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COMPARATIVE REPRODUCTIVE BIOLOGY OF KINGBIRDS (*TYRANNUS* SPP.) IN EASTERN KANSAS

MICHAEL T. MURPHY[1]

ABSTRACT.—Data on body size, timing of breeding, clutch size, egg weight and patterns of nestling growth are reported for sympatrically breeding populations of Eastern and Western kingbirds (*Tyrannus tyrannus* and *T. verticalis*) and Scissor-tailed Flycatchers (*T. forficatus*) in eastern Kansas. Body size and breeding dates were similar for the three species, but all other traits showed significant variation. Eastern Kingbirds laid the smallest clutches, the largest eggs, and their young gained weight fastest. The rate of weight increase by Eastern Kingbirds varied inversely with brood size. Scissor-tailed Flycatchers produced the largest clutches, the smallest eggs, and their young gained weight significantly slower than the young of Eastern Kingbirds. Western Kingbirds were intermediate in most respects. Variation among species in egg and clutch size represent fixed, apparently genetic differences. It is less clear whether variation in the rate of growth reflects phenotypic responses to stress or intrinsic species differences. Comparisons of tarsus growth indicate little variation among species, but primary development was faster in Western Kingbirds and Scissor-tailed Flycatchers than in Eastern Kingbirds. I propose that egg and clutch size vary independently among species in response to climatic stresses within the respective geographic ranges of each species.
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Life histories are commonly viewed as sets "of coadapted traits designed, by natural selection, to solve particular ecological problems" (Stearns 1976). Implicit in this definition is the notion that life histories represent optimal solutions to ecological pressures impinging on reproductive success. Furthermore, it is often assumed that organisms operate at maximal rates and efficiencies (Calow and Townsend 1981), and that optimal amounts of energy are allocated to reproduction (Smith and Fretwell 1974). Hence, theory predicts the existence of compromises among such life history traits as reproductive rate and survival (Williams 1966, Charnov and Krebs 1974), number and size of offspring (Smith and Fretwell 1974, Brockelman 1975, Lloyd 1987), and number and rate of offspring development (Fretwell et al. 1974).

Recently, questions have arisen over the most appropriate taxonomic level for testing life history theory. Ideally, comparative tests should be made within species to control for genetic differences. However, attempts to test theory in birds through intraspecific geographic comparisons of reproductive traits have proved inconclusive (Hussell 1972, Murphy 1978,

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[1] Dept. Biology, Hartwick Coll., Oneonta, New York 13820.

King and Hubbard 1981, Jarvinen and Vaisanen 1983, Murphy 1983a, Winkler 1985, but see Blondel 1985). Except for timing of breeding and/or clutch size, most species showed little variation in reproductive characters among allopatric populations. Differences found to exist were often attributed to body size (Murphy 1978, King and Hubbard 1981), the physiological state of the female (Murphy 1978, Jarvinen and Vaisanen 1983, Winkler 1985), or to seasonal factors (Hussell 1972, Jarvinen and Vaisanen 1983, Murphy 1986a), suggesting that tests of life history theory within species may be limited by allometry, low genetic variability, physiology (Stearns 1980), phylogeny (Jones and Ballinger 1987), or gene flow (Slatkin 1987). Work on classes of animals other than birds indicate similar problems (e.g., Hart and Begon 1982, Brown 1983, 1985, Dobson and Murie 1987). Thus, although work at the population level is essential for identifying the causes for shifts in life history characters, the most profitable tests of theory may be made by comparing closely related species (Stearns 1980, Ekman and Askenmo 1986, but see comments by Jones and Ballinger 1987).

As part of a larger study examining life history evolution in the Eastern Kingbird (*Tyrannus tyrannus*), I gathered reproductive data on Western Kingbirds (*T. verticalis*), and Scissor-tailed Flycatchers (*T. forficatus*) that bred sympatrically with Eastern Kingbirds over the same period in eastern Kansas. Bent's (1942) life history summaries suggest that modal clutch size is 3, 4, and 5 eggs in Eastern and Western kingbirds and Scissor-tailed Flycatchers, respectively. Clutch size declines seasonally in kingbirds (Davis 1955; Murphy 1983a, 1986a; Blancher and Robertson 1985a, b, 1987), and at least in Eastern Kingbirds, differences in clutch size among years and among some populations can be accounted for by variation in timing of breeding (Murphy 1986a; see also Jarvinen and Vaisanen 1983 for the Pied Flycatcher *Ficedula hypoleuca*). Hence, one possible explanation for interspecific variation in clutch size is early breeding by Scissor-tailed Flycatchers and late breeding by Eastern Kingbirds. In this report I provide comparative data on timing of breeding, clutch and egg size, and nestling growth for all three species of kingbirds. I test: (1) the breeding date hypothesis, and, at the interspecific level, the theoretical predictions that inverse relationships should exist between: (2) egg and clutch size (Smith and Fretwell 1974, Lloyd 1987), and (3) number and rate of offspring development (Fretwell et al. 1974).

SPECIES AND STUDY AREA

Eastern Kingbirds (henceforth EKB) have the widest and northernmost distribution of the three species. They breed from the Yukon to south Texas and Florida, and from the Pacific northwest over all of eastern North America in habitats ranging from forest edge to old field and pasture. Western Kingbirds (WKB) also breed in open habitats, including riparian forest, deserts and urban areas. In general, WKBs breed in drier habitats and are found mainly in western North America. However, over the past 50 years WKBs have spread eastward across the Great Plains. Scissor-tailed Flycatchers (STF) have the southernmost distribution, being restricted to grassland habitats in the southcentral United States (all distributional data from the A.O.U. Checklist 1983). All three species are migratory, breed monogamously, and normally raise a single brood per year (Bent 1942, Fitch 1950, Davis 1955, Murphy 1983a, Blancher and Robertson 1987). Diets and foraging behaviors during the breeding season are also very similar (see Murphy 1987), i.e., all three species typically hawk for flying insects. Likewise, all three build open cup nests that are usually placed 2 m or more above the ground (MacKenzie and Sealy 1981, Murphy 1983b, Blancher and Robertson 1985a).

Breeding ranges of the three species overlap in portions of Kansas, Oklahoma, and Texas. I collected data in Douglas County, Kansas, from 1980 through 1983. Additional data on adult body sizes were taken in June, 1986 from Douglas and neighboring counties. My principal research area extended west from the edge of Lawrence, Kansas, to Clinton Reservoir (38°57′N, 78°95′W), a distance of about 6.5 km. Habitats consisted of pastures, grassland with scattered trees, hedgerows, and, near the city and reservoir, parks and campgrounds. "Natural" habitats are described in greater detail elsewhere (Murphy 1986a). EKBs were the most plentiful species and bred in all the above habitats. WKBs were found only near human habitations, but were often very abundant in city parks, campgrounds, or other mowed areas. STFs were found almost exclusively in open grasslands and were the least abundant species. WKBs and STFs rarely bred in the same habitat, but EKBs were syntopic with both species.

METHODS

Field procedures.—Field methods have been described thoroughly in previous publications (Murphy 1983a, 1985a, 1986a, b). I did not make special attempts to locate breeding STFs or WKBs, but included them in my daily activities when nests were located. I used identical methods to record timing of breeding (=date of laying of the first egg in a clutch), clutch size, egg dimensions (maximum length and breadth) and weight, and nestling growth in all species. All weights and length measurements were measured to the nearest 0.1 g and 0.05 mm, respectively, with a 50-g Pesola spring scale and dial calipers. Dates of clutch initiation for nests found after egg laying were determined by backdating from events such as hatching of eggs or age-determination of nestlings (Murphy 1981).

Upon hatching (=day 1 of nestling period), I visited nests at regular intervals up to day 13 or 15 of the nestling period. At each visit I recorded the weight, tarsus length, and 9th primary length for each nestling present. Nestlings were marked individually by clipping toenails. Nest checks occurred daily in 1980. Nest predation increased in 1981 and 1982, presumably due to my disturbance of nests. I therefore attempted to decrease my impact on nest success by reducing the frequency of nest checks to every 1–4 days. I created broods of five EKB young in 1980 (N = 2) and 1981 (N = 1) by adding one nestling to broods of four. Transfers occurred by day 2 of the nestling period and were of same age individuals. Growth was also measured in a natural brood of 5 young in 1981. Except for one STF brood, no growth data were taken in 1983.

In 1983 and 1986 I collected adults of all three species using .22 caliber rifle and "dustshot." Immediately after the specimen was collected, I recorded body weight, wing chord length (unflattened), tarsus length, bill length (anterior edge of the nares to the tip), and keel length. The length of the keel was taken as the distance from the base of the sternum to the base of the furcula, and was averaged from three separate measurements. Sex was determined from plumage characters (two outer primaries emarginate in males, only the outermost primary emarginate in females; Bent 1942).

Data analysis.—I determined fresh egg weight (weight on day of laying) for eggs measured during incubation using length and breadth measurements in the formula, egg weight $W = [C(L \times B^2)]$, where L and B are maximum egg length and breadth, respectively. The conversion factor, C, relating L and B to W was determined for each species separately from a sample of eggs weighed and measured on the day of laying. I took a random sample of 15 EKB clutches from each of the four years to compare to the cumulative four-year totals of the WKB and STF. Sample sizes in all analyses involving comparisons of egg size and nestling growth equal the number of nests from which data were collected. I used average weight, length, and breadth of all the eggs in a clutch in comparisons among species and years.

I computed growth curves for body weight and tarsus and 9th primary lengths for each brood. I then calculated each brood's average rates of weight gain using Crossner's (1977) weight-specific regression method. Crossner's technique permits simultaneous estimation of asymptotic weight (A) and rate of growth (K). I also computed the absolute rate of weight gain by regressing weight against age for the period when growth was approximately linear (days 3–11). Absolute rates of growth for the lengths of the tarsus and 9th primary were determined using the same method, but over different ages (tarsus, days 1–11; 9th primary, days 6–14). The resulting least-squares regression coefficients equalled the absolute rate of increase in weight or length.

I used standard parametric statistics throughout when the assumptions of the models were not violated. I checked distributions visually for normality, and used the F-max Test to determine if variances were homoscedastic. When variances proved to be heteroscedastic, I used a t-test (t_s) based on unequal variances (Sokal and Rohlf 1981) or substituted an appropriate nonparametric test. Most statistical analyses were performed using the BMDP statistical package (Dixon 1981). Statistical significance was accepted at $P \leq 0.05$. Specific tests are described in the Results.

RESULTS

Sexual size dimorphism and adult body size.—Patterns of sexual size dimorphism varied among characters. No dimorphism existed in tarsus length, bill length, or body weight, whereas in all three species keel lengths were 5–8% larger in males than females (Table 1). Wing chord lengths were significantly longer in males than females in 2 of 3 species. Sampling error resulting from small sample size was the probable cause for the lack of significant sexual size dimorphism in wing chord length of WKBs (Table 1).

Because of the lack of dimorphism in bill and tarsus lengths and weight, I combined the sexes for comparisons among species. Bill lengths varied significantly (Table 1) due to the short bills of STFs compared to both WKBs and EKBs (Sums of Squares simultaneous test procedure [SS-STP, Sokal and Rohlf 1981], $P < 0.05$ for both). Tarsus lengths also varied among species (Table 1). In this case STFs were the same size as WKBs and EKBs (SS-STP, $P > 0.05$), but EKBs had shorter tarsi than WKBs (SS-STP, $P < 0.05$). Weight differences among species were not significant

TABLE 1

MORPHOLOGICAL COMPARISONS AMONG ADULTS OF THREE SPECIES OF KINGBIRDS BREEDING IN EASTERN KANSAS. VALUES ARE MEANS (SD)

Sex (N)	Weight (g)	Wing (mm)	Tarsus (mm)	Keel (mm)	Bill (mm)
		Eastern Kingbird			
Male (32)	42.4 (3.64)	117.6 (2.28)	19.26 (0.79)	28.12 (1.01)	13.97 (0.69)
t-test[b]	0.8 ns[a]	11.4****	0.2 ns	7.5****	0.6 ns
Female (34)	41.8 (2.69)	110.9 (2.49)	19.22 (0.75)	25.96 (1.31)	13.86 (0.77)
		Western Kingbird			
Male (2)	41.2 (1.48)	125.8 (1.06)	20.20 (0.42)	28.68 (0.32)	13.65 (0.35)
t-test[b]	0.7 ns	1.6 ns	0.3 ns	4.1***	0.8 ns
Female (5)	45.8 (5.63)	122.1 (3.07)	20.16 (0.47)	26.49 (0.70)	13.91 (0.39)
		Scissor-tailed Flycatcher			
Male (5)	40.7 (1.70)	121.9 (1.29)	19.24 (0.67)	28.07 (0.80)	13.48 (0.72)
t-test[b]	0.1 ns	13.4****	1.6 ns	3.1**	0.9 ns
Female (5)	40.4 (5.10)	111.6 (1.14)	19.96 (0.77)	26.64 (0.63)	13.13 (0.49)
		Statistical Comparisons among Species (ANOVA)[c]			
Male	—	21.1****	—	0.6 ns	—
ANOVA (*F*)[c]	2.6 ns	—	5.6***	—	3.6*
Female	—	45.1****	—	1.0 ns	—

[a] * $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$, **** $P < 0.001$, ns = not significant.

[b] *t*-test for comparison of males and females within species.

[c] *F*-test from an analysis of variance (ANOVA) comparing species. Sexes combined when dimorphism was absent, but analyzed separately when it existed.

(Table 1). Within sex comparisons of wing chord yielded significant differences among species (Table 1). Female STFs and EKBs did not differ significantly (Table 1), but both had significantly shorter wing chords than WKBs (SS-STP, $P < 0.001$). Male differences were also significant (Table 1) because EKBs had shorter wing chords than both WKBs and STFs (SS-STP, $P < 0.001$). None of the within sex comparisons of keel length was significant (Table 1).

Timing of breeding and clutch size.—Breeding dates were variable in all species (Table 2; Fmax = 3.09, df = 2, $P > 0.05$). For this reason, I used nonparametric methods to test for interspecific differences in timing of breeding. Clutch initiation dates overlapped broadly in all three species (Table 2), with no evidence for early- or late-breeding on the part of any of the species (Kruskal-Wallis, $H = 2.25$, $P = 0.40$).

Clutch sizes differed substantially among species (Fig. 1 and Table 2), and in all three species clutch size declined seasonally (Table 2). Regression coefficients describing the relationship between clutch size and date

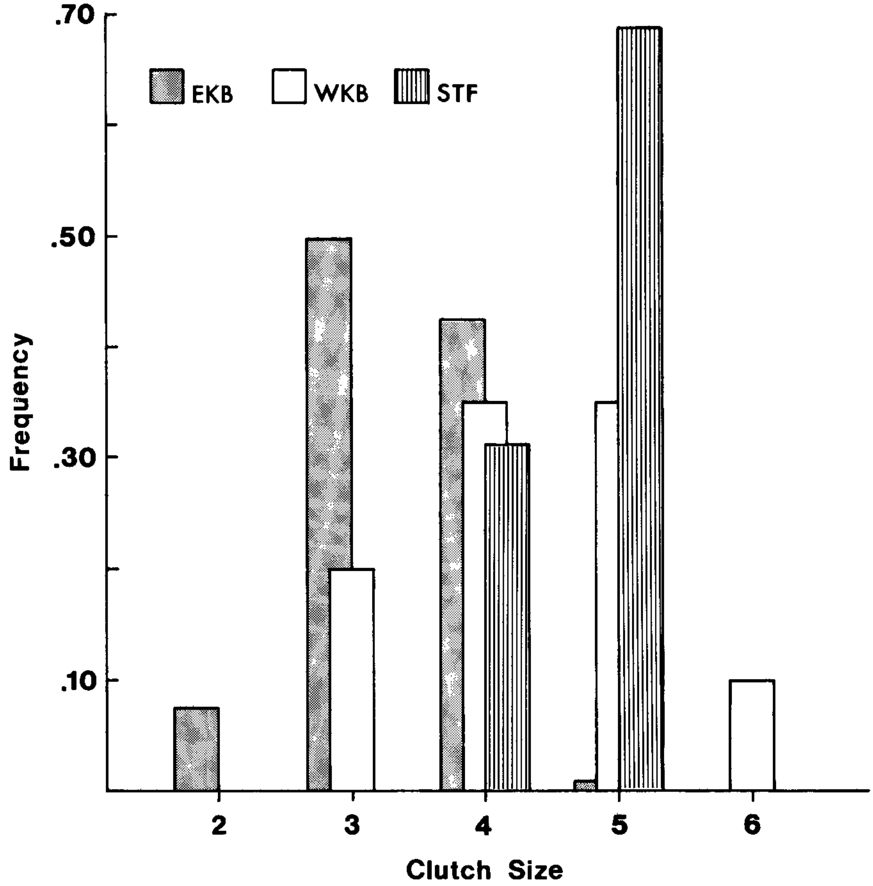

FIG. 1. Interspecific variation in the frequency of different sized clutches in Eastern Kingbirds, Western Kingbirds, and Scissor-tailed Flycatchers breeding in eastern Kansas.

did not differ among species (analysis of covariance, $F = 2.14$, df = 2, 229, $P = 0.12$). Comparisons of clutch size among species after controlling for date effects showed that EKBs laid significantly fewer eggs than both WKBs ($t = 7.29$, $P < 0.001$) and STFs ($t = 8.78$, $P < 0$ .001), but the difference between WKBs and STFs was not significant ($t = 1.57$, $P >$ 0.10).

A potential complicating factor in the above species comparisons of clutch size is variation in food abundance among years. The availability of typical kingbird prey (Hymenoptera, Coleoptera, Orthoptera; Dick and Rising 1965) was significantly higher in 1981 than in other years (Murphy

TABLE 2

REPRODUCTIVE CHARACTERISTICS OF WESTERN AND EASTERN KINGBIRDS AND SCISSOR-TAILED FLYCATCHERS BREEDING IN EASTERN KANSAS. VALUES ARE MEANS (SE, N)

Variable	Eastern Kingbird	Western Kingbird	Scissor-tailed Flycatcher
Breeding date	11 June (0.84 d, 168)	9 June (1.61 d, 19)	10 June (2.96 d, 17)
Clutch size	3.37 (0.043, 214)	4.35 (0.209, 20)	4.69 (0.120, 16)
Seasonal decline[a]	−0.026 (0.0034, 200)	−0.066 (0.0270, 19)	−0.021 (0.0085, 16)
Egg weight (g)	3.90 (0.046, 60)	3.83 (0.091, 14)	3.41 (0.086, 17)
Egg length (mm)	23.48 (0.143, 60)	23.45 (0.269, 14)	22.59 (0.203, 17)
Egg breadth (mm)	17.50 (0.067, 60)	17.45 (0.156, 14)	16.74 (0.151, 17)
Conversion factor	0.541 (0.0015, 57)	0.536 (0.0029, 7)	0.536 (0.0044, 10)

[a] Values given are regression coefficients from the least squares linear regression of clutch size on date. Y-intercepts and coefficients of determination for EKBs, WKBs and STFs, respectively, are 4.45 eggs ($r^2 = 0.233$), 5.77 eggs ($r^2 = 0.262$), and 5.57 eggs ($r^2 = 0.309$).

1986a), but periodical cicadas (*Magicicada* spp.) also emerged during the 1981 laying period (Murphy 1986a). Food was thus very plentiful, and I showed previously that clutch sizes of EKBs were largest in 1981 mainly as a result of early breeding (Murphy 1986a). Nonetheless, the only 5-egg EKB clutches and 6-egg WKB clutches were found in 1981, suggesting that food supply might have directly influenced clutch size. To investigate the potential impact of high food abundance in 1981 on the interspecific results described above, I examined residual clutch size (effects of laying date removed by the common regression equation, CLUTCH SIZE = 4.66 − 0.027DATE, $r = 0.402$, N = 235, $P < 0.001$) using a two-way analysis of variance (ANOVA; BMDP2V) with the main effects being species and year of breeding. For the latter variable, I grouped clutches from 1980, 1982, and 1983 (i.e., "normal" years) and contrasted them with 1981 (i.e., high food abundance).

Comparisons of residual clutch size among the three species and two "years" showed that species effects were again significant ($F = 55.2$, df = 2, 229, $P < 0.001$), but effects of year were not ($F = 1.87$, df = 1, 229, $P = 0.17$). However, the interaction between species and year was significant ($F = 3.23$, df = 2, 229, $P = 0.04$), indicating that the three species responded differently across "years". Pairwise species comparisons of clutch size (date-corrected) between 1981 (high food abundance) and the other years (low food abundance) showed that the only significant interaction effects was in the contrast of WKBs and STFs (two-way ANOVA, $F = 5.33$, df = 1, 31, $P = 0.028$). Mean clutch sizes did not differ between species ($F = 0.38$, $P = 0.54$), but WKBs produced larger clutches in 1981 than in other years (5.0 eggs [SD = 0.89, N = 6] compared to 4.1 eggs [SD = 0.83, N = 14]; $t = 2.25$, $P = 0.04$), whereas the nonsignificant trend was for STFs to lay smaller clutches in 1981 (4.5 eggs [SD = 0.55, N = 6] compared to 4.8 eggs [SD = 0.42, N = 10]; $t = 1.23$, $P > 0.20$).

Because of the significant year-species interaction involving 1981 for WKBs and STFs, I compared date-corrected clutch sizes between species after excluding clutches from 1981. Results indicated that in "normal" years STFs produce significantly larger clutches than WKBs (Wilcoxon Two-sample, $U_s = 102.5$, $P < 0.025$). This result held when the slightly smaller STF clutches of 1981 were included in the analysis ($U_s = 151.5$, $P < 0.025$).

Egg and clutch weight.—Conversion factors relating fresh egg weight to length and breadth (Table 2) were the same for all species ($F = 1.34$, $P > 0.05$), but average egg weights and linear dimensions varied among species (Table 2: ANOVA, $F_{\text{mass}} = 13.0$, $P < 0.001$, $F_{\text{length}} = 4.1$, $P = 0.01$, $F_{\text{breadth}} = 12.7$, $P < 0.001$). Size differences were a result of the small eggs laid by STFs (SS-STP, $P <$ at least 0.01 for all 3 comparisons). None of the comparisons between EKBs and WKBs was significant (SS-STP, $P > 0.05$). Egg sizes among EKBs exhibited significant annual variation, being largest in the year of high food abundance (1981, 4.0 g; Murphy 1986a). STFs also laid significantly larger eggs in 1981 (3.63 g, SD = 0.278, N = 6 nests) compared to other years (3.28 g, SD = 0.344, N = 11 nests; $t = 2.13$, df = 15, $P = 0.05$). WKB eggs in 1981 (3.99 g, SD = 0.103, N = 5 nests) tended to be larger than in other years (3.75 g, SD = 0.401, N = 9 nests), but the difference was not significant ($t = 1.29$, df = 12, $P = 0.23$).

Clutch and egg size varied independently in EKBs (Murphy 1983a), WKBs ($r = 0.141$, df = 12, $P > 0.5$) and STFs ($r = -0.304$, df = 14, $P > 0.50$), hence in all species total clutch weight (clutch size × mean egg mass) increased with clutch size. Given the interspecific differences in clutch and egg size (largest clutches but smallest eggs in STFs), I compared total clutch weight among species to determine if reproductive expenditures at the time of egg laying were similar. They were not (Kruskal-Wallis, $H = 20.9$, $P < 0.001$). EKBs produced the smallest clutch weight ($\bar{x} = 13.0$ g, SD = 2.71, N = 168; median = 12.6 g), followed by STFs ($\bar{x} = 15.9$ g, SD = 2.38, N = 16; median = 15.7 g), and WKBs ($\bar{x} = 16.5$ g, SD = 4.24, N = 14; median = 16.1 g). Differences between EKBs and the latter two species were significant (Wilcoxon Two Sample, $P < 0.001$ for both), but differences between WKBs and STFs were not (Wilcoxon Two Sample, $P = 0.76$). None of the conclusions changed when data from 1981 (year of high food abundance) were excluded.

Nestling growth.—Average body weight and tarsus and 9th primary lengths for days 1–14 are given in Table 3 for EKBs for 1981 and 1982. Growth data for 1980 are presented elsewhere (Murphy 1981). Statistics on nestling WKBs and STFs over the same period are presented in Table 4. General patterns of development (Murphy 1981) are very similar in all species. Differences in size at hatching (weight and tarsus length) correspond well with egg size differences (Tables 2, 3, and 4).

Despite extremely different feeding conditions (Murphy 1986a), and highly different absolute rates of weight increase across years (Table 5; ANOVA, $F = 20.8$, df = 2, 28, $P < 0.001$), weight-specific growth rate (K) did not vary with year in EKBs (Table 5; ANOVA: $F = 1.19$, df = 2, 28, $P = 0.34$). Growth rates in the year of high food abundance (1981) were only 5.6% higher than in the drought year (1980). Growth rates in the drought year and an "average" year (1982) were nearly identical (Table 5). The three year average growth rate from 31 broods ($K = 0.450$, SD = 0.0398) was also very close to the growth rate calculated from each year's average growth curve for weight (1980, $K = 0.444$; 1981, $K = 0.452$; 1982, $K = 0.455$). However, as would be predicted from the different absolute

TABLE 3

MEAN DAILY WEIGHT, TARSUS LENGTH, AND 9TH PRIMARY LENGTH OF EASTERN KINGBIRDS BREEDING IN EASTERN KANSAS FOR THE YEARS 1981 AND 1982. VALUES ARE MEANS (SD)

Age	Eastern Kingbird (1981)				Eastern Kingbird (1982)			
	N	Weight (g)	Tarsus (mm)	Primary (mm)	N	Weight (g)	Tarsus (mm)	Primary (mm)
Day 1	20	3.7 (0.52)	6.65 (0.32)	—	6	3.4 (0.62)	6.43 (0.40)	—
2	19	5.7 (0.72)	7.76 (0.40)	—	6	5.3 (1.04)	7.49 (0.56)	—
3	14	8.2 (1.03)	8.96 (0.57)	—	8	8.0 (1.16)	8.80 (0.90)	—
4	15	11.3 (1.38)	10.31 (0.87)	0.68 (0.42)	7	10.6 (1.65)	10.01 (0.81)	0.73 (0.49)
5	11	14.8 (1.72)	11.82 (0.75)	2.23 (0.66)	7	13.9 (1.74)	11.56 (1.06)	2.05 (0.86)
6	10	19.1 (1.48)	13.68 (0.47)	4.99 (0.95)	6	18.1 (1.13)	12.80 (0.38)	3.98 (0.68)
7	8	22.4 (2.61)	14.79 (1.12)	7.67 (1.81)	6	20.9 (2.70)	14.00 (1.18)	7.17 (1.14)
8	9	25.7 (1.62)	15.95 (0.64)	11.55 (1.06)	5	24.6 (0.98)	15.31 (0.31)	10.65 (1.29)
9	9	30.1 (2.87)	17.13 (0.43)	16.00 (1.34)	3	28.0 (1.33)	16.10 (0.83)	14.13 (0.74)
10	11	31.5 (1.48)	17.54 (0.69)	19.01 (2.35)	5	30.3 (1.34)	16.94 (0.37)	19.06 (1.29)
11	10	33.7 (1.57)	18.34 (0.52)	23.63 (2.16)	4	32.4 (2.08)	17.62 (0.58)	22.96 (0.42)
12	10	34.5 (1.75)	18.55 (0.49)	27.62 (2.72)	4	33.2 (1.80)	17.84 (0.68)	27.98 (0.74)
13	11	34.8 (1.43)	18.83 (0.63)	31.97 (2.43)	4	33.9 (1.15)	18.31 (0.47)	31.33 (0.51)
14	6	33.8 (1.63)	18.78 (0.58)	36.10 (1.92)	0	—	—	—

TABLE 4

MEAN DAILY WEIGHT, TARSUS LENGTH, AND 9TH PRIMARY LENGTH OF WESTERN KINGBIRDS AND SCISSOR-TAILED FLYCATCHERS BREEDING IN EASTERN KANSAS. VALUES ARE MEANS (SD)

Age	Western Kingbird				Scissor-tailed Flycatcher			
	N	Weight (g)	Tarsus (mm)	Primary (mm)	N	Weight (g)	Tarsus (mm)	Primary (mm)
Day 1	4	3.4 (0.67)	6.42 (0.19)	—	2	2.9 (0.32)	5.78 (0.25)	—
2	4	5.1 (0.81)	7.27 (0.39)	—	4	4.4 (0.37)	6.90 (0.47)	—
3	5	6.9 (0.94)	8.42 (0.46)	—	4	6.2 (0.68)	8.12 (0.45)	—
4	4	10.1 (2.48)	9.51 (1.15)	0.53 (0.60)	4	8.3 (1.21)	9.46 (0.36)	0.70 (0.62)
5	4	12.9 (1.81)	11.08 (0.84)	1.42 (0.54)	5	11.0 (1.04)	10.81 (0.30)	1.87 (0.28)
6	4	18.0 (2.00)	13.44 (0.37)	3.73 (0.61)	3	14.2 (1.43)	12.57 (0.14)	3.90 (0.53)
7	3	21.2 (3.04)	14.77 (0.83)	5.99 (0.91)	5	17.5 (1.86)	13.55 (0.27)	6.61 (0.94)
8	4	23.5 (4.13)	15.51 (1.04)	8.63 (1.18)	3	19.4 (3.04)	14.59 (0.66)	9.91 (2.12)
9	4	27.2 (3.87)	16.39 (0.90)	12.57 (1.92)	3	23.2 (2.58)	16.04 (0.11)	14.95 (1.02)
10	4	31.1 (2.97)	17.64 (0.44)	18.38 (0.93)	3	25.7 (1.57)	16.87 (0.18)	18.75 (1.60)
11	4	33.3 (1.71)	18.10 (0.53)	23.08 (1.26)	3	27.3 (3.55)	17.57 (0.26)	23.86 (0.67)
12	4	33.9 (3.30)	18.64 (0.37)	27.25 (1.21)	3	29.1 (3.87)	18.11 (0.40)	27.21 (1.45)
13	4	35.4 (2.18)	18.75 (0.48)	31.64 (1.42)	4	30.6 (4.10)	18.44 (0.41)	31.36 (1.63)
14	4	36.0 (2.27)	19.08 (0.21)	35.78 (1.83)	3	30.1 (2.90)	18.61 (0.57)	35.82 (0.36)

TABLE 5

GROWTH RATES FOR BODY WEIGHT, TARSUS LENGTH, AND 9TH PRIMARY LENGTH FOR EASTERN KINGBIRDS (EKB), WESTERN KINGBIRDS (WKB), AND SCISSOR-TAILED FLYCATCHERS (STF) BREEDING IN EASTERN KANSAS

	Weight (mean [SD])		Tarsus (mm/day)	Primary (mm/day)
Species[a]	K	g/d[b]	Mean (SD)[b]	Mean (SD)[b]
EKB 80 (N = 16)[c]	0.441 (0.045)	2.63 (0.354)	1.20 (0.044)	3.85 (0.140)
EKB 81 (N = 10)	0.466 (0.032)	3.34 (0.187)	1.24 (0.057)	3.99 (0.198)
EKB 82 (N = 5)	0.448 (0.033)	3.05 (0.098)	1.20 (0.046)	4.01 (0.061)
WKB (N = 4)	0.416 (0.029)	3.18 (0.302)	1.26 (0.112)	4.10 (0.165)
STF (N = 4)	0.394 (0.019)	2.92 (0.381)	1.20 (0.067)	4.12 (0.104)

[a] 80, 81, and 82 refer to growth rates from 1980, 1981 and 1982.

[b] Growth rate is the regression coefficient calculated from the least squares regression of weight, tarsus and primary length versus age for days 3–11.

[c] N = sample size, which refers to the number of broods from which data were collected.

rates of increase, asymptotic weights differed widely according to year (ANOVA, $F = 18.8$, df = 2, 28, $P < 0.001$), averaging only 31.5 g in 1980 (SD = 2.24, N = 16 broods) compared to 36.2 g (SD = 1.15, N = 10 broods) and 34.9 g (SD = 1.28, N = 5 broods) in 1981 and 1982, respectively. Differences in the latter two years were not significant (SS-STP, $P > 0.05$). Nestlings starved in 5 of 17 nests in which initial and final brood size were known in 1980, versus 3 of 17 nests in 1981 and 1982 (G-test, $G = 0.16$, df = 1, $P > 0.05$). Yearly conditions had no influence on EKB tarsus or primary growth (Table 5; ANOVAs: tarsus, $F = 2.37$, 9th primary, $F = 2.14$; df = 2, 28, $P > 0.10$ for both).

Because weight-specific rates of growth in EKBs were insensitive to wide changes in food abundance, I directly compared species for weight-specific growth rates (Table 5). Differences were significant (ANOVA: $F = 4.71$, df = 2, 36, $P < 0.025$). STFs and WKBs grew at similar rates, as did WKBs and EKBs (SS-STP, both $P > 0.05$), but STFs grew significantly slower than EKBs (SS-STP, $P < 0.05$). Because asymptotic weight varied with year in EKBs, and because sample sizes were small for WKBs and STFs, I did not compare species for differences in the absolute rate of weight gain or asymptotic weight. However, asymptotic weights in the latter two species were similar to EKBs (WKB: 36.6 g, SD = 3.39, N = 4 broods; STF: 33.5 g, SD = 4.03, N = 4 broods).

Comparisons of the rate of tarsus growth (Table 5) indicated that tarsi grew at the same rate in all species (ANOVA, $F = 1.49$, df = 2, 36, $P > 0.05$). On the other hand, primary growth differed (Table 5; ANOVA, $F = 4.68$, df = 2, 36, $P < 0.025$). WKB and STF primaries grew at equal rates (SS-STP, $P > 0.05$), but the primaries of both species grew significantly faster than those of EKBs (SS-STP, $P < 0.025$).

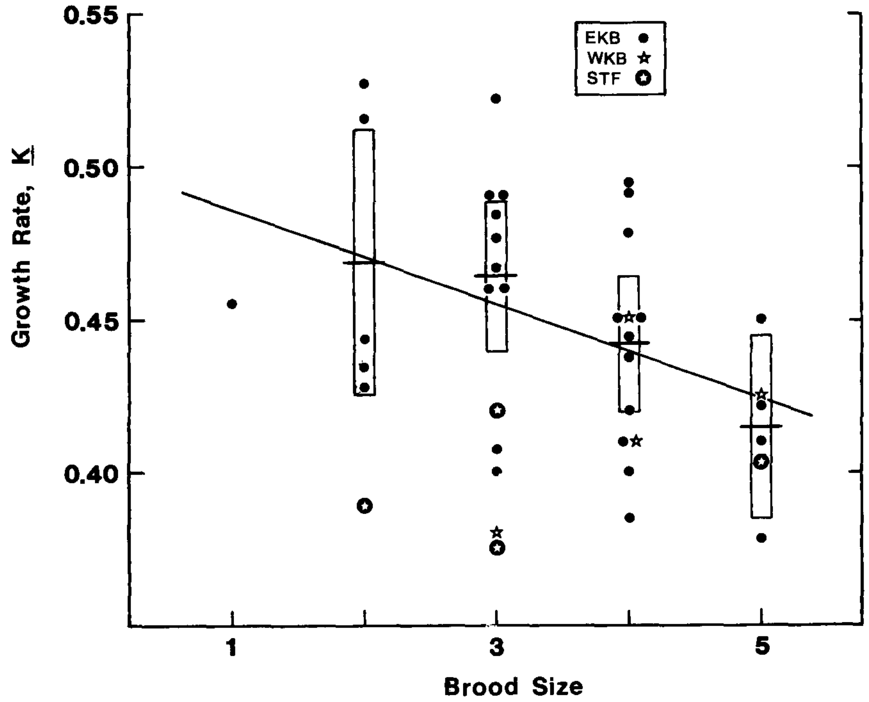

FIG. 2. Variation in the rate of nestling weight gain with respect to brood size in kingbirds. Eastern Kingbird values are indicated by the solid dots. Average growth rate of Eastern Kingbirds ±2 SE are indicated at each brood size by the horizontal line and open box, respectively. The regression equation describing the relationship between growth rate (K) and brood size (BS) for EKBs ($K = 0.503 - 0.0155\text{BS}$, $r = -0.398$, N = 31 broods, $P = 0.033$) is plotted. Observations of growth rate in individual broods of Western Kingbirds (stars) and Scissor-tailed Flycatchers (enclosed open stars) are also plotted.

Mean clutch size and mean growth rate varied inversely in these species (see Tables 2 and 5). Among EKBs brood size and growth rate also varied inversely (Fig. 2; $r = -0.398$, N = 31 broods, $P = 0.033$), especially in the drought year ($r = -0.608$, N = 16 broods, $P = 0.014$). The relationship was not significant in 1981 and 1982 ($r = -0.256$, N = 15 broods, $P > 0.10$). Three of the four WKB growth rates fell within the range of variation for EKBs at the same brood sizes (Fig. 2). Indeed, 2 of 4 points were within ±2 standard errors (SE) of the appropriate EKB mean. When matched for brood size with EKBs, 3 of 4 STFs broods tended towards slow growth (Fig. 2). The only point to fall within ±2 SE of the appropriate EKB mean was the brood of five young (Fig. 2). Thus, the slower growth of STFs did not appear to be the result of the proximate "stress" of raising more young.

DISCUSSION

Body size.—Sexual differences in body size are similar in all species: bill and tarsus lengths did not vary with sex, but wing chord and keel lengths were 3–9% larger in males than females. Body weight did not vary with sex, but this was probably a result of the high variances in weight associated with variable fat stores and growth of female reproductive tissues (e.g., Ricklefs and Hussell 1984). The absolute and relative fat content of female EKBs exceeds that of males throughout the breeding season (Murphy 1986a), but lean dry muscle weight is substantially greater in males (Murphy 1985b. Therefore, overall structural "size" is greater in male than female EKBs and probably other kingbird species as well.

Neither weight nor bill length seem useful for detecting interspecific size differences. Weights are highly variable, and bill size is likely influenced by slight differences in feeding ecology and prey characteristics. Comparisons of wing chord and tarsus and keel (nonsignificant difference) lengths suggest WKBs are the largest species. EKBs and STFs appeared to be about the same size, except that wing chords were larger in male STFs. However, I doubt that wing chord is a good estimator of body size in these species since ecological factors have probably favored different wing shapes (Leisler and Winkler 1985). I suspect that a variable such as lean dry mass must be measured to test definitively for size differences, but at present, I have little evidence of interspecific variation in size.

Timing of breeding and clutch size.—Timing of breeding was the only reproductive trait which did not differ among species (see also MacKenzie and Sealy 1981). Data presented elsewhere (Murphy 1986a, b) suggest that initiation of breeding is energy-limited in EKBs, and given the similar breeding schedules for all species, it seems likely that timing of breeding is energy-limited in the other two species as well.

Clutch size differences appear to be genetically fixed and species-specific. On average, EKBs laid about 1.3 (39%) and 1.0 (29%) fewer eggs than STFs and WKBs, respectively (Fig. 1). The WKB average includes the significantly larger 1981 clutches. Excluding 1981, average EKB clutch size was 0.7 (20.8%) eggs below that of WKBs. The latter WKB average (4.1 eggs) is similar to the value reported for WKBs in Arizona by Blancher and Robertson (1987; 3.9 eggs, SD = 0.77, N = 73; $t = 0.73$, df = 85, $P > 0.50$) and is probably a more accurate measure of normal WKB clutch size. Fitch (1950) reported significantly smaller clutch sizes for STFs in Texas (3.9 eggs, SD = 0.81, N = 16; $t = 3.46$, df = 30, $P < 0.01$). The larger clutch sizes of WKBs (nonsignificant difference) and STFs in Kansas compared to Arizona and Texas, respectively, are consistent with known latitudinal and longitudinal gradients in clutch size variation in birds

(Ricklefs 1980, Crowell and Rothstein 1981). Such trends might "explain" the difference in WKB clutch sizes between Kansas and Arizona, but the difference between Kansas and Texas for STFs seems unusually large. Independent estimates of clutch size for STFs from museum egg sets (mean = 4.6 eggs, SD = 0.65, N = 220 clutches) suggest that Fitch's (1950) estimate of clutch size is low.

Seasonal declines in clutch size occur in all three species (Table 2), and after controlling for effects of date, differences in clutch size persisted. The rate of decline in STFs (0.021 eggs/day) was similar to that of EKBs (0.027 eggs/day) and fell within the EKBs range of annual variation (Murphy 1986a). The rate for WKBs was greater (0.066 eggs/day), but did not differ statistically from either of the other species. The large WKB value probably resulted from sampling error due to small sample size as Blancher and Robertson (1987) reported a seasonal rate of decline in WKBs (0.018 eggs/day) that was much lower and closer to values for EKBs and STFs.

EKBs and WKBs appeared to respond positively to increased food abundance in 1981 by laying larger clutches. Most of the EKB response was due to earlier breeding, but after controlling for date, 1981 EKB clutches were larger than those produced in the drought year ($P < 0.05$, Murphy 1986a). Likewise, date-corrected clutch sizes of WKBs were larger in 1981 compared to other years. Unlike its congeners, STFs failed to lay more eggs in 1981. I suspect this resulted from differences in kingbird habitat use and differential availability of cicadas in each kingbird species breeding habitat. Mature trees, on which cicadas oviposit, were much more common in EKB and WKB breeding sites than in the grass-dominated habitats of STFs. Cicadas were no doubt less available to STFs than to either EKBs or WKBs. The larger STF eggs in 1981 presumably resulted from the increased availability of normal insect prey.

Egg size.—Differences in egg size were nearly as dramatic as for clutch size. Fitch (1950) commented previously that STF eggs were smaller than EKB eggs. My data confirm his statement, yet also show that STF eggs are smaller than those of WKBs. EKBs and WKBs produced eggs of nearly identical size. The small eggs of STFs are not due to small adult body size (Table 1). Small STF egg size may result from limited energy for clutch formation and trade-offs in number and size of eggs (i.e., Smith and Fretwell 1974, Lloyd 1987). This reallocation argument gains support from comparisons of total clutch weight for WKBs and STFs. Despite differences in clutch and egg size, the two species allocate very similar amounts of energy to clutch formation. However, given that small clutch size in EKBs is not matched by a further increase in egg size (compared to WKBs), I am doubtful of the applicability of the reallocation hypothesis.

Possible alternative explanations for the egg size differences are provided by a macrogeographic examination of egg size variation in EKBs. The smallest EKB eggs are produced within the geographic range of the STF, and from there egg size increases clinally with latitude (Murphy 1983a, 1985b). Small egg size in STFs may therefore reflect relaxation of selective pressures that are strong at high latitudes, and which EKBs experience regularly. One possibility is cold stress on eggs. Male kingbirds do not incubate, and large eggs at high latitudes may reduce the rate of heat loss from eggs when females are off foraging. Jarvinen and Vaisanen (1983) noted poor hatching success of small Pied Flycatcher (*Ficedula hypoleuca*) eggs at northern locations and suggested that selection for large eggs was strong at high latitudes. Alternatively, since the size of nestlings within the first week of hatching is primarily a function of the size of the egg from which they hatched (Murphy 1985a; Tables 2, 3 and 4), selection to minimize nestling heat loss may favor large eggs at high latitudes.

Nestling growth.—Pattern and rate of growth were similar in nestlings of the three species. Early size differences were determined by egg size, but as has been demonstrated for EKBs (Murphy 1985a), the influence of egg size waned as nestlings aged. Yearly variation in the growth of EKB tarsi and primaries was nonexistent despite variation in annual egg size and feeding conditions. Likewise, weight-specific rates of EKB growth did not vary with year, but did vary with brood size (Fig. 2), especially in the drought year. Asymptotic weights were also lowest in that year.

The similarity of EKB growth rates among years (Table 5), despite variable food regimes and small sample size in 1982, agrees with data for other species (Ricklefs and Peters 1979, King and Hubbard 1981) and suggests that the growth rates recorded for WKBs and STFs are sufficient for interspecific comparisons. Indeed, the rate which I calculated for WKBs in Kansas ($K = 0.416$) was very similar to the value reported by Blancher and Robertson (1984) from Arizona ($K = 0.414$). My interspecific comparisons indicated that EKBs grew significantly faster than STFs. Growth rates of only 1 of 4 STF broods fell within ±2 SE of the mean growth rate of EKBs at the same brood sizes (Fig. 2), suggesting that nestling STF growth is intrinsically slower than that of EKBs.

Interspecific differences in clutch size.—The failure of timing of breeding to account for interspecific variation in clutch size leaves open the question of why clutch size differs among such equal-sized and ecologically similar species. Interestingly, the interspecific differences are opposite of what is considered the "usual" pattern for birds (Ricklefs 1980, Crowell and Rothstein 1981). The species with the northernmost distribution, the EKB, lays the fewest eggs whereas the southernmost breeding species, the STF, produces the largest number. A possible explanation is that interspecific clutch size differences reflect adaptation to climatic variability over North America. Northern and eastern portions of the continent experience cooler temperatures and more precipitation during summer than southern and western regions of North America (Climatic Atlas of North and Central America 1979), and evidence indicates that such weather impedes kingbird foraging success (Blancher and Robertson 1987, Murphy 1987). Previous experimental brood size manipulations have also shown that unlike broods of 3, broods of 5 young grow poorly and experience heavy starvation during extended periods of cool, wet weather (Murphy 1983c). Hence, attempts to raise large broods within most of the EKB's geographic range possibly entails great risk to the survival of the parent's entire seasonal reproductive effort. Threats of this magnitude are theorized to favor the production of smaller clutches which can be raised with greater certainty (G. Murphy 1968, Stearns 1976, Boyce and Perrins 1987).

If greater exposure to environmental uncertainty has selected for smaller clutch size in EKBs compared to its congeners, then EKB clutch size should vary geographically in a manner that mimics the interspecific differences, i.e., large clutches should be produced where EKBs breed with WKBs and especially STFs. Indeed, based on museum egg sets, EKB clutches are significantly smaller in eastern North America than in western and middle portions of the continent where they breed with WKBs and STFs (Murphy 1985b). However, EKB clutch sizes are still significantly smaller than clutch sizes of sympatric populations of congeners (Murphy 1985b, this study). Furthermore, although EKB clutch size varies little with latitude, the largest EKB clutches are produced at northern sites (Manitoba and Saskatchewan), which does not conform to predictions of the environmental uncertainty hypothesis.

Why intraspecific geographic patterns of clutch size variation are of lesser magnitude than interspecific patterns is unknown. Conceivably, adaptation of EKB clutch size to local conditions may be prevented by frequent dispersal and gene flow among geographically separated populations (Slatkin 1987). However, this seems unlikely given that EKB egg size shows strong geographic differentiation that is unrelated to food availability or body size (Murphy 1983a, 1985b). I also doubt that a lack of genetic variability is a problem because all species have been recorded to lay between 3 and 6 eggs (Fitch 1950; Davis 1955; Murphy 1983a, 1985b, 1986a; Blancher and Robertson 1985a, b, 1987). Presumably, at least some of this reflects underlying genetic variability (e.g., Noordwijk et al. 1981).

Clearly, further study is needed to answer the question of why clutch size differs among these species. Of particular need are estimates of age-specific survival (Stearns 1976) and measures of dispersal and population genetic structure for all three species. The latter will permit inferences on the extent of recent past gene flow (Slatkin 1987). Parental time-budgets (see Hussell 1985) and food availability must also be measured among geographically separated populations of all three species. Finally, additional brood size manipulation experiments must be performed to assess the importance of stochastic variability in food supplies to the evolution of clutch size in the genus *Tyrannus.*

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