



Size, ornamentation, and flight feather morphology promote within-pair paternity in a sexually dimorphic passerine

Diane V. Roeder^{1,2,3} · Michael S. Husak¹ · Michael T. Murphy⁴ · Michael A. Patten^{2,3}

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Abstract

Morphology in sexually dimorphic species is related to increased opportunity for sexual selection when traits reflect individual quality. In socially monogamous species, it may function to increase variance in reproductive success if exaggerated traits are related to the opportunity to engage in extra-pair paternity (EPP). Nonetheless, it is poorly understood if ornamental versus functional traits are differentially related to the distribution of paternity across individuals. We examined EPP in the Scissor-tailed Flycatcher (*Tyrannus forficatus*), a sexually dimorphic suboscine passerine, to determine how flight feather morphology (both ornamental and related to flight performance), ornamental coloration, and flight performance were related to paternity for males and females. We assessed paternity at 140 nests across 7 years and found that 73% of nests contained extra-pair young with 59% of nestlings resulted from extra-pair fertilizations. Males that secured paternity with their social mate had larger size (wing chord and tail length), better body condition, and more exaggerated ornamental traits (color, primary notch, and streamer length) than cuckolded males. When compared directly to the social males they cuckolded, however, cuckolders had shorter primary notches and had duller coloration. Elongated flight feather features were associated with greater maneuverability during flight, and longer primary notches and tail streamers were associated with maintenance of within-pair paternity, possibly via flight displays. Females that cuckolded their mates had less exaggerated flank coloration but better body condition than those that did not. We posit that in this system, there is a lack of strong selection on extra-pair mate morphology; rather, high-quality males maintained WPP while females in good condition were more likely to cuckold social males of poorer quality, signaling a role of reciprocal selection in extra-pair mate choice. Determinants of the frequency and extent of extra-pair paternity are central to our conception of mating systems, population genetics, and sexual selection. Morphological determinants can influence faithfulness to a mate and are a key aspect of locomotion, limiting or enhancing an individual's ability to interact with others. We examined how ornamental (coloration and tail streamers) and functional traits involved in flight (wing and tail structure) correlated with cuckoldry. Male condition, size, and ornamental traits were negatively associated with cuckoldry; yet, social males were

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✉ Diane V. Roeder
droeder@cameron.edu

¹ Present address: Department of Agriculture, Biology, and Health Sciences, Cameron University, 2800 W Gore Blvd, Lawton, OK 73505, USA

² Oklahoma Biological Survey, University of Oklahoma, 111 E Chesapeake Street, Norman, OK 73019, USA

³ Ecology and Evolutionary Biology Program, Department of Biology, University of Oklahoma, 730 Van Vleet Oval Room 314, Norman, OK 73019, USA

⁴ Department of Biology, Portland State University, 1719 SW 10th Avenue Room 247, Portland, OR 97201, USA

cuckolded by males of poorer quality. Flight feather characteristics were positively associated both with flight performance and maintenance of paternity, suggesting a role of flight in cuckoldry. Female body condition was related to cuckoldry and perhaps indicates reciprocal choice by males for healthy extra-pair mates. We posit a lack of strong selection on extra-pair mate morphology in this system; rather, high-quality males maintained WPP while females were more likely to cuckold social males of poorer quality.

Keywords Cuckoldry · Sexual selection · Flight performance · Asymmetry · Color · *Tyrannus forficatus*

Introduction

Reproductive success is driven in large part by the mating system of a species, which ultimately determines patterns of

gene transmission across generations (Emlen and Oring 1977). In lekking and polygamous species, only some individuals are able to reproduce, causing strong competition for mating opportunities and high variance in reproductive success. Conversely, most individuals in monogamous systems reproduce so competition for mating opportunities is weak and variance in reproductive success is low (Emlen and Oring 1977). However, it is now well recognized that social reproductive systems are not always representative of genetic systems (Griffith et al. 2002). In socially monogamous species, for example, individuals may engage in extra-pair mating to increase their own reproductive success, thereby increasing variance in reproductive success and generating more intense sexual selection pressure across males (Webster et al. 2007).

Sexual infidelity and extra-pair paternity (EPP) are common in socially monogamous birds (Griffith et al. 2002; Westneat and Stewart 2003). The evolutionary benefit of EPP to males is clear; males can increase their reproductive success without the costs of providing parental care, particularly when they can also maintain paternity in their own nests (Dolan et al. 2007). In some cases, males not only lose paternity in their own nests, but are also unable to secure extra-pair copulations (EPCs), leading to low reproductive success. These two opposing scenarios lead to high variance in reproductive success within populations (Dolan et al. 2007; Lebigre et al. 2013).

Benefits to females are more contentious, but a number of studies provide evidence for adaptive consequences of EPP. When females are not coerced into EPCs, benefits have been attributed to fertility insurance (Sheldon 1994; Slatyer et al. 2011; cf. Morrow et al. 2002), access to male-guarded resources (Griffith et al. 2002), or, indirectly, increased embryo survival (Kempnaers et al. 1999), higher fitness (Jennions and Petrie 2000; Gerlach et al. 2012; cf. Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007), and increased heterozygosity of young (Jennions and Petrie 2000; Arct et al. 2015; cf. Hsu et al. 2014). Females may also engage in EPCs with extra-pair males to increase uncertainty in paternity and thus create a cooperative neighborhood in which many males respond together to potential predators because each has young in multiple nests (Eliassen and Jørgensen 2014).

Ultimate benefits aside, it has been argued that females select extra-pair mates that are healthy (Podmokła et al. 2015; Whittingham et al. 2015), experienced (Tarof et al. 2012; Ramos et al. 2014), and have more exaggerated sexually dimorphic traits (Bitton et al. 2007). These qualities may allow males to secure within-pair paternity (WPP) or to coerce EPCs (Cleasby and Nakagawa 2012). Males may benefit from assessing extra-pair female mates on the basis of similar qualities (Hill 1993; Amundsen et al. 1997; Pryke and Griffith 2007; Moreno et al. 2015) to ensure that EPC attempts are worth the risk if multiple mating depletes sperm (Birkhead

and Fletcher 1995), increases risk of contracting disease (Sheldon 1993; Westneat and Rambo 2000), or results in damage to sexual ornaments when social males defend their mates (Mays and Hopper 2004). If males coerce EPCs, then they should be successful most often with small, young, or less agile females unable to escape pursuit (Low 2005). If EPCs are the result of reciprocal selection, cuckoldry should involve females that are more experienced breeders and in good condition (Amundsen et al. 1997). Regardless of whether cuckoldry is driven by females or males, sexual selection should favor a similar suite of traits in males successful at maintaining WPP and gaining EPCs. It should, however, result in two opposing sets of traits for females that participate in EPCs, depending on whether they participate via coercion (i.e., less experience and characteristics that make it more difficult for females to escape coercion) or choice (i.e., greater experience and characteristics that allow females to escape mate guarding).

If traits that help a male to gain paternity are costly ornaments, then those traits are expected to serve as honest signals of quality (Evans 1993; Pryke and Andersson 2005). Good body condition in birds with exaggerated ornaments may signal quality in both developmental and disease-resistance pathways (Whittingham et al. 2015) as well as in foraging performance and predator evasion (Møller 1993; Brown and Brown 1998). For example, sexual selection drives colorful plumage in sexually dimorphic species via intra- or intersexual selection for brighter colors (Møller and Höglund 1991; Dunn et al. 2015) in healthier individuals (Whittingham et al. 2015). When ornaments are feathers of exaggerated length, size, or shape, competition for paternity will select for further exaggeration if they are honest signals (Pryke and Andersson 2005), even if some signals vary over time (Chaine and Lyon 2009). Yet, bilateral ornaments such as elongated tail feathers or sound-producing wing feathers must still function in flight. Elongated tail feathers have been shown to increase lift and subsequent flight performance (Norberg 1994; Hedenström 1995). Birds with long, symmetrical ornaments should perform better during flight (Evans 1993; Thomas 1993), be favored during intrasexual contests and intersexual mate choice (Møller 1991, 1993), be better able to provision and protect nestlings, and survive longer via higher foraging efficiency (Brown and Brown 1998). If flight feather morphology signals individual quality or shapes a male's ability to successfully pursue or a female's ability to evade EPCs, we should expect morphology important for flight to also play a role in EPP.

The link between sexual and natural selection on ornamental morphology seems clear, yet no studies have concurrently investigated whether the morphological characteristics involved in cuckoldry are also those involved in flight. We used a breeding population of the sexually dimorphic and socially monogamous Scissor-tailed Flycatcher (*Tyrannus forficatus*)

to investigate how coloration, flight feather morphology, and body condition were related to cuckoldry by females and whether social males differed from extra-pair cuckolders. We also investigated the relationship between flight feather morphology and flight performance, such as obstacle navigation success and in-flight collisions. We made four predictions: (1) population-wide, males in poor condition and with dull coloration, relatively short flight feathers, or asymmetrical tails will be cuckolded more often than males with brighter coloration, longer flight feathers, and more symmetrical tails; (2) when directly compared to their extra-pair cuckolders, cuckolded males will be in poorer condition and have duller color, shorter flight feather characteristics, or more asymmetrical tails; (3) if females are subject to mate guarding, females in poor condition and with dull coloration, short flight feather features, or asymmetrical tails will cuckold social mates less often than those in better condition and with longer flight feathers or more symmetrical tails, however, this will be reversed if coercion by males can control EPCs; and (4) morphology associated with cuckoldry and extra-pair mate selection, such as longer flight feathers and symmetrical tails, will be associated with enhanced flight performance.

Methods

Study species

The Scissor-tailed Flycatcher is a suboscine passerine with high rates of EPP (66% of nests and 49% of nestlings; Roeder et al. 2016). Adult males are of similar mass (49.2 g vs. 49.4 g; Regosin and Pruett-Jones 2001) and wing chord (male range = 110–129 mm; female range = 105–120 mm; Pyle 1997) as females. Feather features tend to be dimorphic, however. Males have brighter salmon-colored flanks and redder axillaries (underwing feathers) than females (Pyle 1997). Both sexes have forked tails, but males have longer outer tail feathers (second year (SY) or older: male range = 190–265 mm; female range = 145–182 mm; Pyle 1997). Wing feather and tail feather asymmetry is uncorrelated with tail length (Regosin and Pruett-Jones 2001). The outermost primary is emarginated on the trailing edge of the feather tip (here called the primary notch), with notch deeper in males (SY or older: male range = 19–22 mm; female range = 10–15 mm; Pyle 1997).

Male breeding flight displays consist of a vertical zig-zag flight in which males call, rapidly flap their wings, and snap their tails open at the top and bottom of each zig-zag. Males produce a buzzing sound during displays associated with rapid wing beats (Smith 1966) that may be produced by their exaggerated primary notch (DVR pers. obs.). Calls and displays are assumed to be important for mate choice, yet they may function in male-male interactions because they continue

throughout the breeding season. Both sexes are strongly territorial and forage and search for nest material primarily in their own territories, although each will foray off-territory when resources are scarce (Regosin 2003). Pairs defend territories that range in size from 0.2–0.4 ha and breeding densities range from 0.5–3.3 pairs/10 ha (Regosin 2003). Females build nests and incubate eggs without male assistance, but both sexes provision young until several weeks post-fledging (Regosin 2003). Median clutch size range-wide is 5 eggs (range 3–6, with 3 or 6 egg clutches occurring only rarely; Regosin 2003), with 87% of fully incubated eggs successfully hatching (Regosin 2003). Nest success is low, with 28% of nests fledging an average of 3.2 young per nest (Regosin and Pruett-Jones 1995).

Study area

Data were collected from April to August of 2008–2014 at the Wichita Mountains Wildlife Refuge (34.747902 N, –98.676882 W) and the adjoining Fort Sill Artillery Base (34.662277 N, –98.562584 W) in Comanche County, Oklahoma. The refuge is 59,020 ha mixed-grass prairie broken by low-lying mountains and riparian corridors composed of oaks (*Quercus* spp.), American elms (*Ulmus americana*), and eastern redcedars (*Juniperus virginiana*). It has minimal human impact in the form of several paved roads, a game fence that runs its length, and hiking trails. Fort Sill is primarily mesquite (*Prosopis glandulosa*) savannah dominated by a mix of native grasses and Johnsongrass (*Sorghum halepense*). Fort Sill's West Range is used for artillery and ground troop exercises and is maintained in a savannah-like state through clearing brush with bulldozers and prescribed fire. It is divided into mile-sections by regularly traveled gravel and paved roads and a fence runs the length of the southern boundary of the artillery range (~18 km). Main human impacts are through vegetation maintenance, foot and artillery exercises, and hunting. Roughly 1810 ha of this range was available for use during this study.

Field methods

We found flycatcher nests by walking appropriate habitat or by sighting birds returning to the nest. Nest locations were recorded with a Garmin 60CSX GPS unit and monitored following standard protocols (Ralph et al. 1993). When nestlings were ≥ 5 days of age, we attempted to capture parents by setting up mist nets around nest trees. We used predator models and vocalization recordings as lures. All captured adults were given a United States Fish and Wildlife Service aluminum leg band and a unique color combination of Darvic leg bands. We used color bands to confirm nest parent identity by observing combinations on birds attending the nest after banding. All nestlings were fitted with a single aluminum

band. We did not color band nestlings because natal philopatry was low (Becker et al. 2018). We collected blood samples from nestlings at 5 days of age or older and from all adults upon capture (50 μ l from adults and 25 μ l from nestlings) by puncture of the brachial vein with a sterile 22-gauge needle. Blood was drawn into a heparinized capillary tube, transferred immediately to a 1.5-ml Eppendorf tube with Longmire's buffer (Longmire et al. 1997), and refrigerated later. If eggs failed to hatch, we collected them when possible and sampled any embryo tissue present ($n = 6$). Because brood reduction via depredation was common, we sampled fewer nestlings than were hatched at $\sim 21\%$ of nests.

Morphological measurements

We recorded body mass to the nearest 0.1 g and measured morphology of all captured adults following Leisler and Winkler (1991) on each side of the body, where applicable. Non-feather measurements were taken with calipers to the nearest 0.1 mm and included culmen length (tip of bill to base of skull), culmen depth and width (at proximal tip of nostril), and tarsus length (notch at back of intertarsal joint to distal end of last complete scale on tarsus). For each side of the body, feather measurements were taken with a wing rule to the nearest 0.5 mm. Wing measurements included flattened wing chord, 9th primary notch depth (from tip of primary to point on feather when the curve switches from angling towards the rachis to angling towards the feather tip), and Kipp's distance (distance from the tip of the first secondary to the tip of the longest primary on a folded wing; Swaddle and Lockwood 2003). Kipp's distance is an important component of wing aspect ratio and indicates wing pointedness (Leisler and Winkler 1991). Longer Kipp's distances are related to faster and more efficient flight, shorter distances, and rounder wingtips with greater thrust and maneuverability (Leisler and Winkler 2003; Dawideit et al. 2009). Length of each tail feather was measured from insertion to tip of each feather. Tail feather lengths were divided into three categories: overall tail length, length of the central six rectrices that are likely to provide most of the lift necessary for flight (i.e., functional rectrices), and the length of the tail streamers that extend beyond the functional surface on the outermost three rectrices on each side of the body (i.e., tail ornaments). We averaged both sides for character length except for the overall tail length because individual feathers overlay to create a single visual signal when a bird is perched. We also calculated tail asymmetry by calculating the difference in the length of the longest tail feather on each side of the body. We used the residuals of a regression of body mass onto wing chord, by sex, as an index of body condition (Brown 1996). We measured the intensity, hue, and saturation of the axillaries and flank using a Konica-Minolta CR-400 handheld chroma meter in 2013–2014. This meter records the average of three measurements for colors

along a light to dark axis (L^*), blue to red axis (a^*), and green to yellow axis (b^*). Any time an adult was recaptured, all morphology was re-measured and used for nesting attempts made during that season. If individuals were not recaptured but were resighted, prior measurements were used. All measurements were blinded in the sense that we could not know in advance which males or females would engage in extra-pair behavior.

Flight measurements

In 2013–2014, we measured flight performance by constructing a portable flight tunnel through which birds were flown (Fig. 1). The flight tunnel (1.2 m \times 1.2 m \times 8.5 m) was framed with PVC pipe and covered in black shade cloth to allow enough light penetration to film. Birds were released into the entrance and had to navigate an obstacle, a 0.2-m-wide mesh panel stretching from top to bottom placed 1.8 m from the entrance. Two 0.4-m-wide panels were set 0.1 m behind and on either side of the first panel. This left an angled opening on either side of the center mesh panel that was narrower than the birds' wingspan, so a bird had to maneuver or tuck its wings to pass between the obstacles. Birds flew to the exit at the opposite end of the flight cage and were allowed to fly away. Flight was filmed by high-speed cameras (64 fps) mounted on each end of the flight cage, to the side of the obstacle, and above the obstacle. We evaluated maneuverability as both (1) obstacle navigation, scored as successful if a bird flew through without any break in forward motion and failed if a bird collided with the obstacle in a manner that stopped forward progress, and (2) hits on the obstacle (Swaddle et al. 1996), assessed as minor if a bird brushed lightly against an obstacle or major if the body, bend of wing, or tail hit an obstacle in a manner that altered the bird's flight path.

Molecular methods

DNA was isolated from blood samples and unhatched embryos with a QIAGEN DNeasy extraction kit (Qiagen, Valencia, CA: #69504). Putative sex of each bird was confirmed following Fridolfsson and Ellegren (1999). We amplified eight microsatellite loci for parentage analysis (Roeder et al. 2016) using polymerase chain reaction (PCR) in a 25 μ l with Type-It Microsatellite PCR Kits (Qiagen, Valencia; #206243). We used non-labeled reverse primers and forward primers labeled with a universal M13(-21) tail that allowed us to incorporate different fluorescent dyes as necessary during multiplexing (Schuelke 2000). PCR conditions were initial denaturation at 95 $^{\circ}$ C for 15 min; 25 cycles of 94 $^{\circ}$ C for 30 s, 59 $^{\circ}$ C for 90 s, and 72 $^{\circ}$ C for 60 s; 15 cycles of 94 $^{\circ}$ C for 30 s, 53 $^{\circ}$ C for 90 s, and 72 $^{\circ}$ C for 60 s; and a 60 $^{\circ}$ C final extension for 30 min. Amplified PCR fragments were separated by capillary

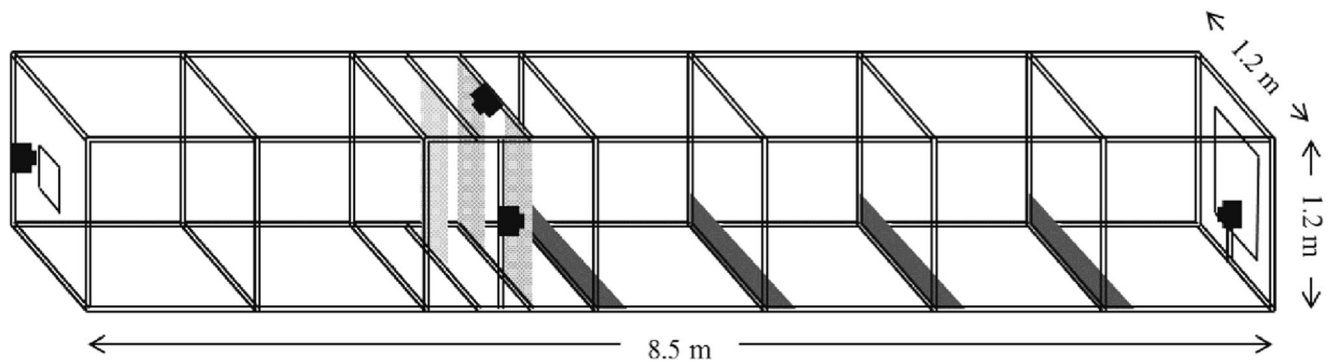


Fig. 1 Schematic for the flight tunnel with measurements, obstacle location, and camera locations. Obstacles are light gray panels set 3 m from the entrance. GoPro cameras are indicated by the black camera icons and were placed at the entrance (left side) and exit (right side), as well as

above and to the side of the obstacle. Mirrors are indicated in dark gray in the last four sections of the cage. Mirrors were angled such that the PVC frame directly above each was reflected and filmed by the camera at the exit of the flight tunnel

electrophoresis using an ABI 3730 DNA Sequencer and analyzed using Peak Scanner 2 (Applied Biosystems, Inc., Foster City, CA).

Parentage assessment

Parentage assignments were carried out using the maximum likelihood method in CERVUS 3.0.7 (Kalinowski et al. 2007). All loci were in Hardy-Weinberg equilibrium and the probability of null alleles was 0, indicating that the microsatellite loci used in this study were likely not under selection. All nestlings matched their putative mothers at all microsatellite loci. The combined probability of exclusion for all loci was > 99.9% for parent pairs.

Nestlings were assigned paternity based on number of allele mismatches and LOD (logarithm of odds) scores that reflect the likelihood ratio for each candidate father/offspring pair across all evaluated loci. The most likely father was assigned paternity if the difference between his and the next most likely father's LOD score exceeds the threshold LOD value (calculated by simulating 100,000 offspring using the observed allele frequencies and an estimate of 0.99 loci typed and 0.01 mistyped). Nestlings were considered extra-pair young (EPY) if the nestling/social male pair had a LOD score lower than the critical value and one or more loci that mismatched the social male. We assigned males as extra-pair sires based on LOD scores only when CERVUS assigned paternity at the 95% confidence level and they had no mismatches with the nestlings. Because we estimate that we captured around 60% of the males in the population, we used these conservative assignment criteria to avoid assigning the wrong male as genetic sire. All males sampled within a site and across all years were included as potential sires for paternity analysis (Wichita Mountains Wildlife Refuge, $n = 101$; Fort Sill $n = 105$). We used males assigned as genetic fathers to calculate the minimum number of males with which each female copulated.

Statistical analysis

We evaluated differences in the frequency of EPP in nests and number of nestlings resulting from EPCs across years using G -tests. We adopted a Bayesian framework to draw inference about how morphology differs based on the incidence of EPP and on flight performance. In essence we adopted Kruschke's (2013) "BEST" (Bayesian Estimation Supersedes the t test) framework, in that we created Bayesian analogs for both paired and two-sample t tests; i.e., we built models in JAGS, run via R, to estimate either the mean difference score (for a paired test) or the difference in means between groups (for a two-sample test). We estimated these parameters via three chains in standard Markov chain Monte Carlo, with 1000 burn-in, 10,000 iterations, and flat priors. We interpreted a predictor as having a biologically meaningful effect only if > 0.9 (i.e., 90%) of the posterior distribution of the parameter of interest was positive or negative; we judged anything less to be of insufficiently low uncertainty to conclude the predictor had an effect. Furthermore, we interpreted only those parameters for which the magnitude of mean estimated effect size (η)—essentially a Cohen's d (Cohen 1988)—exceeded 0.40, generally considered to be at the low end of a moderate effect. Because some individuals occurred as the social parent for more than one brood, we ran this analysis twice. In the first analysis, we excluded all but the first appearance of any bird as a social parent. In the second, we included all birds for whom we had data on cuckoldry, including all instances of repeated individuals. All statistical analyses were performed using the R statistical software (version 2.3.2; R Core Team 2013). Analyses were blinded in that they were accomplished by someone other than the person who gathered the field measurements.

Data availability The datasets analyzed during the current study are available in Dryad (<https://doi.org/10.5061/dryad.2qv284p>).

Results

EPP rates

We assessed parentage at 140 nests and for 550 nestlings. Of these, we genotyped known mothers at 123 nests and known social males at 119 nests. We were able to genetically identify extra-pair fathers at 61 nests (77 nestlings). Scissor-tailed Flycatchers had a high rate of EPP across sites and years: 73% of nests contained at least one EPY, and 59% of all nestlings sampled resulted from EPCs (Table 1). The proportion males cuckolded at their own nests was similar when we included all social males sampled, when we included only the first nest in our dataset at which a male appeared as a social parent, and when we looked only at males that were social fathers at more than one nest. This was also true for the proportion of females cuckolding their social mates (Table S1). These rates may be underestimates, given that we were unable to sample all potential offspring in every nest as a result of the failure of some eggs to hatch and high partial depredation rates. Extra-pair sires in our dataset produced between 1 and 13 extra-pair young across all years in which they were present as breeders. The most prolific male sired 13 EPY, which equated to a complete clutch of four nestlings and one of five nestlings in 1 year, and another complete clutch of 4 nestlings in another year. We were able to identify genetic fathers at the nests of 24 males that appeared as extra-pair fathers in the nests of other males. Half of these were cuckolded at their own nests. Of 123 nests at which we were able to identify the genetic sire of at least one nestlings, nests most often had one ($n = 63$) or two genetic sires ($n = 41$), although three were confirmed for 18 nests,

and a single nest had 4 sires. These represent minimum estimates of number of sires, as we were unable to identify every father in every nest. Because the prevalence of EPP in nests or the total number of EPY did not differ among sites ($G_1 = 0.1$, $P = 0.2$) or years ($G_6 = 6.2$, $P = 0.6$), we grouped paternity data for statistical analyses.

Morphology and cuckoldry

On average, cuckolded males had poorer body condition, shorter tail length, shorter wing chord, shallower primary notches, and yellower flanks than males that maintained paternity (Table 2). Several other characteristics of smaller effect ($\eta < 0.4$) may also have been different between males that were and were not cuckolded, with cuckolded males having shorter tarsi and shorter ornamental streamer length. Because body condition and wing chord were highly correlated ($r = 0.87$), it may be that larger males (i.e. longer wing chord and tarsus) were not cuckolded. These results were qualitatively similar when we included all males, including those for whom we had cuckoldry data for more than one nest (Table S2).

When social males were directly compared to the males that cuckolded them, we found evidence of a weak effect of several characteristics given the posterior distributions of the mean difference score (proportions > 0.9) but low effect sizes ($\eta < 0.4$). Social males had longer primary notches and more intense axillary feather coloration (higher redness and yellowness values) than did the males that cuckolded them (Table 3).

Females that did not cuckold their mates had yellower flanks and poorer body condition than those that did, although body condition had a low effect size ($\eta < 0.4$) (Table 4). When all females were included in this

Table 1 Summary of paternity in Scissor-tailed Flycatcher (*Tyrannus forficatus*) broods between sites and across years. WPP (within-pair paternity) only, EPP (extra-pair paternity) only, and mixed paternity refer to the proportion of broods containing only young sired by the social

father, only young sired by extra-pair fathers, and a mix of young sired by both social and extra-pair fathers, respectively. WPY is the proportion of all young sired by a social father while EPY is the proportion sired by extra-pair males

Location	Broods				Nestlings		
	<i>N</i>	WPP only	EPP only	Mixed paternity	<i>N</i>	WPY	EPY
Fort Sill	74	0.26	0.35	0.39	296	0.42	0.58
WMWR	66	0.29	0.41	0.30	254	0.41	0.59
2008	4	0.50	0.25	0.25	14	0.71	0.29
2009	8	0.13	0.25	0.62	31	0.45	0.55
2010	13	0.23	0.39	0.38	52	0.33	0.67
2011	21	0.57	0.19	0.24	71	0.68	0.32
2012	21	0.19	0.48	0.33	84	0.32	0.68
2013	37	0.24	0.38	0.38	144	0.47	0.53
2014	36	0.20	0.47	0.33	151	0.28	0.72
Totals	140	0.27	0.38	0.35	547	0.41	0.59

Table 2 Results of a Bayesian comparison of morphology between male Scissor-tailed Flycatchers (*Tyrannus forficatus*) that were (EPP = extra-pair paternity) or were not (no EPP) cuckolded by their mates. HDI refers to the lower and upper Bayesian highest density credible interval,

proportion > 0 (< 0) refers to the proportion of the posterior distribution that is positive (or negative), and η is the effect size. Proportions > (or <) 0.9 are italicized

	<i>n</i>	No EPP	EPP	Difference (HDI)	Proportion > 0 (< 0)	η
Body condition	91	2.80	0.91	1.90 (0.54, 3.28)	<i>0.997</i> (0.003)	0.666
Mass (g)	91	37.74	37.78	-0.04 (-0.96, 0.86)	0.462 (0.538)	-0.025
Tarsus length (mm)	91	18.76	18.58	0.18 (-0.15, 0.52)	0.860 (0.140)	0.271
Wing chord (mm)	91	123.77	121.77	2.00 (0.46, 3.52)	<i>0.994</i> (0.006)	0.603
Notch depth (mm)	91	20.57	19.73	0.84 (-0.04, 1.76)	<i>0.966</i> (0.034)	0.438
Kipp's distance (mm)	49	14.97	12.95	2.03 (-2.84, 6.47)	0.813 (0.187)	0.309
Tail						
Length (mm)	86	230.42	219.71	10.71 (-2.07, 23.39)	<i>0.954</i> (0.046)	0.403
Asymmetry (mm)	76	1.58	1.92	-0.34 (-1.67, 1.01)	0.294 (0.706)	-0.192
Functional rectrices (mm)	91	74.42	74.23	0.20 (-1.23, 1.64)	0.605 (0.395)	0.064
Ornaments (mm)	86	150.39	141.72	8.67 (-3.42, 21.04)	<i>0.918</i> (0.082)	0.331
Flank feather color						
Darkness (L^*)	49	72.42	72.15	0.27 (-1.50, 2.00)	0.620 (0.380)	0.096
Redness (a^*)	49	12.90	13.17	-0.27 (-2.63, 2.04)	0.412 (0.588)	-0.070
Yellowness (b^*)	49	29.39	31.44	-2.06 (-4.92, 0.82)	0.076 (<i>0.924</i>)	-0.458
Axillary feather color						
Darkness (L^*)	49	46.30	47.16	-0.86 (-4.46, 2.94)	0.315 (0.685)	-0.159
Redness (a^*)	49	34.47	32.31	2.16 (-2.69, 6.90)	0.820 (0.180)	0.320
Yellowness (b^*)	49	39.68	38.99	0.69 (-1.76, 3.18)	0.720 (0.280)	-0.180

analysis, including those for whom we had cuckoldry data for more than one nest, any differences between females that did and did not cuckold their mates disappeared.

Morphology and flight

We filmed flight of 53 birds, including 17 females and 36 males. Thirteen failed to navigate the flight obstacle: they either landed on it or collided with it and subsequently landed on the ground. On average, birds that successfully navigated the flight tube had longer wing chords, deeper primary notches, longer tails (overall length, functional rectrix length, and ornament length), and greater Kipp's distance (Table 5). Rectrix asymmetry may have been lower in birds that successfully navigated the obstacle, as well ($\eta = 0.43$ but proportion = 0.84). Much of the pattern we detected was driven by males (mean η 0.59 for ♂ vs. 0.43 for ♀), and in one key case—wing chord—females had the opposite pattern, with shorter-winged birds performing better ($\eta = 0.74$). In contrast, we found no strong evidence that morphology was related to whether an individual collided with barriers during the flight performance trials ($n = 50$, all proportions < 0.86 for Bayesian posterior distributions of estimates of differences in means, with all $|\eta| \leq 0.32$).

Discussion

We document a highly promiscuous system (Roeder et al. 2016) in which putative measures of male quality differed between males that were and were not cuckolded. Males that suffered paternity loss were smaller (i.e., shorter wing chord) and in poorer condition than those that maintained all paternity within their own nests. Body size and condition have been linked to maintenance of WPP in a number of other species, as well (Griffith et al. 2002). Males that maintained paternity within their own nests had a lower yellow saturation in the flank feathers. Assuming the red carotenoid pigments in Scissor-tailed Flycatcher feathers are converted from other dietary pigments (Weaver et al. 2018), these males may have been more efficient at converting yellow pigments to red, and thus have been both healthier, as converted carotenoid concentrations have been linked with immunocompetence and disease-resistance pathways (McGraw and Ardia 2003; Whittingham et al. 2015) and parasite resistance (Weaver et al. 2018), and better able to hold high quality territories, mate guard, and produce more offspring (Wolfenbarger 1999; Hoi et al. 2013). Females may choose not to cuckold males that are likely high quality social mates.

We also found that flight feather characteristics played a role in maintenance of WPP, as has been found in other studies (Griffith et al. 2002; Møller et al. 2003). Males maintaining all

Table 3 Results of a Bayesian comparison of morphology between social males and their cuckolders in male Scissor-tailed Flycatchers (*Tyrannus forficatus*). Mean difference refers to the mean across all pairs of the difference between the social male and his cuckolder. HDI

refers to the lower and upper Bayesian highest density credible interval, proportion > 0 (< 0) refers to the proportion of the posterior distribution that is positive (or negative), and η is the effect size. Proportions > (or <) 0.9 are italicized

	<i>N</i>	Mean difference (HDI)	Proportion > 0 (< 0)	η
Body condition	77	0.52 (− 0.36, 1.39)	0.88 (0.12)	0.14
Mass (g)	77	− 0.14 (− 0.76, 0.49)	0.34 (0.66)	− 0.05
Tarsus length (mm)	77	− 0.10 (− 0.35, 0.14)	0.20 (0.80)	0.10
Wing chord (mm)	77	0.29 (− 0.64, 1.17)	0.73 (0.27)	0.08
Notch depth (mm)	77	0.47 (− 0.13, 1.06)	<i>0.94</i> (0.06)	0.18
Kipp's distance (mm)	44	0.57 (− 0.87, 2.02)	0.79 (0.21)	0.14
Tail				
Length (mm)	77	2.89 (− 7.39, 13.39)	0.70 (0.30)	0.07
Asymmetry (mm)	54	− 0.38 (− 1.15, 0.38)	0.16 (0.84)	0.19
Functional rectrices (mm)	77	0.52 (− 0.40, 1.46)	0.87 (0.13)	0.13
Ornaments (mm)	77	− 1.91 (− 10.58, 6.53)	0.32 (0.68)	− 0.07
Flank feather color				
Darkness	43	0.81 (− 0.86, 2.47)	0.84 (0.16)	0.17
Redness	43	1.07 (− 0.67, 2.78)	0.89 (0.11)	0.20
Yellowness	43	− 0.33 (− 2.37, 1.69)	0.37 (0.63)	− 0.05
Axillary feather color				
Darkness	41	− 0.42 (− 3.27, 2.53)	0.39 (0.61)	− 0.05
Redness	41	2.87 (− 0.83, 6.29)	<i>0.94</i> (0.06)	0.26
Yellowness	41	2.10 (− 0.01, 4.27)	<i>0.97</i> (0.03)	0.33

paternity in their own nests had a weak association with longer overall tail and ornamental streamer lengths. Such males may be of higher quality given the cost of producing and maintaining ornaments (Pryke and Andersson 2005) as they also maintained good body condition. Such ornaments likewise may affect flight itself. Elongated tail ornaments can act to increase lift and improve flight performance when they increase proportionally to overall tail length (Norberg 1994; Hedenström 1995), providing birds with more aerodynamic flight and maneuverability during foraging, flight displays, and possibly during inter- or intrasexual interactions, such as flight displays, mate guarding, or male-male contests. Males that were not cuckolded also had longer primary notches, which may function to fine-tune wing position during flight, although they also produce a buzzing sound during male flight displays (DVR pers. obs.).

When we evaluated how flight feather morphology was associated with flight performance, we found that wing chord, Kipp's distance, and primary notch depth were longer for birds that successfully navigated the flight tube. These results agree with the relationship between primary feather length and flight in European Starlings (*Sturnus vulgaris*), for which individuals with shorter primary feathers had reduced flight performance (Swaddle et al. 1996). Likewise, longer and more pointed wings should help compensate for exaggerated tail ornaments during flight (Norberg 1995). We also found that

successful birds had longer tail surfaces that provided lift (i.e., functional tail length) as well as longer ornamental streamer length. As noted above, elongated tail ornaments may provide additional lift and stabilization, particularly when present in birds with forked tails (Thomas 1993; Norberg 1994; Hedenström 1995).

Given the association of primary notch depth, ornamental tail length, and overall tail length with maintenance of WPP and flight performance, we suggest that evaluation of flight displays, which include an auditory element (provided by calls and sound generated by the primary notch), a visual element (display of axillary and flank color patches as well as tail ornaments), and a maneuverability element (aerial tumbling) together play a role in female faithfulness to social mates. They also may play a role in initial mate choice (Manica et al. 2016) and serve to reinforce territory boundaries and reduce intrusion by strange males (Green et al. 2000), thereby reducing cuckoldry. By contrast, we conclude that it is unlikely cuckoldry in this system resulted from male coercion of females or female escape of mate guarding, as many of the functional features associated with flight performance were not associated with cuckoldry.

When we directly compared social males to their cuckolders, we found that cuckolders had somewhat less exaggerated ornaments (i.e., shallower primary notches and grayer flank feather coloration). These cuckolded males were

Table 4 Results of Bayesian comparison of morphology between female Scissor-tailed Flycatchers (*Tyrannus forficatus*) that did (EPP = extra-pair paternity) or did not (No EPP) cuckold their mates. HDI refers to the lower and upper Bayesian highest density credible interval,proportion > 0 (< 0) refers to the proportion of the posterior distribution that is positive (or negative), and η is the effect size. Proportions > (or <) 0.9 are italicized

	<i>n</i>	No EPP	EPP	Difference (HDI)	Proportion > 0 (< 0)	η
Body condition	93	- 0.90	0.19	- 1.09 (- 2.66, 0.42)	0.080 (0.920)	- 0.359
Mass (g)	93	34.98	35.01	- 0.03 (- 1.00, 0.92)	0.479 (0.521)	- 0.015
Tarsus length (mm)	93	18.72	18.66	0.06 (- 0.17, 0.29)	0.689 (0.311)	0.112
Wing chord (mm)	93	112.35	112.00	0.35 (- 1.16, 1.89)	0.677 (0.323)	0.123
Notch depth (mm)	93	10.31	10.34	- 0.02 (- 0.81, 0.73)	0.474 (0.526)	- 0.017
Kipp's distance (mm)	50	37.93	36.84	1.09 (- 1.32, 3.49)	0.823 (0.177)	0.348
Tail						
Length (mm)	93	148.05	147.87	0.19 (- 9.75, 10.38)	0.514 (0.486)	0.009
Asymmetry (mm)	72	1.50	1.66	- 0.17 (- 1.22, 0.96)	0.374 (0.626)	- 0.105
Functional rectrices (mm)	93	69.78	69.17	0.60 (- 0.97, 2.18)	0.775 (0.225)	0.186
Ornaments (mm)	93	73.75	76.71	- 2.95 (- 10.13, 4.31)	0.206 (0.794)	- 0.198
Flank feather color						
Darkness (L^*)	50	73.94	74.58	- 0.64 (- 3.02, 1.69)	0.287 (0.713)	- 0.180
Redness (a^*)	50	8.69	6.83	1.86 (- 1.07, 4.82)	0.897 (0.103)	0.486
Yellowness (b^*)	50	31.23	28.38	2.85 (- 1.12, 6.89)	0.927 (0.073)	0.532
Axillary feather color						
Darkness (L^*)	50	53.36	55.05	- 1.70 (- 5.97, 2.76)	0.212 (0.788)	- 0.301
Redness (a^*)	50	24.11	22.14	1.97 (- 4.79, 8.49)	0.734 (0.266)	0.243
Yellowness (b^*)	50	39.13	37.53	1.61 (- 3.03, 6.36)	0.762 (0.238)	0.259

of lower quality than males that maintained WPP yet were cuckolded by males of even lower quality than themselves. This counter-intuitive result may stem from their more female-like appearance (i.e., shallower notches and paler ornamental feather color), which is common among young Scissor-tailed Flycatcher males during their first breeding season (Pyle 1997; Regosin 2003). Adult males may have been less likely to approach and attack sub-adult males with female-like plumage, allowing sub-adults to gain access to and attempt EPCs with extra-pair females. This idea that sub-adult males with

delayed plumage maturation may be able to increase their reproductive success via a lower adult male aggressive response to their presence has empirical support (Rohwer 1978; Hawkins et al. 2012) and, indeed, delayed plumage maturation is more common in species with sexual plumage dimorphism and more intense sexual selection (Beauchamp 2003). We suggest these males make the best of a bad job by attempting to gain EPCs and secure some level of reproductive success in the face of a high incidence of lost paternity within their own nests (Lyon and Montgomerie 1986; Rohwer

Table 5 Results of a Bayesian comparison of morphology between Scissor-tailed Flycatchers (*Tyrannus forficatus*) that failed to navigate or successfully navigated flight tube obstacles. HDI refers to the lower andupper Bayesian highest density credible interval, proportion > 0 (< 0) refers to the proportion of the posterior distribution that is positive (or negative), and η is the effect size. Proportions > (or <) 0.9 are italicized

	<i>n</i>	Failure	Success	Difference (HDI)	Proportion > 0 (< 0)	η
Body condition	53	- 0.87	- 0.38	- 0.49 (- 3.39, 2.48)	0.37 (0.64)	- 0.12
Wing chord (mm)	53	114.48	117.80	- 3.32 (- 6.79, - 0.06)	0.03 (0.97)	- 0.65
Notch depth (mm)	53	13.04	16.88	- 3.83 (- 6.89, - 0.73)	0.01 (0.99)	- 0.82
Kipp's distance (mm)	53	39.30	42.73	- 3.43 (- 6.36, - 0.68)	0.01 (0.99)	- 0.77
Tail						
Length (mm)	53	152.53	177.67	- 25.14 (- 43.90, - 5.83)	0.01 (0.99)	- 0.73
Asymmetry (mm)	53	2.28	1.64	0.64 (- 0.69, 2.00)	0.84 (0.16)	0.43
Functional rectrices (mm)	53	70.37	71.71	- 1.34 (- 3.29, 0.77)	0.09 (0.91)	- 0.41
Ornaments (mm)	53	105.70	105.70	- 18.71 (- 41.96, 6.09)	0.06 (0.94)	- 0.50

and Butcher 1988), as half of cuckolders were likely to be cuckolded by other males. Alternately, because only a small proportion of males were not cuckolded (27%), most males do not have an optimal phenotype, resulting in a high chance of cuckoldry by males of lower quality than themselves. Our data do not allow distinction between these two possible explanations for differences between social males and their cuckolders.

We found no evidence of male coercion of females for EPCs in this system, as smaller females were not more likely to cuckold their mates than larger females nor were feather features that were important in flight performance different between females that did and did not cuckold their mates. However, we did find weak evidence of extra-pair selection on female morphology, as body condition was higher in females that cuckolded their mates. This weak effect may be the result of either escape of male mate-guarding by females in good condition (Low 2005) or reciprocal male selection for healthier extra-pair partners (Amundsen et al. 1997; Westneat and Rambo 2000). Likewise, females that did not cuckold their mates had yellower flanks. As in males, greater yellow intensity may be a signal of lower quality in pathways that convert dietary carotenoid pigments into other carotenoids, such that flanks had less intense red coloration. Pigment conversion pathways have been linked with disease and parasite resistance (Weaver et al. 2018), so these females of potentially low quality or with poorer parasite resistance pathways may have been less able to attract extra-pair mates or escape mate-guarding by their social mates (Whittingham et al. 2015). Because size and flight feather features were not related to cuckoldry, we propose escape of mate-guarding did not drive cuckoldry in this system. Instead, it appears there is some degree of reciprocal selection, where males avoided engaging in EPCs with females in poor condition. Another possibility is that males are not choosy and will mate with any female, given the opportunity. If so, then EPC is driven by the female, in which case it is possible that female of poorer condition are both less vagile and more susceptible to forced EPC.

In sum, our results suggest that associations between cuckoldry and condition, size, ornamental characters, and flight feather features important in maneuverability reflect female faithfulness to social partners of good quality. Social mates of these males may be less inclined to copulate outside of the pair bond if body size, condition, and ornament quality are good cues of overall male quality (Podmokła et al. 2015; Whittingham et al. 2015). Direct comparison of social males with the extra-pair males to whom they lost paternity revealed that cuckolders had duller, more female-like coloration and ornamentation, potentially suggesting a role of delayed plumage maturation (Hawkins et al. 2012) in increasing reproductive success of young breeders in this system. This conjecture will need thorough investigation before we can eliminate other explanations. Still, we posit that in this system there is a lack

of strong selection on extra-pair male morphology; rather, high quality males maintained WPP while females in good condition were more likely to cuckold social males of poorer quality.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflicts of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards of the institution at which the studies were conducted. The study was conducted under the United States Department of the Interior Federal Bird Banding permit #23215 and University of Oklahoma Institutional Animal Care and Use Committee protocols R09-024, R12-101, and R15-006. All necessary permissions and permits were provided by the Oklahoma Department of Wildlife Conservation, Wichita Mountains Wildlife Refuge, and Fort Sill Artillery Base.

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