex*site + sex*nest fate	6	179.299	2.267	----	----
age + nest fate + age*nest fate	5	179.344	2.312	----	----
mass, site, age, sex, nest fate	7	180.586	3.554	----	----
site + mass + age + nest fate + sex + age*nest fate + sex*site + sex*nest fate	10	182.117	5.085	----	----
site + mass + age + nest fate + sex + age*nest fate + sex*site + sex*nest fate + age*sex	11	185.030	7.998	----	----

Table 2.3 Importance weights of variables, model averaged parameter estimates, and confidence intervals (85%) for variables included in the top model set emerging from the generalized linear models analysis of variation in breeding dispersal distance of Scissor-tailed Flycatchers breeding near Lawton, OK, between 2008 and 2015 (N = 64).

Variable	**Importance weight**	**Parameter estimate (SE)**	**Confidence interval**	
			lower	**upper**
Age	1.000	-0.964 (0.448)	-1.620	-0.308
Nest fate	1.000	-1.132 (0.468)	-1.817	-0.447
Age*nest fate	1.000	1.085 (0.538)	0.298	1.872
Body mass	0.860	0.192 (0.097)	0.051	0.334
Site	0.778	-0.418 (0.243)	-0.774	-0.061
Site*Sex	0.357	0.207 (0.176)	-0.052	0.465

Fig. 2.1 Visual depiction of criteria used to distinguish between territories classified as reuse of same territory (left), use of an adjacent territory (center), or use of a distant territory (right).



Example of "same" territory
(BDD ≤ 400 m)

Example of "adjacent" territory
(401 < BDD ≤ 600 m)
A BDD of 399 m would create a situation in which the edge of the new territory included the center of the old territory; at 401 m it does not

Example of "distant" territory
BDD ≥ 600 m)

Fig. 2.2 Distribution of breeding dispersal distances of Scissor-tailed Flycatchers at Fort Sill Military Reservation and Wichita Mountain Wildlife Refuge near Lawton, Oklahoma, 2008 – 2015.

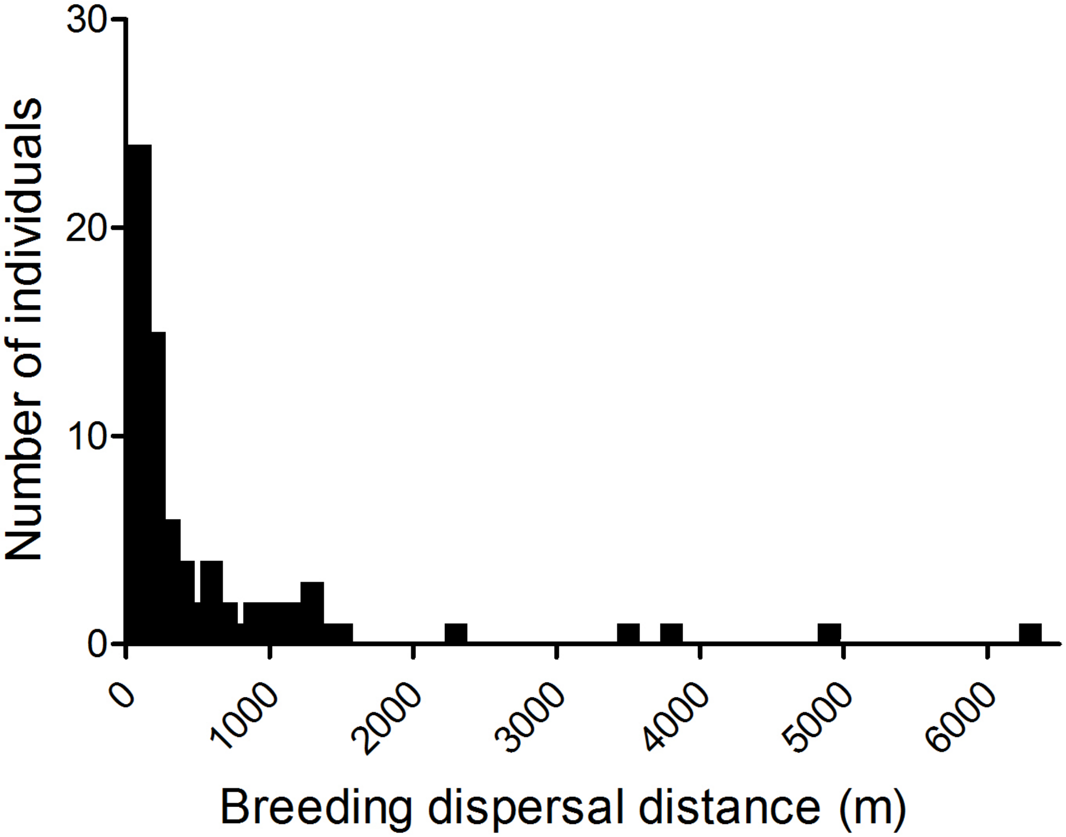


Fig. 2.3 Breeding dispersal distance (BDD) of Scissor-tail Flycatchers from Fort Sill Military Reservation and Wichita Mountain Wildlife Refuge near Lawton, Oklahoma, 2008 – 2015. Body mass is scaled as a z-score to account for sexual size dimorphism and BDD is $\log_{10}$ transformed. The female and male regression lines are depicted as heavy and light lines.

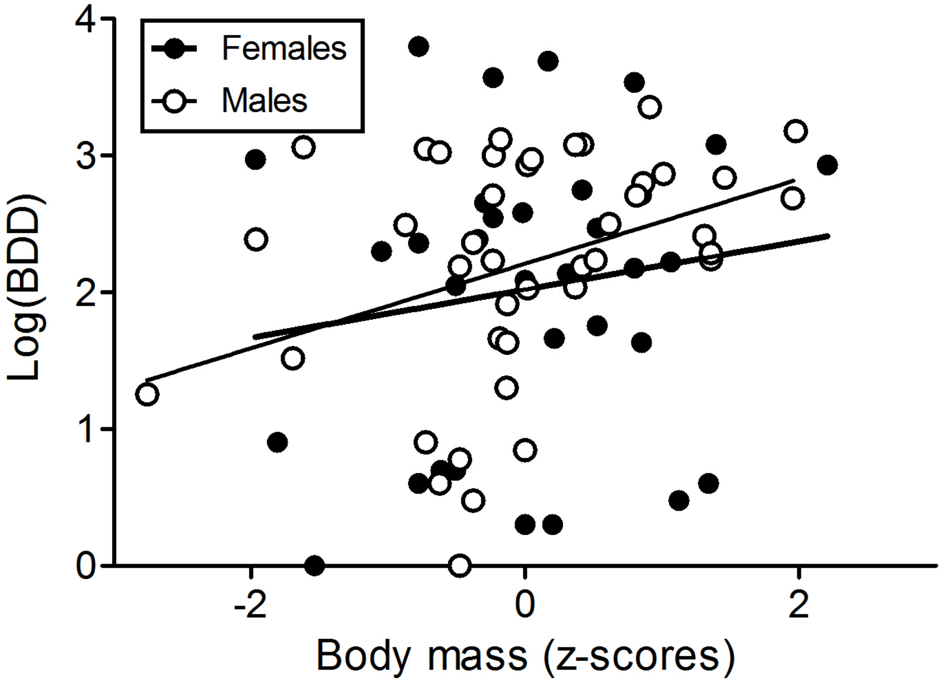
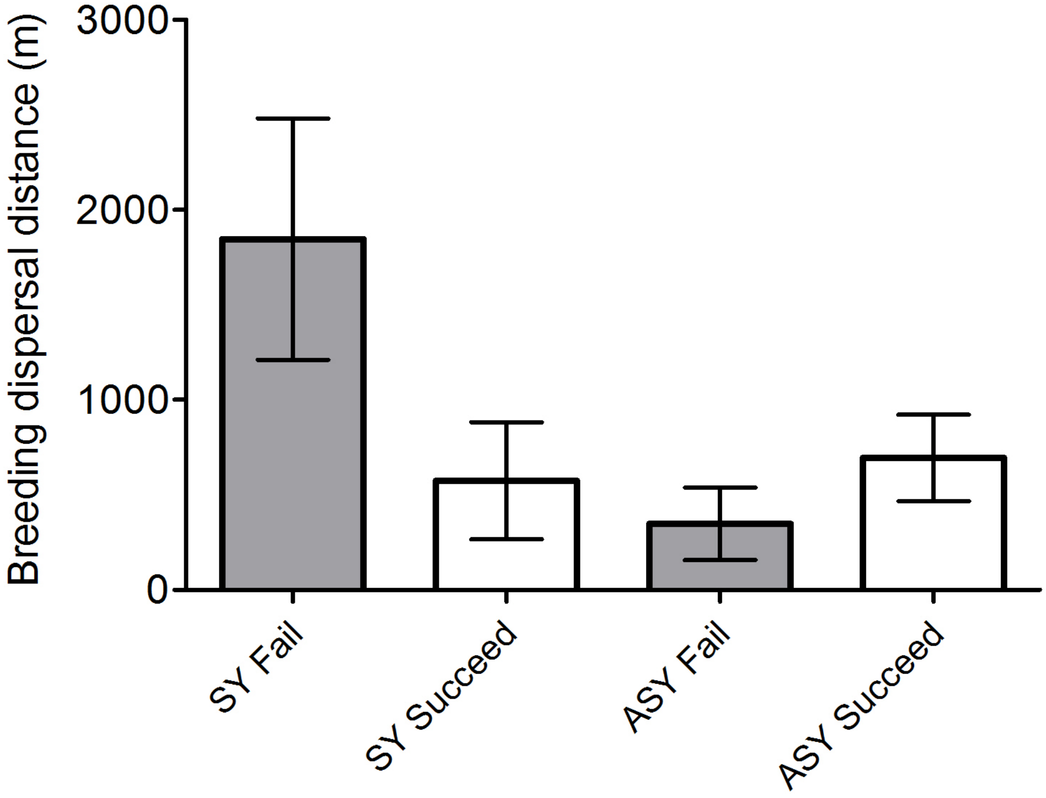


Fig 2.4 Breeding dispersal distance of Scissor-tail Flycatchers from Fort Sill Military Reservation and Wichita Mountain Wildlife Refuge near Lawton, Oklahoma, 2008 – 2015. Mean ± 95% confidence intervals are shown for the four categories defined by age (SY = second year, ASY = after second year) and nesting success from the past year (either failed ["Fail"] or successful ["Success"]).



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