SURVIVAL, LONGEVITY, AND BREEDING DISPERSAL BY EASTERN KINGBIRDS IN CENTRAL NEW YORK

Michael T. Murphy
Department of Biology, Portland State University
P.O. Box 751, Portland, OR 97207
murphym@pdx.edu

Abstract.—Eastern Kingbirds (*Tyrannus tyrannus*) are Nearctic-Neotropic migrants that breed in trees in open savannah-like habitats across New York. Preliminary study of survival and dispersal behavior of male and female Eastern Kingbirds suggested relatively high return rates (~annual survival), infrequent dispersal, but no information on maximum lifespan was reported. Here I report the results of a 13 year study of banded Eastern Kingbirds from Delaware and Otsego Counties, New York, and show that most individuals bred for only 1 or 2 years before dying, but roughly 20% of birds lived ≥4 years. Average and maximum number of years lived was 2.2 and 8 years for females, and 2.7 and 10 years for males. Comparative analyses with other passerines suggest that maximum lifespan was close to that predicted based on body mass. Females dispersed more than males, but both sexes were more likely to disperse over their lifetime when they experienced low average annual reproductive success. Site fidelity of Eastern Kingbirds is high and possible reasons are discussed.

The greater longevity of birds compared to mammals of similar body size is generally attributed to the flight ability of birds (Pomeroy 1990). Bats (*Chiroptera*) are the exception that proves the rule (Wilkinson and South 2002). Flight reduces the probability of capture by predators, makes possible long distance migration to either escape physically stressful conditions or exploit abundant resources, and within the same landscape, increases access to a much wider array of habitats in which to find food. Birds are not known to experience menopause (Ricklefs 2000), and the capacity for long productive reproductive life in some bird species is remarkable, highlighted in 2014 by the successful incubation and hatching of an egg by a wild female Laysan Albatross (*Phoebastria immutabilis*) that was at least 63 years of age (http://www.livescience.com/43288-oldest-bird-hatches-new-chick.html).

However, the difference between maximum longevity and the ages achieved by most individuals is often dramatic. Most individuals have limited time in which to reproduce and decisions must be made that maximize the probability of producing young (Williams 1966). Amongst annual breeders, this often involves the decision over where to breed. Breeding dispersal is defined as movement by an adult that has bred previously at one site to a new location, and the general rule among birds is that females exhibit less breeding site fidelity than males (Greenwood 1989, Greenwood and Harvey 1982, Clarke et al. 1997, Serrano et al. 2001). Social monogamy and biparental care are characteristic of

most avian species (~81%; Cockburn 2006), as is territorial defense of resources for breeding. Typically, males establish territories, and failure to do so precludes a male from breeding. Prior ownership of a territory often enables males to not only hold but also repossess territories from other males (e.g., Krebs 1982, Jakobsson 1988, Cooper et al. 2009), and this presumably underlies the lower dispersal probability of male birds compared to females. By contrast, females are freer to move and they presumably use a combination of territory and male characteristics to choose where to settle. In many species, breeding dispersal is often associated with reproductive failure at a previous breeding site (Hoover 2003, Catlin et al. 2005; but see Bernard et al. 2011), and by moving to "greener pastures" females have the potential to improve reproductive success.

The Eastern Kingbird (*Tyrannus tyrannus*) is a regular inhabitant of New York's open spaces and is known for its pugnacious attitude towards nest predators, and as some have claimed, belligerence towards other birds (Davis 1941). They migrate long distances to South America (Jahn et al. 2013) where breeding season insectivory and territoriality are replaced by frugivory and flocking (Morton 1971). Although not abundant, kingbirds are often conspicuous because of their behavior and penchant for nesting near homes and farms. Indeed, numerous authors have commented on their continual presence year-after-year in the same locations (see Bent 1942), but how long do they live and are those individuals seen year-after-year the same individuals? To answer these questions, in the present paper I report on a population study of Eastern Kingbirds that I conducted in central New York over a 13 year period.

METHODS

Field procedures.—I conducted my research between 1989 and 2001 in Delaware and Otsego Counties. My 1996 publication included data from between 1989 and 1993 and thus the present manuscript expands considerably the data available for analysis. Kingbirds regularly nest near bodies of water, but are also strongly associated with abandoned orchards and otherwise open habitats with scattered trees (Murphy et al. 1997). I therefore centered my principal study site in Delaware County along Charlotte Creek and surrounding floodplain and upland habitats near Davenport and West Davenport. In Otsego County I surveyed the roads and fields bordering the town of Oneonta.

I began searching for returning birds and nests beginning in mid to late May in all years. The majority (>75%) of nests were found before incubation, and once found, nests were checked every 2-4 days to determine breeding date (= date of 1st egg), clutch size (number of eggs/nest), hatching success (proportion of eggs to hatch), and number of young to fledge (young alive 13 days after hatching). Kingbirds raise only a single brood per year, but regularly replace failed nests, and therefore, I located replacement nests for failed attempts and collected identical data to allow me to determine seasonal productivity for all pairs. I captured parents at the nest (with mist nets) mainly during the latter half of the nestling period as they made flights to feed their young. I individually

marked adult birds with one numbered federal band and three plastic colored leg bands (Murphy 2000, 2001). Young were banded as the adults when 13-14 days of age.

Return rates of birds between years were based on sightings and recaptures of individually color-banded birds. Eastern Kingbirds exhibit high site fidelity and high detection probability (Murphy 1996) and therefore return rate (i.e., the proportion of birds to return) provides a reliable estimate of apparent survival (Murphy 1996, Redmond and Murphy 2012). Nonetheless, birds do occasionally disappear for one or (rarely) two years only to reappear. However, in my study no bird ever reappeared after an absence of two years and thus a two year absence almost certainly represented death. The last adults were banded in 1999, and of those seven, three were detected in 2001.

Every bird that I observed on a territory attempted to breed. I thus assumed undetected birds that reappeared in a later year made an attempt to breed at an unknown location in the year they went undetected. Because dispersal occurs more often after nest failure than success in kingbirds (Murphy 1996), I assumed that failure of the bird at the unknown site prompted it to disperse back to its known site of capture. In the very few cases in which a bird was missing for two years and then reappeared, I assumed that it was successful in the first year away, but unsuccessful in the second. I assigned the average number of young fledged in that year by successful pairs to the bird in the assumed year of success.

I revisited the same sites every year over the course of the 13 year study, and as others have found (see Bent 1942), kingbirds repeatedly used the same sites. On the basis of site fidelity I identified over 100 traditionally used sites that I refer to as "territories" (Murphy 2004). I used these territories to determine when a dispersal event occurred, which I defined as a move from one traditionally used site to another. The only uncertainty involved birds that disappeared for two year before returning. In these few cases I assumed that the birds were site faithful in the first year they were missing. Hence, two dispersal events occurred for every bird that disappeared for either 1 or 2 years (i.e., it dispersed away to go missing, and then dispersed back to be resighted).

Data analyses.—For every individual I determined the number of years it was present in the population. I refrain from referring to this as "age" because aging techniques are not known for kingbirds (Pyle 1997), and some were undoubtedly not breeding for the first time when I first banded them. I instead refer to years present in the population as "years lived". I was also able to quantify the number of times every individual dispersed over the period of study, and for most birds I was also able to measure average annual reproductive success. The latter was calculated as the total number of young fledged over their known life divided by the number of years they were known to have lived.

I previously reported apparent annual survival for the first four years of this study (Murphy 1996). Here I compared the number of years lived between the sexes across 11 years using a median test and Kolmogorov-Smirnov test for

differences in distribution. Unlike my earlier study, where I compared dispersal behavior to the past year's breeding success, I now compared the number of instances of site fidelity or dispersal over a lifetime between males and females using a 2 x 2 table and X^2 test. Dispersal tendencies were also compared between the sexes by analysis of covariance (ANCOVA). For the latter, number of years lived was included as a covariate to account for the possibility that number of dispersal events and years lived were correlated.

In an attempt to account for variation in dispersal behavior among individuals within each sex, I used multiple regression to evaluate whether the likelihood of dispersal changed with years lived and with average annual reproductive success. To place kingbird survival in context, I also compared their maximum longevity to that of other species of North American breeding passerine birds obtained from the Bird Banding Laboratory and reported in Blumstein and Møller (2008). Lifespan is expected to vary positively with body mass, and maximum longevity records are probably affected by number of band recoveries; exceptionally old individuals are more likely to be recorded as number of recoveries increases. I therefore used multiple regression analysis to examine maximum longevity for 107 species of passerine birds (including kingbirds) in relation to body mass and number of band recoveries for all species. Body mass and number of recoveries were both $\log_{10}$ transformed. I used STATISTIX (Analytical Software 2008) for all statistical tests, and a $P \leq 0.05$ to establish statistical significance. Sample sizes sometimes vary among tests because I lacked full information on reproductive success in a few individuals.

RESULTS

Most of the 143 male and 158 female kingbirds that I banded lived for just one (male = 40.6%; females = 46.2%) or two years (males = 22.4%; females = 26.6%). However, if they lived beyond two years, lifespans extended to as many as 8 (females) or 10 (males) years (Fig. 1). On the basis of comparison of medians, there was no difference between the sexes in the years lived, (Table 1), but a comparison of the distribution of ages lived between the sexes (Fig. 1) suggested that females tended to be represented in the youngest age class more often than males (one-tailed Kolmogorov-Smirnov test, $P = 0.032$).

Most individuals of both sexes that returned from migration used the previous year's territory. Only 39 of the 211 possible transitions from one year to the next by males that returned for at least a second year was dispersal to a new territory (18.4%). Females were more likely to disperse as 64 of 189 possible year-to-year transitions (33.9%) involved dispersal to a new territory ($X^2 = 12.33$, df = 1, $P < 0.001$). Over the course of their lives, number of dispersal events was 60% higher in females than males (Table 1); nearly 90% of males returned to use former territories from one year to the next compared to 80% of females. Number of dispersal events increased with years lived in both

sexes (F = 34.2, df = 1, 166, P < 0.001), but at any given age, female dispersed more than males (ANCOVA: F = 6.91, df = 1, 166, P = 0.009).

Considering only individuals for whom dispersal was possible (i.e., individuals that returned from migration at least once), nearly half the females (41 of 85) and a quarter of males (21 of 85) dispersed at least once in their known life. In males, regression of number of known dispersal events (DE) against number of years lived and average annual reproductive success (AARS) indicated that dispersal varied with years lived (YL: t = 3.12, P = 0.003) and average annual reproductive success (AARS: t = 2.23, P = 0.028); dispersal was more likely to occur the longer an individual lived and as AARS declined, and together they accounted for 20% of variation in number of dispersal events in an individual's lifetime (DE = 0.398 + 0.164 [SE = 0.052]YL – 0.237 [SE = 0.106]AARS; R^2 = 0.202, n = 81, P < 0.001). Likewise, number of dispersal events increased as females aged (t = 4.58, P < 0.001) and as average annual reproductive success declined (t = 2.39, P = 0.019; DE = 0.402 + 0.261 [SE = 0.057]YL – 0.258 [SE = 0.108]AARS), and in this case, a quarter of individual variation in dispersal was accounted for by the two variables (R^2 = 0.248, n = 83, P < 0.001).

Interspecific comparison of maximum longevity.— Maximum age increased with body mass for the North American breeding passerines (Fig. 2), and mass accounted for about a third of the variation in maximum life span (maximum life span = 2.97 + 5.105[$\log_{10}$Body mass]; r^2 = 0.346, n = 107 species, P < 0.001). Explained variation in maximum lifespan increased to 55% with the addition of number of band recoveries to the regression (maximum lifespan = 1.111 + 3.740[$\log_{10}$Body mass] + 1.540[$\log_{10}$Number of band recoveries]; r^2 = 0.548, n = 107, P < 0.001). Body mass of Eastern Kingbirds (40 g) predicted maximum lifespan of 11.1 years (95% confidence interval [CI] = 5.7 to 16.6 years). Combining body mass with the number to survive beyond the year of capture (i.e., equivalent to band recoveries [n = 170]), predicted maximum lifespan for Charlotte Valley/Oneonta kingbirds was 10.5 years (95% CI = 6.0 to 15.1 years).

Table 1. Comparison of average number of years lived, and average number of dispersal events over the known life of male and female Eastern Kingbirds breeding in Delaware and Otsego Counties, New York (1989 to 2001). Some birds were more than one year old by the year of banding and therefore "Years alive" only approximates age.

Trait	Males	Females	Test (P)[a]
	Mean (SE; range; median)	Mean (SE; range; median)	
Years lived[b]	2.5 (0.15; 1 – 10; 2)	2.2 (0.13; 1 – 8; 2)	2.65 (0.104)
Dispersal events[c]	0.46 (0.095; 0 – 4; 0)	0.74 (0.102; 0 – 4; 0)	7.32 (0.006)

[a] Sexes compared using Median test for Years lived, and Kruskal-Wallis test for number of dispersal events.
[b] Sample size for males and females 143 and 158, respectively.
[c] Sample size for males and females 84 and 85, respectively.

Fig. 1. A comparison of the percentage of male (n = 143) and female (158) Eastern Kingbirds banded in Delaware and Otsego Counties, New York, and known to have lived for between 1 and at least 10 years.

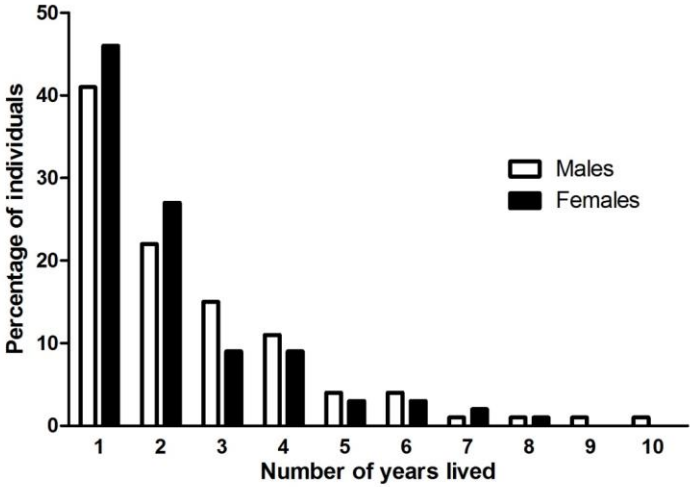
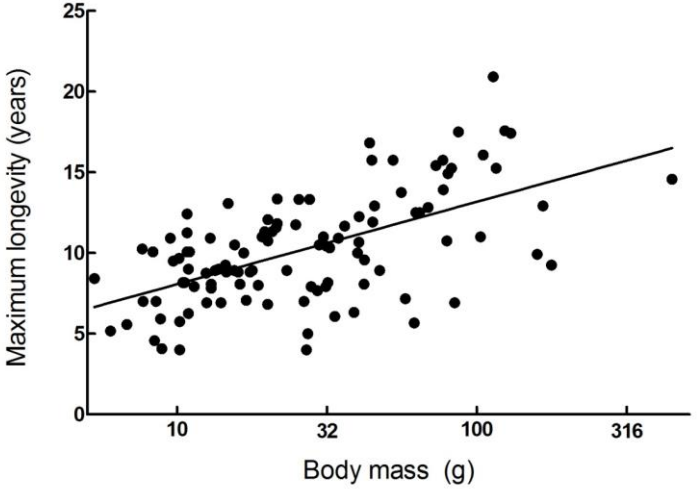


Fig. 2. The maximum number of years lived for 107 North American breeding passerine species plotted against body mass (log_{10} transformed). Longevity data are based on Breeding Bird Survey records as reported by Blumstein and Møller (2008).



DISCUSSION

Natal philopatry, the return of an individual to its birth place, is extremely low for Eastern Kingbirds breeding in the Charlotte Valley/Oneonta region, making it difficult to establish true lifespans for birds in this population. Annual survival rates (S) for males and females estimated from Cormack-Jolly-Seber methods of mark-and-recapture are 0.690 and 0.625, respectively (Murphy 2000). Given mortality rate, M, where M = 1 – S, average life expectancy can be estimated as (2 – M)/2M (Botkin and Miller 1974). This yields values of 2.7 and 2.2 years for males and females, respectively, which are not statistically different from the observed average number of years lived (Table 1). This suggests most individuals were probably in their first or second year of life when first captured. The slighter lower estimate of number of years lived by females compared to males (Table 1) possibly represents higher female mortality associated with greater investment in parental care (Woodard and Murphy 1999, Murphy 2000). However, it seems equally plausible that more frequent female dispersal (Murphy 1996; present study) led to more permanent emigration by females, which cannot be distinguished from mortality.

Ideally, demographic studies end only when all marked individuals are dead. This was not possible, and the abrupt termination of my study possibly led to at least a moderate underestimate of years lived by birds in the middle to older age groups. Contrary to former views (Deevey 1947), birds experience senescence (Ricklefs and Scheuerlein 2001). If this was not the case, and given annual survival rates of 0.69 and 0.625 and the marked populations of 143 males and 158 females, steady attrition should have yielded maximum ages of 15 years for males and 12 years for females. With only a 13 year study it was not possible to detect 15 year old birds, but with so few birds older than seven years (Fig. 1) it seems likely that senescence claimed an accelerating number of individuals as kingbirds aged.

Nevertheless, the ages to which wild birds live can be surprising. For instance, maximum reported ages of American Robin (*Turdus migratorius*), Northern Cardinal (*Cardinalis cardinalis*), Brown-headed Cowbird (*Molothrus ater*), and Common Grackle (*Quiscalus quiscula*) from the data plotted in Figure 2 are 13.9, 15.8, 16.8, and 20.9 years, respectively. The numbers of band recoveries that yielded these age estimates were large (i.e., 11,053, 14,490, 14,458, and 37,065 respectively), which greatly increase the probability of detecting very old individuals. Might maximum kingbird lifespan have been much greater had I had many more recoveries? The multiple regression equation relating maximum lifespan to body mass and number of recoveries predicted maximum age of 11.0 years when I doubled the number of recoveries. Predicted maximum lifespan increased to 13.3 years when the number of recoveries increased to 10,000 (the same order of magnitude as the four aforementioned species). My extrapolations suggest that it would be an exceedingly rare kingbird to live beyond 10 or 11 years.

One of the clearest patterns to emerge from the present study was the much higher probability of female dispersal (see also Murphy 1996). Female-biased dispersal in birds is considered typical (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997), and like most other birds, female Eastern Kingbirds are not only more likely to disperse, they disperse greater distances than males (Murphy 1996). Indeed, many of the dispersal movements by males were between adjacent territories. For example, the male that lived 10 years dispersed four times, but all occurred between two adjacent territories, the centers of which were only ~300 m apart. Because of its brevity I was unable in my earlier study to evaluate whether the likelihood of dispersal varied over an individual's life. My expanded data set indicates that dispersal did not appear restricted to early life (contra Serrano et al. 2001, Bernard et al. 2007) because older individuals, especially females, continued to disperse as they aged. By contrast, some 7 and 8 year old individuals of both sexes used the same territory for their entire history.

Whether an individual dispersed over the course of its life was affected by average annual reproductive success. As with other species (Martin 1993), nest predation is the main cause of nest failure for Eastern Kingbirds (Blancher and Robertson 1985, Murphy 2000). Selection presumably favors individuals that respond adaptively to nest predators and nest loss, and assuming past nest fate at a site is the best predictor of potential future success at that site, individuals that experience the lowest reproductive success would be expected to disperse the most (Hoover 2003). The statistical evidence indicated that, indeed, less successful kingbirds of both sexes were more likely to disperse. However, the combination of years lived and average annual reproductive success accounted for only small amounts (20% in males and 25% in females) of among individual variation in dispersal behavior. Undoubtedly the decision to disperse is influenced by numerous factors beyond simple reproductive success. For males, selection may favor strong attachment to a site if reuse of a former site yields advantages in contests over territory ownership (Krebs 1982, Cooper et al. 2009). For females, an important additional influence on the decision to disperse or remain site faithful may be the reproductive success of neighbors (i.e., "conspecific reproductive success"; Boulinier and Danchin 1997, Serrano et al. 2001). Individuals that integrate the success of neighboring conspecifics with personal success may better evaluate the potential benefits of staying or dispersing. As shown in another Eastern Kingbird population, reproductive success of conspecifics affects dispersal decisions (Redmond et al. 2009).

The picture that emerges from my study of the Charlotte Valley Eastern Kingbird population is that, while the potential for a relatively long reproductive life exists (8 to 10 years), few individuals achieve those lofty ages. Most have only 1 or 2 opportunities to breed, and it appears that the production of a relatively few individuals contribute most of the young to the population (Murphy 2007). Male Eastern Kingbirds are faithful to breeding sites, and for most, the same territory is the destination each spring as males return from

migration. Lower site fidelity of females, and greater distances dispersed compared to males (Murphy 1996), make estimation of survival using females somewhat more difficult, but the majority of females likewise exhibit lifelong fidelity to one breeding site.

Older literature accounts of Eastern Kingbirds regularly reported yearly reuse of particular sites and even specific nest trees (see Bent 1942). The orchards of older farms were repeatedly used by Eastern Kingbirds from one summer to the next, often times even after surrounding habitats changed. An unanswered question was always whether it was the same pair or simply a traditional site used year-after-year by a revolving door of different kingbirds. My study suggests it is both. Many kingbird territories in the Charlotte Valley were occupied in all 13 years of my study, and given that an 8 or 9 year old bird was rare, the only explanation possible is continual use by different individuals. However, 20% or more of birds lived at least 4 years and most were site faithful. Hence, it is indeed often the same bird occupying that same tree in that same field from one year to the next. Why such high site fidelity exists remains only partially answered (reproductive success), and my suggestion is to look towards the benefits of stable social networks. For instance, does reestablishment of territories amongst known neighbors reduce agonistic interactions and promote earlier onset of breeding? Or does proximity to known opposite sex individuals facilitate choice of extra-pair mating partners (Rowe et al. 2001, Dolan et al. 2007)? The eventual explanation may elude us, but the journey to answering the question will no doubt continue to provide fascinating glimpses into the lives of birds that continue to amaze us.

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