

## SEXUAL SELECTION AND TAIL-LENGTH DIMORPHISM IN SCISSOR-TAILED FLYCATCHERS

JONATHAN V. REGOSIN<sup>1</sup> AND STEPHEN PRUETT-JONES

Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street,  
Chicago, Illinois 60637, USA

**ABSTRACT.**—Scissor-tailed Flycatchers (*Tyrannus forficatus*) exhibit elongated tails in both sexes, and sexual dimorphism in tail length. At Fort Sill, Oklahoma, during 1991 and 1992, Scissor-tailed Flycatchers exhibited sexual dimorphism (male–female) in tail length (1.48), with more moderate sexual dimorphism in wing length (1.09) and beak length (1.04). Based on an analysis of museum specimens, immature birds (<1 year of age) of both sexes in their first calendar year exhibited significantly shorter tails than adults (measured in the field). Furthermore, tail length was highly variable among both sexes relative to other morphological traits. Male tail length was correlated with early clutch initiation by the male's mate and, in 1991, with larger clutch size. Similarly, female tail length was correlated with early clutch initiation, and, in one year, larger clutches. Longer-tailed females also tended to arrive earlier on the breeding grounds in 1992, the only year for which such data were available. Assortative mating by tail length was observed. Those findings support the hypothesis that tail length is a sexually selected trait in this socially monogamous species, and that female tail length may be correlated with measures of female quality (e.g. early arrival and breeding, large clutches). However, confounding effects of age on tail length make it difficult to distinguish among various hypotheses for evolution of elongated tails in this species. Received 27 October 1999, accepted 5 September 2000.

SCISSOR-TAILED FLYCATCHER (*Tyrannus forficatus*) are common summer residents in the south-central United States and northeastern Mexico occurring in most open habitats, including agricultural and urban areas, where there are perches for feeding and trees and shrubs for nesting (Fitch 1950, Regosin and Pruett-Jones 1995, Regosin 1998). The species' social organization is best characterized as social monogamy, with males defending large, dispersed territories, and individual males pairing with single females (Regosin and Pruett-Jones 1995). Although the female alone carries out nest building, incubation, and brooding of young, both males and females feed nestlings (Regosin and Pruett-Jones 1995).

Scissor-tailed Flycatchers (and Fork-tailed Flycatchers [*T. savana*]) of both sexes exhibit dramatically elongated tails relative to other kingbirds of the genus *Tyrannus*, and that elongation is not explained by interspecific variation in body size (J. Regosin unpubl. data). Furthermore, tail length in both Scissor-tailed and Fork-tailed flycatchers is highly sexually di-

morphic. In this study, we examined sexual dimorphism and breeding phenology in Scissor-tailed Flycatchers in an effort to document the relationship between tail-length dimorphism and the species' social organization. Here we present a quantitative analysis of tail-length dimorphism, and examine variability in tail length as it relates to various aspects of the species' life history and mating system. Our data are consistent with the sexual selection hypothesis for the evolution of tail-length elaboration and sexual dimorphism in this socially monogamous species.

### METHODS

This study was conducted from March to August during 1991 and 1992 on the range of Fort Sill Military Reservation in Comanche County, southwestern Oklahoma, in the mixed plains biotic district (Blair and Hubbell 1938). The study area consisted of four noncontiguous zones covering approximately 8 km<sup>2</sup> of mesquite (*Prosopis juliflora*) savanna dominated by little bluestem (*Andropogon scoparius*) and 1 km<sup>2</sup> of landscaped area with mowed grass and planted trees including hackberry (*Celtis reticulata*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*). An extensive system of dirt and paved roads runs through the study area. For a

<sup>1</sup> Present address: Department of Biology, Tufts University, Medford, Massachusetts 02155, USA. E-mail: jregos01@tufts.edu

complete description of the study area, see Regosin and Pruett-Jones (1995).

Nests were located through extensive searches on foot and by car. Birds were captured with mist nets set around nest trees during egg laying, incubation, and brooding periods. Birds were banded with a numbered U.S. Fish and Wildlife Service aluminum band as well as with a unique combination of three plastic, colored bands. Morphological measurements of body mass, flattened wing chord length, tarsus length, and tail length were made for each individual that was captured. All linear measurements were taken on both sides of a bird's body in 1991, but only tail length was measured on both sides in 1992. In 1992, measurements of beak length, beak width, and beak depth were also taken. In our analyses, we used measurements of left tarsus, left wing chord, and maximum tail length, unless otherwise noted.

Sex of some females could be determined at the time of banding through the presence of a vacularized brood patch. To determine sex of other banded individuals (or of unbanded birds), we relied on behavioral characteristics: singing and display behavior, nest building, copulation, egg laying, and incubation. Male Scissor-tailed Flycatchers have never been observed to construct nests or incubate eggs, and females do not engage in singing behavior or perform tumble flight displays (Fitch 1950, Smith 1966, Regosin and Pruett-Jones 1995). Only those banded birds for which sex could be determined were included in our analyses; banded birds for which we never observed display or reproductive behavior were excluded.

Because immature, hatching year (HY) birds in their first calendar year could not be captured and measured in the field, we obtained wing, tail, and tarsus length measurements from specimens at the American Museum of Natural History (AMNH) that had been collected between September–December in Texas, Mexico, and Guatemala. Specimens of HY individuals and birds in their second calendar year (SY) can be identified by shape and extent of notching of the outer (P10) primaries (Pyle et al. 1987). That criterion is reliable for individuals measured through March, but is unreliable for identifying SY individuals returning for the first time to the breeding grounds (but see Pyle 1997). At the time of the study, there were no known plumage criteria for ageing older, after-second-calendar-year (ASY) individuals.

We calculated asymmetry in tail length as the difference between the longest left tail feather and the longest right tail feather. Asymmetry values were not corrected for tail length because asymmetry was not correlated with body size (regression of asymmetry against tarsus length: males,  $n = 49$ ,  $r = 0.090$ ,  $P = 0.536$ ; females,  $n = 52$ ,  $r = 0.147$ ,  $P = 0.297$ ) or mean tail length (males,  $n = 49$ ,  $r = 0.129$ ,  $P = 0.377$ ; females,  $n = 52$ ,  $r = 0.142$ ,  $P = 0.316$ ). To examine asymmetry values for fluctuating asymmetry, we

compared the mean asymmetry value against a mean value of 0 and compared the distribution of asymmetry values against a normal distribution (Palmer and Strobeck 1986, Palmer 1994, Møller and Swaddle 1997) and tested for skewness and kurtosis. For analyses of asymmetry as it relates to aspects of life history, the absolute value of asymmetry values were used.

Data on clutch initiation date, clutch size, egg dimensions and weights, hatching date, fledging date, and brood size were collected for each nest found at which there was at least one banded adult. For nests located after egg laying began, we back-calculated to determine clutch initiation date using mean incubation period for each season and knowledge that only one egg is laid each day (Regosin and Pruett-Jones 1995). Clutch initiation dates were standardized such that day one was the first date of clutch initiation in each year.

In 1992, beginning on 26 March and before any Scissor-tailed Flycatchers had returned from the wintering ground, the study site was searched daily for returning banded birds. The date of first sighting of a given bird was treated as date of arrival for that bird. The date of 26 March is eight days earlier than the average spring date of first arrival (4 April) for Scissor-tailed Flycatchers in southwestern Oklahoma (Tyler 1979; based on data from 21 years between 1938–1974).

For analyses (those characterizing morphology and dimorphism) that combined data from both years of the study, individual birds were only used once in each analysis. In those cases, the data that we used were those from the first capture of individuals. For those analyses in which we examined correlations between morphology and reproduction or life-history traits, data from each year were analyzed separately.

## RESULTS

*Morphological variation.*—Among breeding birds, tail length was highly variable relative to other morphological traits (Table 1), with considerable overlap between sexes (Fig. 1). Male tail length ranged from 140.2 to 263.0 mm (CV = 13.6), whereas female tail length ranged from 109.0 to 185.0 mm (CV = 14.0). For both males and females, variance in tail length was significantly greater than variance in all other morphological traits ( $F$ -tests,  $P < 0.001$  in all comparisons). Tail length was not correlated with tarsus length, perhaps the best univariate measure of overall body size in birds (Rising and Somers 1989), or any other morphological trait except wing length (Table 2).

TABLE 1. Means and coefficients of variation for morphological traits of male and female Scissor-tailed Flycatchers. Sample sizes are indicated in parentheses. Traits were measured in both 1991 and 1992, except for beak measurements, which were obtained in 1992 only.

Morphological trait	Males		Females		Sexual dimorphism (male/female)
	Mean	CV	Mean	CV	
Body mass (g)	39.2 (51)	5.3	39.4 (55)	8.7	0.99
Wing length (mm)	124.4 (51)	2.9	114.3 (57)	3.0	1.09 <sup>1</sup>
Tail length (mm)	216.8 (51)	13.6	146.7 (56)	14.0	1.48 <sup>1</sup>
Tarsus length (mm)	20.1 (51)	4.0	19.98 (57)	3.3	1.01
Beak length (mm)	13.8 (30)	3.4	13.28 (34)	4.1	1.04 <sup>1</sup>
Beak width (mm)	7.4 (30)	6.3	7.55 (34)	4.2	0.99
Beak depth (mm)	6.1 (30)	4.2	6.12 (34)	5.7	1.00

<sup>1</sup>  $P < 0.001$ .

There was statistically significant sexual size dimorphism (male–female) in tail length (1.48), wing length (1.09), and beak length (1.04, Table 1). To determine whether tail-length sexual dimorphism could be explained by the observed wing-length dimorphism, an analysis of covariance (ANCOVA) was performed with tail length as the dependent variable, sex as a factor, and wing length as the covariate. The results indicate a significant tail-length sexual dimorphism, controlling for wing length ( $F$ -ratio = 23.48;  $P < 0.001$ ). Despite the overlap in wing and tail length between sexes, results of the ANCOVA suggest that males have longer tails

than females for a given wing length. When we classified any bird with tail length <190 mm length and wing length <120 mm as a female, then only 1 of 51 (2.0%) males and 0 of 56 females were misclassified.

Museum specimens of immature birds in their first calendar year (HY) exhibited significant differences in tail length between males and females ( $t = 10.74$ ,  $df = 25$ ,  $P < 0.001$ ; sexual dimorphism ratio = 1.20). Tail- and wing-length measurements of the museum specimens are presented in Table 3. Both HY males and females exhibited significantly shorter tails than their older (SY/ASY) male and female counterparts measured in the field (males,  $t = 8.75$ ,  $df = 64$ ,  $P < 0.001$ ; females,  $t = 3.75$ ,  $df = 66$ ,  $P < 0.001$ ).

We were unable to age breeding birds in the field (see methods). In 1992, however, we recaptured 11 females and 7 males originally banded in 1991. Mean tail length of recaptured birds increased 15.4 mm in males ( $SD = 28.2$ , paired  $t = -1.44$ ,  $df = 6$ ,  $P = 0.198$ ), and 8.4 mm in females ( $SD = 13.6$ ; paired  $t = -2.05$ ,  $df$

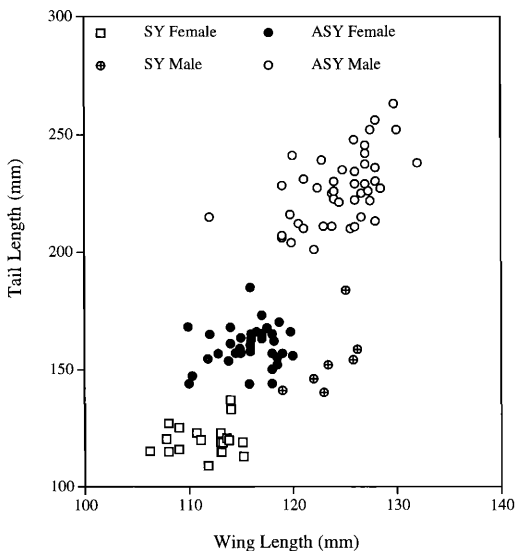


FIG. 1. Plot of cluster analysis of Scissor-tailed Flycatchers by wing length and tail length. The two fairly discrete clusters within each sex may represent distinct age classes (see text).

TABLE 2. Product-moment correlations between tail length and other morphological traits in male and female Scissor-tailed Flycatchers. Sample sizes are indicated in parentheses.

Morphological trait	Males	Females
Weight	0.108 (51)	0.230 (54)
Wing length	0.356 <sup>1</sup> (51)	0.607 <sup>2</sup> (56)
Tarsus length	0.165 (51)	-0.044 (56)
Beak length	-0.256 (30)	0.313 (33)
Beak width	-0.195 (30)	0.297 (33)
Beak depth	-0.089 (30)	0.330 (33)

<sup>1</sup>  $P < 0.01$ , <sup>2</sup>  $P < 0.001$ .

TABLE 3. Tail and wing lengths for After Second Year (ASY) and Second Year (SY) birds as determined through cluster analysis (see text) and ASY and Hatch Year (HY) birds as confirmed by field recapture or shape of the tenth (outer) primary (p10).

	Age assigned by cluster				Age confirmed by recapture or p10			
	Mean	<i>n</i>	CV	(Range)	Mean	<i>n</i>	CV	(Range)
<b>Males</b>								
Tail length	226.9	44	6.6	201.0–263.0)	234.3	7	4.9	(222.2–258.3)
Wing length	124.6	44	3.0	(112.0–132.0)	128.0	7	3.2	(122.0–133.8)
Tail length	153.7	7	9.7	(140.2–183.8)	149.5	15	4.5	(136.0–162.0)
Wing length	123.5	7	2.0	(119.0–126.2)	116.2	15	2.4	(112.0–120.0)
<b>Females</b>								
Tail length	160.2	37	5.3	(143.9–185.0)	157.1	11	3.8	(147.0–164.6)
Wing length	115.8	37	2.3	(109.9–120.0)	116.3	11	1.7	(112.5–119.8)
Tail length	120.5	19	5.6	(109.0–137.0)	124.2	12	4.1	(114.5–129.8)
Wing length	111.4	20	2.5	(106.2–115.2)	111.6	12	2.1	(108.0–116.0)

= 10,  $P = 0.067$ ). In both sexes, there was a statistically significant negative relationship between tail length in 1991 and magnitude of tail-length change between years (males:  $r = -0.924$ ,  $P = 0.029$ ; females:  $r = -0.927$ ,  $P < 0.001$ ; Fig. 2). Long-tailed birds showed little change in tail length, whereas short-tailed birds exhibited dramatic increases in tail length between years. In general, changes in wing length between years showed a similar pattern. Mean wing length of recaptured birds increased 2.8 mm in males (SD = 2.5, paired  $t = -2.96$ ,  $df = 6$ ,  $P = 0.025$ ) and 1.4 mm in females (SD = 3.0, paired  $t = -1.44$ ,  $df = 10$ ,  $P$

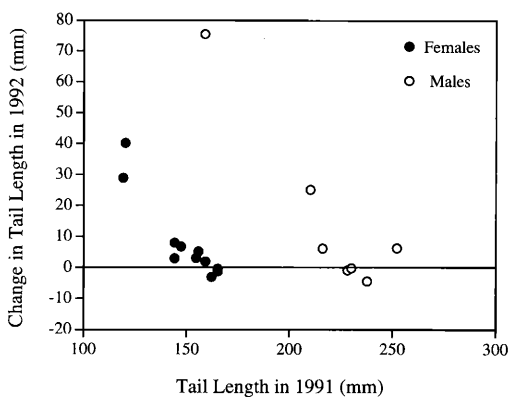


FIG. 2. Relationship between tail length of males and females in the first year of the study and the magnitude of tail length change that those individuals experienced between years.

= 0.159). There was a statistically significant negative relationship between wing length in 1991 and magnitude of wing-length change between years in females ( $r = -0.813$ ,  $P = 0.023$ ) but not in males ( $r = -0.540$ ,  $P = 0.211$ ). Nevertheless, changes in tail length and in wing length appeared to be independent of each other. There was no relationship between change in tail length and change in wing length (males:  $r = 0.289$ ,  $P = 0.530$ ; females:  $r = 0.417$ ,  $P < 0.202$ ).

The observed bimodal distribution of tail lengths, as well as the pattern of changes of wing and tail length between years, suggested the possibility of performing a cluster analysis to identify putative first-time (SY) breeders. Because we were interested in effects of tail length on breeding success independent of age (see below), we performed a "K-means" cluster analysis (SYSTAT), based on tail and wing length (Fig. 1). Mean tail lengths for putative ASY birds were similar to means of confirmed ASY birds banded in 1991 and recaptured in 1992, whereas putative SY birds exhibited measurements similar to confirmed HY museum specimens (Table 3).

*Relationship of tail length to breeding phenology and reproduction.*—Male Scissor-tailed Flycatchers arrive on the breeding grounds earlier than females, and the sex ratio remains highly skewed for about 4–6 weeks after males begin arriving (Regosin and Pruett-Jones 1995). During 1991, tail length in males was negatively

TABLE 4. Product-moment correlations between tail length and other traits of male and female Scissor-tailed Flycatchers. Sample sizes are indicated in parentheses.

Year and trait	Males		Females	
	<i>r</i>	<i>P</i> <	<i>r</i>	<i>P</i> <
	<b>1991</b>			
Egg laying date	-0.781 (22)	0.001***	-0.728 (26)	0.001***
Clutch size	0.413 (21)	0.063	0.439 (24)	0.032***
Fledging success	0.059 (20)	0.806	-0.047 (25)	0.822
	<b>1992</b>			
Egg laying date	-0.367 (24)	0.077	-0.521 (25)	0.008**
Clutch size	0.098 (19)	0.690	-0.332 (18)	0.178
Fledging success	0.112 (23)	0.609	-0.192 (22)	0.392

correlated with their mates' clutch initiation dates (Table 4). That relationship was also negative but not significant in 1992 (Table 4). Longer-tailed males tended to obtain mates that initiated egg laying earlier in the breeding season. Similarly, tail length in females was negatively correlated with clutch initiation date in both years of study (Table 4). Longer-tailed females produced larger clutches in 1991, but not 1992 (Table 4).

During 1991, but not 1992, clutch initiation date for a female's first clutch of the season was negatively correlated with clutch size (Table 5). In addition, considering those pairs that made multiple nesting attempts (all of which failed because of depredation or weather-related events), there was a strong negative correlation between clutch initiation date for the first clutch of the season and number of nesting attempts in both 1991 ( $r = -0.939$ ,  $n = 7$ ,  $P = 0.002$ ) and 1992 ( $r = -0.795$ ,  $n = 18$ ,  $P < 0.001$ ; Fig. 3). However, no direct correlation was detected between clutch initiation date and fledging success (Table 5).

We can correct for relative age of birds in some analyses. First, birds banded in 1991 that returned to the study site in 1992 were at least two years old (ASY). For that subset of birds,

clutch initiation date was correlated with their arrival date (Table 5). Furthermore, among ASY females, longer-tailed individuals tended to arrive earlier on the breeding grounds ( $r = -0.785$ ,  $n = 6$ ,  $P = 0.064$ ) although no such correlation was detected for males ( $r = -0.073$ ,  $n = 6$ ,  $P = 0.891$ ). Second, we combined data from both years but deleted putative SY birds from the analysis. For that sample, the negative correlation between tail length and clutch initiation date remained significant for males ( $r = -0.418$ ,  $n = 39$ ,  $P = 0.008$ ), but not females ( $r = -0.154$ ,  $n = 31$ ,  $P = 0.407$ ). Again considering only putative ASY females, there was a tendency for females laying early clutches (egg-laying date) to have larger clutches (size of first clutch;  $r = -0.400$ ,  $n = 22$ ,  $P = 0.065$ ).

*Assortative mating.*—Combining data from both 1991 and 1992, but counting each pair only once, males always exhibited longer tails than their mates, and birds mated assortatively by tail length ( $r = 0.477$ ,  $n = 30$ ,  $P = 0.008$ ; Fig. 4). If, however, putative SY birds are deleted from the analysis, the significant correlation between tail length in males and that of their social mates disappears ( $r = 0.233$ ,  $n = 27$ ,  $P = 0.242$ ). Thus, assortative mating occurs across

TABLE 5. Product-moment correlations between egg laying date (the first egg of the first clutch) and other aspects of seasonality and reproduction. Sample sizes are indicated in parentheses.

Trait	1991		1992	
	<i>r</i>	<i>P</i> <	<i>r</i>	<i>P</i> <
Date of arrival				
Males	—	—	0.612 (10)	0.060
Females	—	—	0.850 (11)	0.001***
Clutch size	-0.387 (31)	0.032*	-0.198 (26)	0.332
Fledging success	-0.152 (30)	0.423	-0.033 (27)	0.870

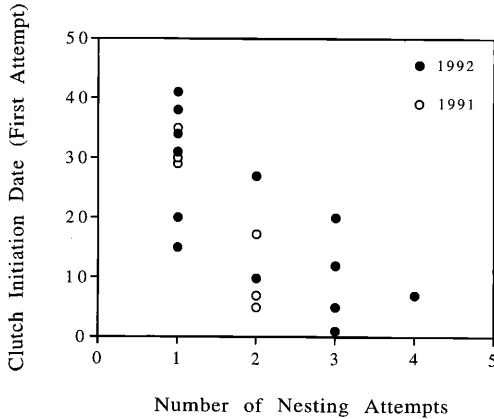


FIG. 3. Plot of clutch initiation date versus number of nesting attempts that reached at least the egg laying stage for pairs that did not nest successfully in a given breeding season. Data from both 1991 and 1992 are plotted. Pairs that initiated breeding early re-nested significantly more frequently (see text).

age categories (SY vs. ASY) but does not within each age group.

*Fluctuating asymmetry.*—The mean signed tail asymmetry value for males and females combined was 0.340 (SD = 3.95,  $n = 97$ ), which was not significantly different from 0 ( $t = 0.847$ ,  $df = 95$ ,  $P = 0.399$ ). The frequency distribution of tail asymmetry did not differ from a normal distribution (Shapiro-Wilk  $W = 0.985$ ,  $P > 0.900$ ), indicating that asymmetry in tail length in Scissor-tailed Flycatchers is correctly classified as fluctuating asymmetry rather than directional symmetry or antisymmetry.

Examining fluctuating asymmetry in males and females separately, the mean signed fluctuating asymmetry was 0.478 (SD = 4.078,  $N = 46$ ) and 0.216 (SD = 3.879,  $N = 51$ ) for males and females, respectively (differences not significant;  $t = -0.263$ ,  $df = 95$ ,  $P = 0.746$ ). Fluctuating asymmetry did not correlate with tarsus length in either sex (males:  $r = 0.090$ ,  $n = 49$ ,  $P = 0.536$ ; females:  $r = 0.147$ ,  $n = 52$ ,  $P = 0.297$ ). Also, fluctuating asymmetry did not correlate with fledging success, clutch initiation date, or clutch size for either males or for females (1991,  $P > 0.20$  in all regressions; 1992,  $P > 0.30$  in all regressions).

#### DISCUSSION

Scissor-tailed and Fork-tailed flycatchers are unique among species within the genus *Tyr-*

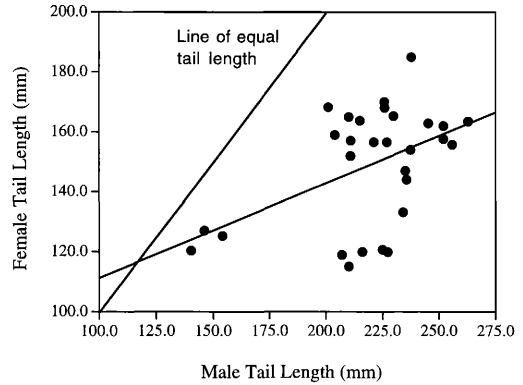


FIG. 4. Regression of male tail length against the tail length of his mate, showing assortative mating by tail length. Assortative mating is not statistically significant when the three outliers to the lower left, which may have been second-year birds, are deleted (see text).

*annus* in that both species show greatly elongated tails in males and females as well as significant dimorphism in tail length between sexes. Fork-tailed Flycatchers have yet to receive detailed study, and the present study represents the first analysis of dimorphism in the Scissor-tailed Flycatcher. Because an accurate phylogeny is not yet available for *Tyrannus*, it not possible to speculate whether dimorphism and tail elongation in those two species evolved once or twice within the genus.

Male Scissor-tailed Flycatchers had tails that were approximately 50% longer than those in females. Nevertheless, tail length in females is elongated relative to other species in the genus *Tyrannus* (except *T. savanna*) and tail length in the Scissor-tailed Flycatcher can thus be said to be partially sex limited (Cuervo and Møller 2000). As is true for other species exhibiting partial sex limitation in dimorphism of ornamental feathers (Cuervo and Møller 2000), Scissor-tailed Flycatchers are socially monogamous and males participate in parental care of offspring. In addition to having significantly longer tails than females, male Scissor-tailed Flycatchers also had significantly longer wings than females. As shown by Balmford et al. (1994), wing dimorphism correlates with tail dimorphism across species within long-tailed families of birds. Larger wings in long-tailed species may evolve as an adaptation to compensate for the aerodynamic costs associated with long tails (Evans and Thomas 1992, Balm-

ford et al. 1994, Møller 1996). Henderström and Møller (1992) and Møller (1996) list other examples of cost-reducing traits that may compensate for high costs of secondary sexual characters.

Tail length in both male and female Scissor-tailed Flycatchers was highly variable, with coefficient of variation (CV) values two to three times greater than for other morphological traits. Phenotypic variation is commonly much larger in secondary sexual characters than other morphological traits (Alatalo et al. 1988, Barnard 1991, Møller and Höglund 1991, Fitzpatrick 1997) although the evolutionary reasons for that pattern are still unclear. As reviewed by Møller (1994), two alternative explanations for the trend of increased phenotypic variance in secondary sexual traits are (1) an interaction between stabilizing and directional selection, and (2) selection for condition-dependence in secondary sexual traits.

Besides the dimorphism in wing and tail length, male and female Scissor-tailed Flycatchers were significantly dimorphic in beak length, with males having longer beaks. We did not quantify diet of males and females in this study, but sexes are known to exhibit differences in foraging modes and foraging location (reviewed by Regosin 1998). Those differences, plus the combined differences in wing, tail, and beak length between males and females may be indicative of different diets between sexes. Sexual dimorphism may evolve through natural selection for sex differences in feeding structures if those differences facilitate a niche divergence between males and females (Selander 1966; reviewed by Hedrick and Temeles 1989; Andersson 1994). Our data do not permit a test of the niche divergence hypothesis for sexual dimorphism in the Scissor-tailed Flycatcher and we acknowledge that this represents a limitation to our understanding of sexual dimorphism in this species.

Natural selection also influences tail length in Scissor-tailed Flycatchers through the obvious aerodynamic function of tails. Aerodynamic studies of tail length and shape in birds (Balmford et al. 1993, Thomas 1993, Nordberg 1994, Thomas and Balmford 1995, Evans and Thomas 1997) have shown that forked tails are optimal in shape relative to graduated or pin shaped tails. Those authors argue, either directly or indirectly, that selection for aerody-

namic efficiency may be sufficient to explain evolution of elongated forked tails. Nevertheless, an aerodynamic natural selection hypothesis for forked tails does not explain why species with forked tails exhibit sexual dimorphism in tail length, particularly in species like Scissor-tailed Flycatchers in which males and females are similar in body size (cf. Henderström 1995, Møller et al. 1998). Furthermore, in species like Scissor-tailed Flycatchers with deeply forked tails, in which the outer tail feathers are greater than twice as long as the inner retrices, tail shape is aerodynamically sub-optimal (Thomas 1993, Evans and Thomas 1997). Thus, although natural selection through aerodynamic efficiency may be important with respect to the general shape of the tail in Scissor-tailed Flycatchers (forked vs. graduated or pin-tailed), it cannot explain the degree of elongation of the tail in males or the degree of dimorphism.

The evidence that tail length in both male and female Scissor-tailed Flycatchers is sexually selected and that there is mutual mate choice is circumstantial. Tail length increased with age in both males and females, at least between SY and ASY birds. Such age-related changes are not predicted under a natural selection hypothesis (either for niche divergence or aerodynamic efficiency) for tail-length exaggeration. Furthermore, there was significant assortative mating by tail length. Both males and females appeared to prefer to mate with longer-tailed individuals. The observation of assortative mating could be due to patterns of active choice by males and females, or it could result from the fact that tail length in females is correlated with their arrival date on the breeding grounds. If longer-tailed males (presumably older males) were the first individuals to pair each season, the result would be assortative mating by tail length. Those alternatives are simply different mechanisms leading to the same outcome—longer-tailed individuals of each sex being more likely to be paired with each other, and both are possible under the hypothesis of mutual mate choice. Regosin and Pruett-Jones (1995) present other behavioral data that suggests that female Scissor-tailed Flycatchers actively choose among males when deciding on which territory to settle.

Tail length in males and females was also indirectly related to aspects of fecundity. As pre-

dicted by the Darwin-Fisher hypothesis for sexual selection in monogamous birds (Darwin 1871, Fisher 1930, Price et al. 1988, Kirkpatrick et al. 1990), longer-tailed males mated with females that nested earlier, and in one year, earlier nests were associated with larger clutches. Longer-tailed males may gain a fitness advantage from early nesting both through increased fecundity of their mates and through an increased opportunity for multiple nesting attempts following nest failure.

There are some indications that tail length may be correlated with increased fecundity or other aspects of female quality. Longer-tailed females tended to arrive earlier on the breeding grounds, and female tail length was negatively associated with clutch initiation date. In 1991 only, female tail length was correlated with clutch size of first nesting attempts.

The negative relationship between tail length and clutch initiation dates in both males and females may be a result of younger, shorter-tailed birds initiating breeding late in the season as first-time breeders. With putative SY birds deleted from the analysis, however, the correlations between tail length and clutch initiation date remained significant for males, and tail length was negatively correlated with arrival date for ASY females. Because of the strong relationship between relative age and tail length, we cannot distinguish between the hypothesis that tail length is simply an indicator of age and the possibility that tail length indicates aspects of male or female quality independent of age. Our data suggest that tail length in both males and females may be a reliable indicator of age up to two years of age (ASY), but possibly not for older aged birds.

Our observation of wing and tail length increasing with age (SY vs. ASY) in Scissor-tailed Flycatchers is a common pattern in passerines (e.g. Fugle and Rothstein 1985, Rothstein et al. 1986, Møller 1994, see measurements in Pyle 1997) and leads to a strong confounding effect of age on analyses such as ours of reproductive success and life-history traits. Age-related differences in morphology are most obvious between SY and ASY individuals, but it may also play an important role in older birds (ASY individuals only) if age is associated with behavioral differences. Furthermore, we identified putative SY birds in our study by comparison of their measurements to confirmed HY mu-

seum specimens (see above). Although measurements of putative SY birds at our field site were similar to those of museum specimens of HY individuals, any geographical variation in size in the Scissor-tailed Flycatcher complicates that comparison; however, it does not influence our analyses of reproduction and life history of just ASY individuals.

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