

# SURVIVORSHIP, BREEDING DISPERSAL AND MATE FIDELITY IN EASTERN KINGBIRDS<sup>1</sup>

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*Abstract.* I measured annual survivorship, breeding dispersal and mate/site fidelity in a color-banded population of Eastern Kingbirds (*Tyrannus tyrannus*) breeding in central New York from 1989 through 1994. I also sought to identify the factors that led to breeding dispersal and to test whether breeding philopatry was based on site or mate fidelity. Survivorship of males did not differ between the first (0.64) and all subsequent years of banding (0.73), and overall, males returned at a higher rate than females. Female survival in the first year following banding (0.68) exceeded that for all subsequent years (0.51). The difference between the sexes and between banding classes of females may be related to high costs of reproduction in older females. Breeding-site fidelity was very high (96% and 72.5% of males and females, respectively, reused former territories), but females dispersed significantly farther than males between breeding seasons. Site fidelity of males was not reduced significantly by poor nest success in the past year, and was independent of whether or not the female returned to breed. Females often dispersed between seasons after nest failures, but were even more likely to move if the male failed to return. Furthermore, 86.5% of pairs reunited when both partners were known to have returned from migration. Female philopatry thus seemed to be influenced heavily by mate fidelity. Females that renested with a former mate advanced their breeding date by about four days for every year of experience together, but they did not lay larger clutches or fledge more broods than females that nested with a new male. Reunited pairs thus made a rapid transition from migration to egg-laying.

*Key words:* breeding dispersal; divorce; mate choice; mate and site fidelity; survivorship; *Tyrannus tyrannus*.

## INTRODUCTION

Mortality and dispersal are fundamental elements of a species' life history that often differ between the sexes (Greenwood 1980, Breitwisch 1989). In most species of birds males must defend a territory to breed (e.g., Arcese 1987, Ens et al. 1993). Young males may often disperse only until an open territory is found (Beletsky and Orians 1993), and older males move infrequently (Part 1995). The reluctance of older males to move stems presumably from the uncertainty, delay and energetic expense of finding and then establishing a new territory (Temeles 1994, Part 1995). Females are seemingly less constrained and usually disperse farther and more frequently than males, possibly to avoid incestuous matings or as a tactical decision to find the best possible mate and/or territory (Orell et al. 1994).

Although widespread, the above generalizations are not without exception. Males in some bird species show lower or at least no higher site

fidelity than females (Brooke 1979, Weatherhead and Boak 1986, Bollinger and Gavin 1989, Bensch and Hasselquist 1991), and dispersal may even be male-biased (Brooke 1979, Bensch and Hasselquist 1991, Caffrey 1992, Alonso and Alonso 1992). For the most part we are ignorant of why species differ in their degree of site and/or mate fidelity, or why sex-biased dispersal exists in some species but not others.

Attachment to former breeding sites is probably beneficial because individuals learn the locations of important resources (food, nest sites and materials) and probable locations of predators. Among males, it may also improve their chances of maintaining a breeding territory (Part 1995). However, in many species, the costs to a female for remaining faithful to a site apparently outweigh the benefits, and divorce (the failure of a former breeding pair to reunite when both return to the breeding ground) is common. Female birds are far more likely than males to divorce their mate (e.g., Ens et al. 1993, Dhondt and Adriaensen 1994), and the choice may be based on either incompatibility with the male or the existence of a higher quality male or territory elsewhere. In other species, individuals may be

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avored as mates regardless of past success because of the advantages of reuniting with a former mate (e.g., earlier breeding, larger clutch size or higher nest success; Newton and Marquiss 1982, Coulson and Thomas 1983, Rowley 1983, Korpimäki 1988, Bradley et al. 1990, Orell et al. 1994). One indication that divorce may be adaptive is the dispersal of females from a site after nest failure (Darley et al. 1977, Shields 1984, Part and Gustafsson 1989, Beletsky and Orians 1991, Hepp and Kennamer 1992, Newton 1993; but see Orell et al. 1994). Such observations, although valuable, do not however answer the question of whether the decision to disperse was based on deficiencies in the male partner or the territory.

In this report I describe the results of an ongoing study that measures survivorship, dispersal and mate/site fidelity in Eastern Kingbirds (*Tyrannus tyrannus*). Kingbirds are intercontinental, neotropical migrants that breed monogamously, lay a clutch of three or four eggs and raise a single brood per year (Murphy 1983a, 1986; Blancher and Robertson 1985). Anecdotal observations suggest that kingbirds are site faithful (Bent 1942, Davis 1955) and Blancher and Robertson (1985) concluded that site fidelity in kingbirds might be based on previous breeding performance. However, Blancher and Robertson (1985) could not separate site- and individual-effects because most birds were not color-banded. Using observations of color-marked individuals over a six-year period, I document survivorship and the proximate causes of dispersal, assess whether breeding site fidelity is based on attachment to the site or mate, and test for advantages to reunification of pairs.

#### STUDY AREA AND METHODS

In 1989, I established a study site centered on Charlotte Creek in Delaware County, New York (42°78'N, 74°53'W). Charlotte Creek is a slow-moving, meandering stream with a rich riparian habitat dominated by hornbeam (*Carpinus caroliniana*) and hawthorns (*Crataegus* spp.). Kingbirds often nest in trees over water (Davis 1955, Blancher and Robertson 1985), in orchards, hedgerows (Bent 1942) or in isolated trees in fields (Murphy 1983b), all of which are abundant throughout the valley. My study area extends from (roughly) West Davenport (42°27'N, 74°57'W) to 4 km east of Davenport (42°28'N, 74°50'W) and includes all the habitat along Char-

lotte Creek and in between the two roads that run parallel on either side of the creek (Charlotte Creek Road and Route 23). The main study area is roughly 1 km × 20 km. Additional areas of excellent habitat along side roads that run perpendicular to Charlotte Creek and Route 23 were included in the study area. I expanded the study in 1990 to include a second site that was located 15 km away and just north of the city of Oneonta, Otsego County, New York (42°28'N, 75°03'W). The Oneonta study sites is best characterized as upland habitat. All territories at this site were located in open fields with scattered trees, and with only a few exceptions, none of the territories were located near bodies of water.

In mid to late May of every year I began to census habitats and former territories for returning adults. Identification of individuals was based on sightings of color bands. My assistants (2 to 4 per year) and I used 10 × 25 binoculars and spotting scopes to determine color-band combinations (see below). In the last three years of the study I also searched habitats along side roads just off the study area to check for dispersal of banded birds. Once nests were located I documented laying date, clutch size, egg masses, hatching and fledging success, and size of the nestlings at fledging (see Murphy 1983a, 1986 for more complete descriptions of methods). Kingbird nest height varied between 1 m to over 20 m high in trees, but most were located between 3 and 5 m (Murphy 1983b, unpubl. data). I checked most nests by either climbing the tree or using ladders, and banded and measured young in accessible nests within one day of day 13 of the nestling period. I also attempted to capture adults at nests during the latter half of the nestling period using mist nets whenever nests were low ( $\leq 5$  m). Adults were banded with an aluminum U.S. Fish and Wildlife Service band and a unique combination of three plastic colored legbands. I then measured body mass (0.1 g with a 50 g Pesola scale), bill and tarsometatarsus lengths (0.05 mm using dial calipers) and unflattened wing chord length (0.5 mm using a flat-ended 15 cm ruler) of each bird. Although individuals could not be aged, I sexed birds based on dimorphism in the 9th and 10th primaries (Pyle et al. 1987) and wing chord length.

#### DATA ANALYSIS

I classified all nests that fledged at least one nestling as successful. Likewise, all adults that were

resighted, regardless of whether or not I found their nests, were considered to have returned from the past breeding season. To obtain a first approximation of survivorship I divided the number of birds marked in year X which returned to breed in year X + 1 by the total number of marked adults alive in year X. I also produced an approximate survivorship curve for each sex by treating the year of banding as year 0 and converting the number of adults banded each year to an initial population size of 1000. I then averaged the number of individuals to return from each cohort in the first year after banding (=year 1) to determine survivorship over the first year of banding. This included all birds banded from 1989 through 1993. To determine survivorship from year 1 to year 2, I excluded those birds banded in 1993 (because they did not yet have a second year of potential survival), and then averaged the number of birds alive for the four cohorts banded from 1989–1992. Identical procedures were followed to measure survivorship for each successive year (Fig. 1). This measure of return rate does not take recapture efficiency (Lebreton et al. 1992) into account and thus generally underestimates true survivorship. The data were thus reanalyzed using RELEASE to test for goodness-of-fit to the Cormack-Jolly-Seber model using results of Test 2 and Test 3 (Burnham et al. 1987). Program SURGE (Lebreton et al. 1992) was then used for selection of the best model and to compute maximum likelihood estimates of survival and recapture probability. Model selection was important because sex and year were possibly varying factors. An artificial dummy age variable was also examined, where age was modeled as two age classes: (1) the first year following banding, and (2) all subsequent years. The best model was chosen based on Akaike's Information Criterion (Akaike 1973) and standard likelihood ratio tests following methods described by Lebreton et al. (1992). Analyses were performed in collaboration with T. E. Martin and J.-D. Lebreton.

I measured breeding dispersal as the shortest distance between nest sites in consecutive years. For nest locations that were within sight of one another I paced or estimated distance to the nearest 25 m. Locations of other nests were plotted on U.S. Geological Survey topographic maps and the shortest distance between nests measured. I then grouped dispersal distances into the following categories:  $\leq 25$  m, 26–50 m, 51–75 m, 76–

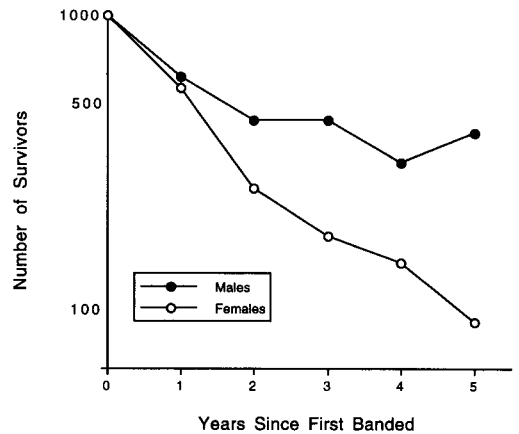


FIGURE 1. Survivorship curves for male (solid points) and female (open circles) Eastern Kingbirds breeding in the Charlotte Valley from 1989 through 1994. All birds were banded as adults at unknown ages. Hence, the minimum age for the oldest bird in the sample was six years. See Methods for a description of how the curve was generated.

100 m, 101–150 m, 151–200 m, 201–300 m, 301–500 m, 501–1000 m, 1001–2000 m and >2 km. Male and female dispersal behavior were compared by classifying each individual as having returned to (a) the territory it used the past year, (b) an adjacent, neighboring territory, or (c) a territory with one or more territories between it and its previous territory (a distant territory). Both measures of dispersal behavior, plus additional behaviors, were compared between the sexes or between birds with failed or successful nests using contingency table analyses and G-tests. I also examined the possible benefits of pairs renesting by comparing breeding performance (i.e., timing of breeding, clutch size, and nest success) of pairs that were known to have bred previously with pairs breeding together for the first time. I did not compare productivity (fledglings/year) because brood sizes were manipulated in all years of study. Brood size substantially affects feeding rates in kingbirds (Rosa and Murphy 1994) and may influence survivorship if parental behavior carries a cost. But, for the purposes of describing average survivorship, I assumed that the effect of enlarging or reducing the size of some broods canceled one another. Because of annual variation in timing of breeding I standardized first egg date for each nest to the population mean for first nests in each year by subtracting the mean laying date for the popu-

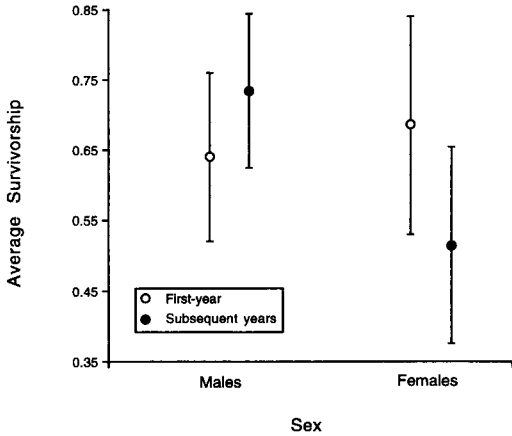


FIGURE 2. Maximum likelihood estimates of adult survivorship for male and female Eastern Kingbirds for the first year their banding (open circle) and for all subsequent years (solid dot). Vertical bars indicate  $\pm 2$  standard errors.

lation from all clutch initiation dates. Repeatability (Falconer 1981) for female breeding date and clutch size were measured using correlation analysis between each trait in consecutive years. Further tests are described in the Results. All claims of significance assume  $P < 0.05$ .

RESULTS

SURVIVORSHIP

Survivorship, based on return rate and calculated by dividing the number of birds that returned to breed by the total number of possible returns, was 69.0% (98/142) for males and 54.3% (75/138) for females. The difference was statistically significant ( $G = 5.201$ ,  $df = 1$ ,  $P < 0.02$ ). Return rates of the sexes over the first year of banding were similar, but in the remaining years males exhibited higher survivorship (Fig. 1).

The maximum likelihood estimates of survivorship yielded very similar results. Of the 54 males banded prior to 1993, only one (2%) disappeared and then reappeared in a later year. Five of the 61 females (8.2%) banded before 1993 disappeared for one or more years before later being recorded as breeding. Recapture probability of males (0.98, SE = 0.022) derived from the Lebreton et al. (1992) survivorship model was significantly higher than that of females (0.77, SE = 0.074). Annual survival rates, corrected for differences in probability of recapture, were cal-

culated for both sexes for (a) the year between the summer of banding and the next summer, and (b) all subsequent years that the bird was known to be present. Male (0.64) and female (0.68) survivorship did not differ in the year following banding, but males (0.73) survived at a significantly higher rate than females (0.51) in subsequent years (Fig. 2). Male survivorship did not differ between year classes (Fig. 2), but females survived better in the year following their initial year of banding than in subsequent years (Fig. 2).

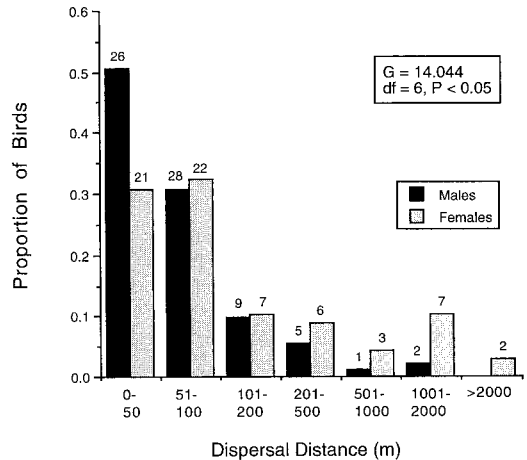
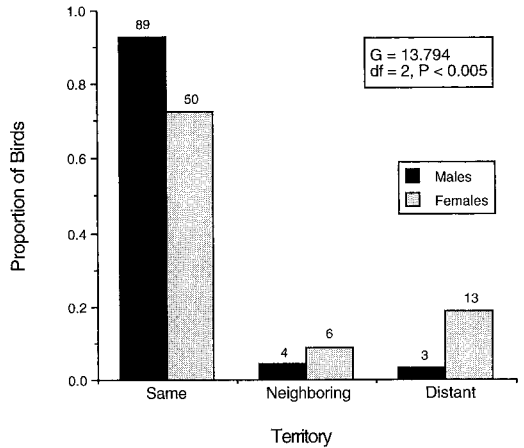


FIGURE 3. Dispersal patterns of adult male and female Eastern Kingbirds. Dispersal refers to breeding dispersal, i.e., movement between breeding sites in consecutive years, and is represented as either movements among territories (upper figure) or into distance classes (e.g., within 0 to 50 m of last year's nest site; lower figure). Numbers above bars give sample sizes.

TABLE 1. Responses of kingbirds to nest fate in the past year. Numbers (percentages in parentheses) indicate the number of male and female kingbirds that returned to the same territory, a different territory, or were never seen again in year  $X + 1$  after their nest in year  $X$  either failed or fledged young successfully.

Adult response	Males		Females	
	Successful	Failed	Successful	Failed
Return, same territory	73 (68.9)	19 (54.3)	47 (45.6)	6 (22.2)
Return, new territory	4 (3.8)	1 (2.9)	10 (9.7)	4 (14.8)
Never seen again	29 (27.4)	15 (42.9)	46 (44.7)	17 (63.0)

## DISPERSAL

Males and females differed substantially in movement patterns between years. Based on the use of the same, neighboring or distant (i.e., at least one territory between former and present territory) territories, female kingbirds ( $n = 69$ ) tended to move to a neighboring (6; 8.7%) or distant territory (13; 18.8%) more than males ( $G = 13.794$ ,  $df = 2$ ,  $P < 0.005$ ; corresponding percentages for males are 4.2% and 3.1%, respectively;  $n = 96$ ; Fig. 3). In accordance, males tended to move shorter distances between nest sites in consecutive years (Fig. 3). Over 50% of males nested within 50 m of their former nest location compared to only 30% of females. Only 2.2% of males moved one or more km between nest locations in consecutive years compared to 13.2% of females (Fig. 3). The greater fidelity of males to past breeding sites is further highlighted by their more frequent use of former nest trees. Although nest trees were seemingly abundant, new mates of 26.1% of returning males nested in the same tree used in the preceding year whereas only 16.1% of females that reused their former territory rebuilt in the preceding year's nest tree.

## FACTORS INFLUENCING THE DECISION TO RETURN

I began my examination of the effect of past nest success on site fidelity by placing adults into one of three categories: (a) return to breed in the same territory, (b) return to breed in a different territory or (c) non-return (i.e., not seen again). Because studies of other species have shown that dispersal often follows nest failure, I used a one-tailed test to determine if nest failure led to dispersal in kingbirds. Males that failed to fledge young were marginally less likely than successful breeders to return to the same territory (Table 1;  $G = 2.407$ ,  $df = 1$ ,  $P < 0.10$ ; males that bred successfully were compared to all others). Nest fate had a much stronger influence on female

behavior (Table 1). Females that failed to breed successfully were only half as likely to be seen on the same territory in the next year as were successful breeders ( $G = 5.157$ ,  $df = 1$ ,  $P < 0.01$ ; females that bred successfully were compared to all others). To further examine the relationship between sex, nest success and breeding dispersal, I compared the behavior of males and females when nests either failed or fledged young. Females changed territories (or were never seen again) 69.9% more often than males when their nest failed ( $G = 8.121$ ,  $df = 2$ ,  $P = 0.021$ ) and 74.4% more often after a success ( $G = 12.179$ ,  $df = 2$ ,  $P < 0.005$ ). Females were thus always more likely to change territories.

The results described above were based on all banded birds, regardless of whether or not a mate was banded. In order to examine the effects of the presence of a former mate and nest fate on the probability of reusing the past territory I restricted further analyses to 90 nests at which I had (a) banded both parents, (b) determined nest success, and (c) knew that at least one pair member had returned to breed in the following year. Pairs reformed 32 of the 37 times (86.5%) that both pair members were known to be alive. The five "divorces" all followed successful nests, whereas all five failed nesting attempts were followed by reunification of the pair. Four of the five divorces entailed the movement of females to new territories. Both males that dispersed to new territories had successfully fledged young in the past year. One of these males moved with his former mate to a neighboring territory. The other male moved without his former mate to a distant territory (> 1 km away) while she moved to an adjacent territory. Overall, 35 of 37 males reused their former territory (94.6%) when their former mate was alive compared to 33 of 37 females (89.2%).

Males returned to their former territory 36 of 37 times (97.3%) when their former mate did not

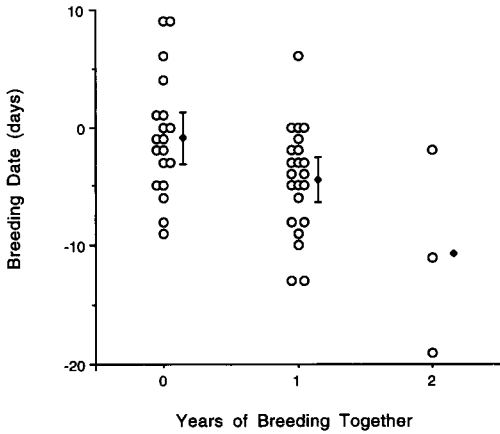


FIGURE 4. The relationship between date of breeding (corrected for annual variation in the onset of breeding in the population) and number of years pairs were known to have bred together. Open circles indicate individual observations. Points have been offset slightly in order to minimize overlap and improve visualization. The three solid points are mean values and the vertical bars represent  $\pm 2$  standard errors. A value of zero for Years of Breeding Together indicates that this was the pair's first year together.

return. The one movement followed a successful nest, whereas six failures were followed by reuse of the former territory. The tendency of a male to reuse his former territory was independent of whether or not his former mate returned ( $G = 0.354$ ,  $df = 1$ ,  $P > 0.50$ ). On 16 occasions only the female returned. Fourteen of the 16 females fledged young in the former year and 9 of the 14 reused their former territory. The two failures, plus five successful nests, were followed by

TABLE 2. Results of a multiple regression analysis that examined the relationship between timing of breeding and pairing patterns (i.e., number of years paired: 0, 1, or  $\geq 2$ ) in female Eastern Kingbirds. The analysis also controlled for repeatability (Falconer 1981) in breeding date and number of years the bird was banded.  $t$ -values represent the significance of each variable when included in the full regression whereas  $R^2$  indicates the amount of variation in timing of breeding that was accounted for by that variable as it entered the model in the sequence given in the table.

Predictor variable	Coefficient	$t$ -value (p)	$R^2$
Former breeding date	0.344	2.71 (.01)	0.265
Years banded	-1.468	2.05 (.05)	0.315
Years paired	-3.288	3.00 (.005)	0.438

movement to a new territory. A comparison of the behavior of females when their former mate was known to have returned to the same territory ( $n = 35$ ) and when she alone returned ( $n = 16$ ) indicated that the presence of the male increased her chances of reusing the former territory (88.6% vs. 56.2%;  $G = 6.375$ ,  $df = 1$ ,  $P = 0.012$ ). This conclusion is reinforced by a direct comparison of male and female reuse of former territories when (a) their partner returned, and (b) when they returned alone. Males and females behaved identically when their former mate returned ( $G = 1.463$ ,  $df = 1$ ,  $P > 0.10$ ), whereas females were more likely to disperse when her former mate was missing ( $G = 13.856$ ,  $df = 1$ ,  $P < 0.001$ ).

#### REPRODUCTIVE CONSEQUENCES OF PAIRING PATTERNS

The significantly greater tendency of females to reuse territories if a former mate was present suggested that advantages accrue to those females that renest with former mates. I therefore compared timing of breeding, clutch size and nest success among females that mated with either a new or former mate (one to two years of past experience). My analysis was restricted to banded females for which I had breeding data for at least two consecutive years, and for which I could establish (through banding) whether or not they paired with their former mate. Egg-laying dates were correlated significantly in consecutive years ( $r = 0.515$ ,  $P < 0.001$ ). In addition, females began to lay earlier as both the number of years mated to the same male (Fig. 4;  $r = -0.468$ ,  $P < 0.005$ ) and the number of years the female was banded increased ( $r = -0.361$ ,  $P < 0.05$ ;  $df = 43$  for all three correlations). Thus, early breeding was associated with early breeding in the past (i.e., repeatability for breeding date was high), pairing with a former mate, and number of years banded. All three variables remained significant when tested in a multiple regression analysis (Table 2) and together they accounted for 44% of the variation in female breeding date ( $F = 10.67$ ,  $df = 3, 41$ ,  $P < 0.0001$ ). After controlling for repeatability of date and number of years banded, pairing with a former mate, on average, advanced breeding date by about four days for each year of experience together. Whether or not a female utilized the same territory had no influence on when she laid her eggs ( $P > 0.25$  in all multiple regression analyses).

As an additional test of the significance of re-

nesting with a former mate, I expanded my analysis to compare timing of breeding for all females known to have bred with different males in consecutive years. Breeding date was not advanced in the second year for females breeding with different males on either the same (paired  $t$ -test for between years comparison = 0.00,  $df = 11$ ,  $P = 1.0$ ) or different (paired  $t$ -test = 0.22,  $df = 8$ ,  $P = 0.93$ ) territories. The results indicated that experience with a particular male, rather than aging or familiarity with a territory, led to early egg-laying by females.

Female clutch size also showed significant repeatability between years ( $r = 0.452$ ,  $P = 0.003$ ), but neither number of years mated to a male ( $r = -0.041$ ), number of years banded ( $r = 0.026$ ), nor patterns of territory use ( $t = 1.41$ ,  $P = 0.16$ ) affected clutch size (clutch size of first nests of the season = 3.4 and 3.1 eggs on the same [34] vs. new [10] territory, respectively;  $df = 42$  for all tests). The latter conclusions held true when all four variables were analyzed using multiple regression ( $P = 0.008$  for former clutch size, but  $P \geq 0.27$  for the remaining variables). Finally, I tested the hypothesis that reuniting with the same male improved a female's chances of breeding successfully by comparing nest success for females that (a) bred on the territory in the previous year, and (b) mated previously with the resident male. Contrary to predictions, the probability of first nests producing young declined significantly as years of breeding experience together increased (Fig. 5; females breeding for the first time with a male were compared to females that had bred previously with a male;  $G = 4.885$ ,  $df = 1$ ,  $P = 0.028$ ). Experienced females (13 of 15) were also no more likely to replace failed nesting attempts than were females with new mates (11 of 15;  $G = 0.846$ ,  $df = 1$ ,  $P > 0.30$ ). Most failed nesting attempts were replaced, hence, overall success of new and experienced pairs did not differ over the season (Fig. 5;  $G = 0.48$ ,  $P > 0.40$ ).

## DISCUSSION

### SURVIVORSHIP AND DISPERSAL

Kingbird survivorship is noteworthy in two respects. First, male survival after the first year of banding (0.73) was at the maximum values recorded for other small- to medium-sized birds breeding in temperate regions, and approached or exceeded that of many similar-sized tropical

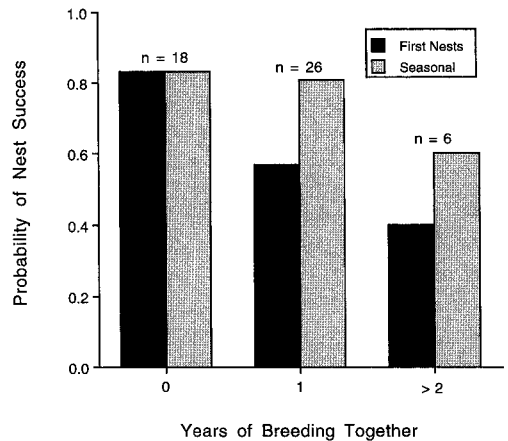


FIGURE 5. Probability of nest success (successful nests fledged at least one nestling) versus number of years of experience a pair had breeding together. Solid bars represent first nests of the season and hatched bars represent the probability of whether or not a pair fledged young before the season ended (sample size =  $n$ ). Data are for females and were limited to only those individuals for which it was known whether or not they had bred on the territory in the past year, and whether they had bred previously with the male.

species (Karr et al. 1990). Second, after the first year of banding males had significantly higher survivorship than females. These patterns were evident in both the direct survivorship measurements (Fig. 1) and the maximum likelihood estimates (Fig. 2). My survivorship estimates thus appear to be robust (especially for males), which is likely the result of the high site fidelity of kingbirds, the use of color-bands to resight individuals, and my intensive recensusing of virtually all former breeding locations. Blancher and Robertson's (1985) survivorship estimates for male (42%,  $n = 12$ ) and female (44%,  $n = 18$ ) kingbirds in Ontario were lower. While possibly reflecting true population differences, the small number of birds banded in Ontario make comparisons difficult because confidence limits around the reported values would be large (P. Blancher, pers. comm.). Comparisons to Karr et al.'s (1990) data for temperate- and tropical species are also difficult because the latter study's estimates were based on recaptures rather than resightings, a method known to underestimate survivorship (Piper et al. 1981, Elder 1985, Buckland et al. 1987). Thus, whether or not kingbirds show unusually high survivorship awaits more comparative data from studies based on resightings of individually marked birds.

Return rates in the years after the initial year of banding are thought to better reflect true survivorship (because handling may cause birds to disperse; Blancher and Robertson 1985; Payne and Payne 1990; T. Martin, pers. comm.). In addition, individuals of both sexes (but especially females) are less likely to disperse as they age (Ens et al. 1993, Newton 1993, Dhondt and Adriaensen 1994, Part 1995). Assuming kingbirds show similar patterns, females survived poorly compared to males after the second year of banding. Two possibilities might explain this finding. First, it may have been an artifact of the combination of (a) the higher probability of females reusing former territories after a successful nest, and (b) my failure to net and band many of the unbanded birds that did not fledge young. The other possibility is that as females aged, and reproductive value declined, they invested more in reproduction than males and experienced high mortality (e.g., Pugsek 1981, Pugsek and Diem 1990).

Large differences in survivorship should have resulted in many males being unmated. In every year a few males did not obtain mates until after nests began to fail, suggesting that females moved in after a failure at her initial nesting attempt. The presence of a few unmated males is consistent with my finding that males were more likely to survive than females. Nonetheless, I suspect that female survivorship was underestimated by the current model because (a) females dispersed more than males and (b) the long, rectangular shape of the main study area increased the probability of females moving permanently off the site. Given that the main study site was only one km wide, and that several females dispersed 2 to 4 km between nest sites in consecutive years, some surviving females probably dispersed permanently to distant sites where they went undetected. I therefore suspect that older female survivorship was probably at least 60%. Still, higher female mortality is not uncommon in monogamous songbirds (Payne and Payne 1990; reviewed by Breitwisch 1989), and the greater mortality of female kingbirds may reflect greater parental investment (Maugret and Murphy, unpubl.), or unknown events on the winter grounds.

#### SITE AND MATE FIDELITY

Males were exceptionally faithful to former breeding territories: the absence of a former mate had no influence on male dispersal, and failure

to fledge young only marginally increased the probability of male dispersal. Indeed, the four males banded in 1989 (from the original 10) that were still alive in 1994 never moved from their original territory and often reused their former nest trees. Females were more likely to move between territories in successive years, but still, most returning females (72.5%) used their former territories and spent their entire known reproductive life at one site. For example, two females did not move from their territories for five and six years, respectively, and many females spent three or four years at one site. Based on a smaller sample, Blancher and Robertson (1985) also showed that female kingbirds were more likely to disperse than males, but they concluded that turnover of individuals on territories was high. Although the populations may have again differed, my results suggest that territory turnover is low, and that site consistency in breeding performance cannot be assessed without analyzing individual performance by marked individuals.

The greater dispersal distances of females is typical of birds (see Introduction) and needs no further discussion. Males dispersed so infrequently that I cannot speculate as to the circumstances surrounding their movements. Hence, my discussion of site fidelity is based on decisions made by females to either return and nest with a former mate on their old territory, or to move to a new territory and breed with a new male. Selection should favor dispersal by females after nest failures if by moving they improve their chances of success, and indeed, female kingbirds did move more often after a failure (for other species see Thompson and Nolan 1973, Darley et al. 1977, Nolan 1978, Shields 1984, Drilling and Thompson 1988, Part and Gustafsson 1989, Beletsky and Orians 1991, Hepp and Kenamer 1992, Newton 1993, Marra and Holmes, unpubl.) Females that moved after a failure were presumably seeking better breeding opportunities elsewhere.

Divorce between seasons in kingbirds is difficult to explain. Among the 37 returning pairs, all five divorces were preceded by successful nests whereas all five breeding failures were followed by reunification of the pair. The two leading hypotheses that attempt to explain divorce ("better options" and "incompatibility"; Ens et al. 1993, Dhondt and Adriaensen 1994) both predict that females will do better by breeding elsewhere, but only the incompatibility hypothesis proposes that



males also benefit by the separation. The better options hypothesis assumes that females mate elsewhere because of the availability of either a higher quality male or better territory, and that her former mate's reproductive success suffers. I cannot test either hypothesis, but the low divorce rate of kingbirds (13.5%) and the association of female dispersal with the male's death suggest that compatibility may be an important factor influencing a female's choice of mate, and possibly of a site. My data also suggest that site fidelity in female kingbirds is largely an outcome of mate fidelity. Compatibility may be based on the willingness of the male to provide parental care (Hayes and Robertson 1989, Rosa and Murphy 1994), and female mate fidelity may exist because male properties or familiarity with a male have a greater impact on reproductive success (possibly assessed on a lifetime basis) than variability in territory quality. As Orell et al. (1994) proposed for Willow Tits (*Parus montanus*), expectations of future success may drive mate choice by female kingbirds.

#### MATE FIDELITY AND MIGRATORY STATUS

Rowley (1983) proposed that mate fidelity in songbirds is based mainly on site fidelity in both males and females. My data suggest the opposite for kingbirds. Rowley's (1983) argument was based on the incorrect assumption that annual mortality rates of migrant songbirds were higher than those of residents (see Greenberg 1980, 1986). He also argued that mate attachment would be especially low in migrants because pair members do not associate with one another on their wintering grounds. Migrants do, on average, have lower mate fidelity than resident birds (Fig. 6), but I suspect that the very high mate fidelity of female kingbirds and many residents is facilitated mainly by the predictable presence of the male on his former territory. It also seems unlikely that high survivorship is a sufficient explanation for low divorce rates. Otherwise, why would species such as migrant Great Reed Warblers (*Acrocephalus arundinaceus*) divorce 88% of the time despite having a 60% annual return rate (for successful breeders; Bensch and Hasselquist 1991).

I propose that low divorce rates may reflect either advantages of associating with a particular individual, or simply be a byproduct of having few opportunities to choose a new mate in a saturated environment (e.g., Freed 1987). In the

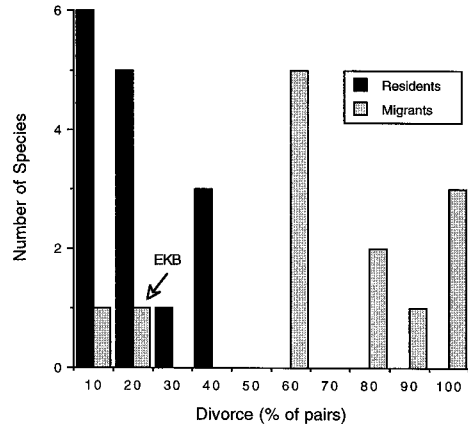


FIGURE 6. A comparison of the frequency of divorce among resident and migrant songbirds breeding in temperate regions around the world. The bars are a tally of the number of species falling into 10 equally spaced categories of divorce (0–10%, 11–20%, etc.). For example, less than 10% of pairs divorced in six resident species, but only one migrant (Welcome Swallow [*Hirundo neoxena*; Rowley 1983]). Data are from Table 5 of Dhondt and Adriaensen 1994, this study (*Tyrannus tyrannus*, EKB; divorce rate = 13.5%) and the following references: Beletsky and Orians 1991 (*Agelaius phoeniceus*; 57%), Drilling and Thompson 1988 (*Troglodytes aedon*; 96.4%), Part and Gustafsson 1989 (*Ficedula hypoleuca*; 94%), Payne and Payne 1993 (*Passerina cyanea*; 50.5%) and Orell et al. 1994 (*Parus montanus*; 12.5%). All species are represented only once. Hence, an average divorce rate was computed for all species with multiple estimates of divorce rate.

case of kingbirds, reestablishing a former pair bond allowed females to shorten the time to egg-laying (Fig. 4; but did not result in either larger clutch size or higher probability of nest success). Orell et al. (1994) obtained identical results for resident Willow Tits and divorce rate was similarly low (12%; see also Ens et al. 1993, Perrins and McCleery 1985). Female kingbirds that bred with new males on either the same or a different territory did not change breeding date between years, indicating that the effect was not related to age or territory. Early breeding is important for kingbirds because it is associated with greater fledgling production (Blancher and Robertson 1985) and a higher probability of replacing failed nests (Murphy 1983a). The latter may be particularly important because nest predators destroy roughly 50% of all nests each year (Blancher and Robertson 1985; Murphy 1983b, unpubl.). Male kingbirds do not courtship feed or assist in nest construction. Hence, preparation for egg-laying

does not change with a female's pairing status. The main benefit thus appears to be a more rapid transition to breeding condition.

Residents may also encounter greater social constraints than migrants and as a consequence have fewer opportunities for finding an open territory if they divorce. Birds in dense populations face intense intraspecific competition and experience greater threats of loss of territory and mates to intruders. O'Connor (1992) showed that resident populations of songbirds in North America were denser than migrant populations, and that resident species showed stronger evidence of density-dependent population regulation. Exploratory behavior may be riskier for residents because it increases the chances of losing a territory. For instance, Blue Tit (*P. caeruleus*) females in a population that maintained territories over winter had the lowest divorce rate (25%) whereas individuals in populations with typical parid mixed species flocks divorced 45% and 85% of the time (Dhondt and Adriaensen 1994). Abandonment of territories and reshuffling of territory ownership, far more than differences in survivorship, thus seem likely to underlie the large differences in the frequency of divorce seen in resident and migrant birds (Fig. 6).

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