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FROM INDIVIDUALS TO ENVIRONMENT: THE RELATIVE ROLES OF MORPHOLOGY, FLIGHT, DENSITY, SYNCHRONY, HABITAT STRUCTURE, AND WEATHER ON EXTRA-PAIR PATERNITY

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DIANE V. ROEDER
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FROM INDIVIDUALS TO ENVIRONMENT: THE RELATIVE ROLES OF MORPHOLOGY, FLIGHT, DENSITY, SYNCHRONY, HABITAT STRUCTURE, AND WEATHER ON EXTRA-PAIR PATERNITY

A DISSERTATION APPROVED FOR THE
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BY

Dr. Michael A. Patten, Chair

Dr. Jeffrey F. Kelly

Dr. Lawrence J. Weider

Dr. Michael T. Murphy

Dr. Phillip B. Chilson

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TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

ABSTRACT

Reproductive success is driven in large part by the mating system of a species, which ultimately determines patterns of gene transmission across generations. In species with socially monogamous mating systems, an important component of reproductive success is extra-pair paternity (EPP), when males obtain fertilizations outside of their social pairing. While social monogamy is rare in most taxa, it is the most common mating system of birds and >75% of species have appreciable rates of EPP. Although, the distribution of EPP in birds has a large phylogenetic component, there is a great deal of variability across populations, suggesting contemporary constraints on extra-pair behavior. Given the prevalence of EPP in birds, it is important that we understand how these factors interact to drive or constrain the opportunity for EPP, and thus sexual selection and the genetic contribution of individuals to the next generation. In this dissertation, I examined the distribution of EPP between the two main passerine suborders, and then attempted to elucidate the influence of individual, ecological, and environment characteristics individually, and finally, in combination, on the probability of EPP in nests of a savannah oscine passerine, the Scissor-tailed Flycatcher (*Tyrannus forficatus*). In Chapter 1, I compared EPP rates in commonly studied oscine species (Suborder Passeri) to those in the less frequently studied suboscines (Suborder Tyranni). I found similar EPP rates between the suborders and suggest that generalizations from oscines may be extended to this group. In addition, I used molecular techniques to investigate EPP rates in the suboscine Scissor-tailed Flycatcher and found that the population under study had high rates of EPP compared to other passerine species, with 73% of nests containing extra-pair young and 59% of

young resulting from extra-pair copulations. In Chapter 2, I used this species to examine whether individual characteristics influence the distribution of EPP in the population. Males in good body condition and with a high degree of tail symmetry, which may have indicated individual quality, were cuckolded infrequently. Females may have been more faithful to high quality males or, alternately, these males may have been better able to continuously guard their mates from extra-pair copulation (EPC) attempts. In Chapter 3, I moved beyond the individual to ask how timing of nesting, breeding density, and breeding synchrony influence the frequency with which individuals interact, and thus rates of EPP. I found that EPP was negatively influenced by the distance to neighbors with synchronously fertile mates and that cuckolded males and their cuckolders were not mate-guarding concurrently. These results suggest that males with fertile mates must invest their time into mate-guarding to assure paternity in their own nests, while males not mate-guarding are free to seek EPCs. I also investigated how habitat structure on breeding territories influenced EPP. I found that EPP declined with an increase in shrub perches from which a male could survey his territory, but increased with greater tree abundance, which likely obscured a male's view of his territory and provided cover for EPCs with intruding males. Cuckoldry was also more likely as fence length increased. Fences were used as foraging perches by birds from neighboring territories, bringing together birds that would normally not have interacted. Man-made structures that influence habitat structure may thus artificially alter reproductive behavior by changing how individuals interact. In Chapter 4, I address the influence of weather conditions, which can be quite extreme in savannah systems, on the probability of EPP. EPP was less prevalent when the social female of a pair was fertile during high vapor pressure deficit conditions. Low vapor pressure deficit indicates moist air and decreases a bird's ability to thermoregulate through evaporative heat loss. Heat stress may make mate-guarding more difficult for males and resisting EPC attempts more difficult for females, resulting in higher EPP rates. EPP was also low when minimum daily temperature was variable, indicating the occurrence of cold mornings in the normally hot summer breeding months. To maintain their energy reserves needed for thermoregulation, all birds likely spent more time foraging and less time seeking EPCs on cold mornings. Finally, in Chapter 5, I assessed the relative importance of predictors from all datasets when examined together using path analysis. I found that morphology was not influential when put in the context of ecological or environmental conditions. Instead, variables that directly and indirectly influenced interaction rates between breeding individuals (nearest synchronous neighbor distance, breeding density, breeding synchrony, fence length) had the strongest relationship with EPP. These were followed in importance by variables that directly and indirectly modified the ability of individuals to interact (vapor pressure deficit directly, minimum daily temperature variability, maximum wind speed average and variability). These results emphasize the importance of the context in which reproductive decisions occur. Morphology may have been under sexual selection at a fine scale, but opportunities for cuckoldry likely depended on ecological and environmental conditions. Interaction rates between social mates and with potential extra-pair partners depended on the distribution and synchrony of breeding individuals, while ambient weather conditions modified the ability of individuals to interact during fertility by constraining the ability of individuals to mate-guard and pursue EPCs.

INTRODUCTION

Variation in 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). Because not all individuals can successfully reproduce, there should be strong competition to contribute genetically to the next generation. This is particularly true when some individuals are able to dominate mating opportunities, resulting in increased intrasexual competition for access to mates and more intense sexual selection (Emlen and Oring 1977).

In promiscuous and polygamous species, few males are able to secure copulations with choosy or unevenly distributed females (Emlen and Oring 1977, Nunney 1993). As a result, these systems are typified by high to moderate variation in male reproductive success (Ligon 1999, Bennett and Owens 2002). In contrast, most individuals of monogamous species, in which a single male and female associate during breeding, have the opportunity to reproduce, leading to substantially lower sexual selection pressure and more evenly distributed reproductive success (Ligon 1999, Bennett and Owens 2002). However, sexual selection and variance in reproductive success can still be relatively high in socially monogamous species if some individuals can monopolize fertilizations both within and outside of the pair bond (Yezerinac et a. 1995, Dolan et al. 2007). When individuals engage in copulations outside of the pair bond (extra-pair copulations; EPC) that result in fertilization, extra-pair paternity (EPP) increases both variance in reproductive success and the opportunity for sexual selection (Yezerinac et a. 1995, Griffith et al 2002).

While monogamy as a social system is rare in the animal kingdom, occurring occasionally in arthropods, fish, mammals, reptiles, and amphibians (Wittenberger 1980, Clutton-Brock 1989, Lukas and Clutton-Brock 2013), it is the predominant mating system of birds (> 90% of species; Lack 1968, Mock and Fujioka 1990, Ligon 1999). In most socially monogamous taxa, EPP is common (78% of mammals - Cohas and Allainé 2009; 61% of fish - Avise et al. 2002; 21% of reptiles - Uller and Olsson 2008). Birds exhibit a high prevalence of EPP, with 75% of monogamous species maintaining appreciable rates of EPP (18.7% of broods, 11.1% of offspring; Griffith et al. 2002). Extra-pair paternity is present at moderate rates in non-passerine birds (48% of species, ~3% of offspring; Westneat and Sherman 1997), but is much higher in species in the Order Passeriformes (> 86% of species; ~11% of offspring; Griffith et al. 2002), which make up over half of all bird species. Because of its link with reproductive success and evolution, it is important to understand not only the benefits and costs to males and females from extra-pair behavior, but also to understand the social, ecological, and environmental factors that influence extra-pair behavior.

The benefits of EPP to males are intuitive; when males can maintain paternity in their own nests while securing extra-pair fertilizations (EPF), they can increase their reproductive success (i.e. fitness), resulting in a greater opportunity for sexual selection among males (Albrecht et al. 2007, Dolan et al. 2007, Lebigre et al. 2013). On the other hand, females typically cannot increase their reproductive output in terms of number of offspring. Although benefits of EPP to females are less clear and more difficult to assess, they are likely of similar importance as those to males given the frequency with which females initiate EPCs (Gray 1997, Ligon 1999, Suter et al. 2007). Direct benefits for females can come in the form of resources or paternal care provided by the extra-pair mate (Davies 1990, Gray 1997, Griffith et al. 2002) or fertility insurance (Sheldon 1994, Pizzari et al. 2004) and increased embryo survival (Kempenaers et al. 1999). Females may engage in EPCs to increase paternity uncertainty among males, thereby creating a “cooperative neighborhood” in which many males respond together to potential predators because they may have young in multiple nests (Eliassen and Jørgensen 2014). Females can indirectly benefit from EPFs if they increase the fitness of their young. The primary ways in which these benefits are realized are through sperm competition to ensure offspring are sired by quality males (Møller and Ninni 1998, Jennions and Petrie 2000, Michl et al. 2002); genetic quality of mates, which increases the quality of offspring (Kempenaers et al. 1992, Whittingham et al. 2015); and genetic diversity and complementarity of extra-pair mates and resulting offspring, which can increase the likelihood that some offspring will survive in an unpredictable environment (Jennions and Petrie 2000, Suter et al. 2007, Arct et al. 2015). Alternately, recent studies suggest that females may seek EPCs as a result of genetic covariance in mating behavior due to strong selection on males to seek EPCs (Reid et al. 2010).

There are also a suite of potential costs for both males and females. Costs for males can come from increased risks of sperm depletion, parasite or disease contraction, injury from a female’s social mate, predation, or of cuckoldry when not mate-guarding their own fertile mates, (Birkhead and Møller 1992). It is likely that the risk of paternity loss is the strongest cost, as males of some species delay seeking EPCs until after their social mates have begun incubation (Canal et al. 2012). Costs to females are similar and include risk of exposure to parasites or disease and injury from a male’s social mate (Ligon 1999, Arnqvist and Kirkpatrick 2005). More importantly, females seeking EPCs risk retaliation by the social mate, either by physical harassment or by the withholding of paternal care of offspring (Clutton-Brock 1991, Ligon 1999). While there is evidence that males decrease care in response to cuckoldry (Sheldon and Ellegren 1998, Hunt and Simmons 2002, Arnqvist and Kirkpatrick 2005), withholding care is counterproductive, especially in relatively short-lived species, if most males maintain at least some paternity in their own nests, as withholding care could result in complete nest failure (Westneat 1995, Varian-Ramos et al. 2012).

Regardless of the costs and benefits to individuals, a diverse array of avian taxa exhibit appreciable rates of EPP. Explanations for cuckoldry in these species seem to be scale dependent. Nearly 50% of variation in EPP among species is accounted for by variation among families and orders (Westneat and Sherman 1997, Arnold and Owens 2002). Accordingly, life history traits of species are associated with rates of EPP. Species with high rates of adult mortality, high fecundity, and reduced paternal care are more likely to exhibit higher rates of EPP (Ligon 1999, Arnold and Owens 2002, Matysiokova and Remes 2013). A considerable degree of variation exists among populations and individuals of the same species, however, and EPP rates on this smaller scale is more likely to be determined by differences in contemporary genetic, ecological, and environmental factors (Arnold and Owens 2002).

While we understand to some extent the relationship between these factors and the probability of cuckoldry in single species, we know little about how they interact to shape reproductive behaviors (Westneat and Stewart 2003). The majority of studies have focused on individual morphological and population characteristics (Griffith et al.

2002). These studies have provided evidence that traits of individuals, such as age, experience, condition, song, color, and feather morphology, can act as honest signals of quality or can influence an individual's ability to mate-guard (males) or escape mate-guarding (females), thus influencing sexual selection and extra-pair paternity (Balmford and Read 1991, Açkay and Roughgarden 2007, Cleasby and Nakagawa 2012). Likewise, some characteristics of breeding populations, including the timing of nesting, spatial distribution of nests, and synchrony of fertile pairs, influence the prevalence of EPP by altering rates of interaction between individuals and the propensity of males to mate-guard (Mayer and Pasinelli 2013, Stewart et al. 2010, Westneat et al. 1990).

In contrast, the idea that EPP may be linked to how individuals move about and respond to conditions on their own territory remains largely unexplored. Flight performance may affect cuckoldry by determining how well or where individuals can forage (Swaddle and Witter 1997), as well as by influencing territorial defense, mate-guarding (Evans and Thomas 1992), and the ability of females to escape mate-guarding. Habitat structure may shape cuckoldry by influencing movements of both territory-holders and extra-pair individuals. As habitat structure can affect both foraging location, via habitat quality and perching structure availability (Westneat et al. 1990, Rubenstein 2007), and visual obstruction of the territory, it may promote or constrain a male's ability to mate-guard (Sherman and Morton 1988, Blomqvist et al. 2006). Only two studies have attempted to address the effect of habitat type; one examined EPP and habitat type across species (Blomqvist et al. 2006) while the other focused on nest locations (Tryjanowski et al. 2007). None have examined habitat structure at a fine scale, and we know very little about this potentially important correlate of cuckoldry.

Lastly, only three studies to date have focused on the impact of weather on the probability of cuckoldry. Their results suggest that EPP was less likely when temperatures were colder and rainfall was greater, likely due to thermoregulatory constraints on seeking EPCs (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006, Hoset et al. 2014). However, because these studies were conducted in cold climates, it remains to be seen how other biologically important weather conditions in hot climates, such as vapor pressure deficit and wind speed, constrain cuckoldry by driving trade-offs between self-maintenance and the pursuit of EPCs.

Only a few studies have simultaneously investigated multiple correlates of EPP in the same population across years because of the difficulty of carrying out such large-scale studies (Olsen et al. 2008, Rubenstein 2007, Johnsen and Lifjeld 2003). However, investigation into temporal variation in EPP rates at multiple levels of biological organization are needed if we are to begin to understand how EPP varies temporally across individuals, populations, and environments. The potential for interactions among levels of ecology is vast and vital to understanding promoters and constraints of extra-pair behavior (Griffith et al. 2002). My dissertation research explored how each of the factors discussed above were related to EPP, how some factors might act indirectly on paternity through their effect on other factors, and on the relative importance of factors that directly predict EPP. My goal was to build an integrative ecological model for EPP to investigate whether and how body condition, flight surface morphology, flight performance, nesting density, synchrony of female fertility, habitat structure, and weather conditions relate to the presence of EPP in nests, and also to test for potentially meaningful relationships among these variables.

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CHAPTER ONE

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FREQUENCY OF EXTRA-PAIR PATERNITY IN SCISSOR-TAILED FLYCATCHERS (*TYRANNUS FORFICATUS*) AND OTHER SUBOSCINES: ARE OSCINES AND SUBOSCINES DIFFERENT?

Diane V. Roeder[1],
Michael S. Husak[2], and Michael T. Murphy[3]

[1] Department of Biology & Oklahoma Biological Survey, University of Oklahoma,
Norman, OK 73019, USA
[2] Department of Biological Science, Cameron University, Lawton, OK 73505, USA
[3] Department of Biology, Portland State University, Portland, OR 97207, USA.

ABSTRACT

Extra-pair paternity (EPP) appears to be widespread in passerine birds, but few studies have focused on suboscine species, and therefore it is unclear if this generalization can be extended to this group. In this study, we document high rates of EPP in a socially monogamous, suboscine passerine, the Scissor-tailed Flycatcher (*Tyrannus forficatus*) in southwest Oklahoma in the summers of 2009—2011. Averaged across years, EPP occurred in 66% of nests in our study population and accounted for 49% of all nestlings. EPP rates were variable (50–88%), but did not differ significantly among years or between two study sites. Our review of the literature yielded EPP data for only 11 other species of suboscines (0.7% of total), which we compared to EPP rates for the 83 oscine species (1.9% of total) reported in Spottiswoode and Møller (2004). EPP was as common and variable in suboscines (21.7% of young) as oscines (17.5% of young). Our study adds to our knowledge of mating systems in the understudied suboscine group, but further sampling of suboscines should be a priority, as they comprise a quarter of all passerine species and comprise a large fraction of passerines in tropical regions.

Key words—cuckoldry, mating systems, oscine, Tyranni, Tyrannidae, *Tyrannus forficatus.*

INTRODUCTION

The mating systems of >90% of bird species are classified as socially monogamous (Griffith et al. 2002), where a prolonged pair bond between a male and a female is established (Lack 1968, Birkhead and Møller 1992). However, males and females in three-quarters of sampled species regularly engage in extra-pair copulations (Griffith et al. 2002), often resulting in young sired by extra-pair males (i.e., extra-pair paternity [EPP]). Males can increase their reproductive success as a result of siring extra-pair young (EPY) in addition to siring young with the social mate. In some species, these gains in extra-pair reproductive success are balanced by paternity lost to neighbors (Lebigre et al. 2012, Schlicht and Kempenaers 2013). However, when males of some species gain extra-pair mating while retaining paternity within their own nest, in effect gaining at the expense of their neighbors, EPP adds to the variance in male reproductive success (Dolan et al. 2007, Webster et al. 2007, Balenger et al. 2009) and creates an opportunity for sexual selection to occur (sensu Webster et al. 1995).

Benefits of extra-pair matings for females are more difficult to elucidate, but if females can evaluate male quality and select high quality males, males with high genetic diversity, or males with whom they are genetically compatible, they may increase their reproductive success via success of higher quality young (Jennions and Petrie 2000). The effect of EPP on reproductive success and fitness vary with age, nest success, and between individuals who lose paternity in their own nests. Extra-pair paternity thus has the potential to greatly influence reproductive success in socially monogamous systems (Lebigre et al. 2013), but the details often vary from species to species.

Our ability to generalize current knowledge on EPP to other bird species is limited, because we still have little or no knowledge of the genetic mating system of the majority of species. This is of concern because it appears that patterns of EPP are not randomly distributed with respect to phylogeny. About half of the variation in interspecific rates of EPP occurs among families or orders, suggesting that the frequency of EPP in avian taxa is a function of their evolutionary history (Griffith et al. 2002). In passerines in particular, EPP has been documented to some degree in the roughly 20 families studied (Westneat and Sherman 1997), and passerines appear to exhibit EPP with much greater regularity than other bird taxa.

Almost all of our knowledge of EPP comes from oscine passerines (suborder Passeri). By contrast, studies on EPP in suboscine passerines (suborder Tyranni) remain scarce, despite the fact that these birds comprise ~26% of the estimated 6015 known species of passerines (Gill and Wright 2006). Because of their abundance and their basal position in the passerine phylogeny, it is important to understand variation in EPP in this group. Some suboscine groups, such as the family Tyrannidae, are speciose (~450; Fitzpatrick et al. 2004) and breed in both temperate and tropical regions of North America and South America. Suboscines thus provide a powerful opportunity to determine whether EPP rates of closely related species differ between temperate and tropical regions as a result of different breeding seasonality (e.g., Stutchbury et al. 2007).

In this study, we report rates of EPP for the Scissor-tailed Flycatcher (*Tyrannus forficatus*: Tyrannidae), summarize previously published data for suboscine EPP rates, and provide an exploratory, non-phylogenetically controlled comparison of EPP rates between oscines and suboscines. The Scissor-tailed Flycatcher is one of two sexually dimorphic species in an otherwise sexually monomorphic genus breeding widely throughout temperate and tropical regions of the Western Hemisphere. Male Scissor-tailed Flycatchers generally have longer tails, are more brightly colored, and are heavier than females (Pyle 1997). Scissor-tailed Flycatchers winter in savannah regions from southern Mexico to northern Costa Rica and breed in similar habitat in the south-central Great Plains of the United States and northeastern Mexico (Regosin 2013). They are biparental and socially monogamous, with high within-season but low between-season mate fidelity (Regosin 2013, Regosin and Pruett-Jones 2001).

The only other species of *Tyrannus* in which EPP has been studied to date, the monomorphic Eastern Kingbird (*T. tyrannus*), exhibits consistently high rates of EPP (61% of nests) and high percentage of young sired by EP males (45% of young; Rowe et al. 2001, Dolan et al. 2007). Given the high rate of EPP in Eastern Kingbirds and the evidence that plumage dimorphism reflects the strength of sexual selection (Pryke and Andersson 2005), we predicted higher rates of EPP in the dimorphic Scissor-tailed Flycatcher than in the monomorphic Eastern Kingbird.

METHODS

Study Site—Our study was conducted annually from April to August 2008–2011 at the Wichita Mountains Wildlife Refuge (N 34.766667, W -98.700278) and the adjoining Fort Sill Military Reservation (N 34.65285, W -98.484501) in Comanche County, Oklahoma, U.S.A. The refuge is characterized by stretches of mixed-grass prairie habitat broken by low mountains, small lakes, and riparian forests primarily consisting of oak species, including blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*). The artillery range on Fort Sill is mesquite (*Prosopis glandulosa*) savannah dominated by little bluestem (*Andorpogon scoparius*) and Johnsongrass (*Sorghum halepense*), as well as landscaped areas with mowed grasses and various tree species, including hackberry (*Celtis reticulata*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*).

Field Methods—We located nests of Scissor-tailed Flycatchers by searching trees in areas of suitable habitat and following adults. Nest locations were marked with Garmin 60CSX GPS units (Garmin International Inc., Olathe, KS, USA) and visited every 2–3 days to track nest status and eventual fate (Ralph et al. 1993). We captured adults attending the nest with mist nets, often with the aid of predator or conspecific models and playback calls, when nestlings were ≥6 days of age (hatching = 0 days). We banded all captured adult birds and all nestlings with an aluminum USGS band. We also banded each adult with a unique combination of three colored Darvic leg bands for individual identification (total of two bands per leg). Social parents at each nest were identified by recording the band colors of the male and female attending the nest the day after banding.

Upon capture, we collected 50 µL blood samples from adults using a heparinized capillary tube following venipuncture of the brachial vein of the wing with a 22-gauge sterile, disposable needle. We collected 25 µL blood samples from nestlings when they were ≥6 days of age using the same procedure. Blood was transferred into Eppendorf tubes containing 1.5 mL Longmire’s buffer (Longmire et al. 1988) and refrigerated until processing.

Molecular Methods—DNA was isolated from blood samples with a QIAGEN DNeasy extraction kit (QIAGEN Inc., Valencia, CA, USA) using the protocol for whole-nucleated blood. We genetically determined the sex of all individuals using 22550F/2718R primers to amplify the CHD|W and CHD|Z introns, which are present in different lengths on the Z and W chromosomes (Fridolfsson and Ellegren 1999). PCR reactions were amplified in 25 µL reactions. Amplified fragments were run on 2% agarose gels, stained with ethidium bromide, and visualized fluorescently.

We used eight polymorphic microsatellite loci in parentage analysis, including EMIC23, ASE9, EMIZ27, ACG5, GATA5 (Dolan et al. 2007), DPU16 (Dawson et al. 1997), EMID46 (Tarof et al. 2001), and SAP22 (Watson et al. 2002). PCR reactions were carried out in 25 µL reactions using PuReTaq Ready-to-Go PCR beads and fluorescently labeled primers (GE Healthcare, Piscataway, NJ, USA; #27-9558-01) following the conditions given in Dolan et al. (2007). PCR was carried out with the following thermal conditions: DNA denaturation at 94°C, primer annealing at 65°C (ACG5 and GATA5) or 61°C (all others), and strand elongation at 72°C. This cycle was repeated 30 times, with a final elongation time of 5 mins. Amplified microsatellite loci were separated by capillary electrophoresis and visualized on an ABI 3130XL DNA Analyzer (Applied Biosystems, Inc., Foster City, CA, USA).

Paternity Analysis—Nestling genotypes were compared directly to female genotypes to confirm maternity. All putative mothers matched their nestlings at each locus, with no evidence of non-amplifying alleles or intraspecific brood parasitism. The nonmaternal genotype was used to assess paternity using direct exclusionary analysis. Because all mothers matched their offspring at all loci, any nestlings that had one or more allele mismatches with the social father were considered extra-pair. Genotypes of EPY were compared with all other sampled males to attempt to identify the genetic father. To be assigned to an EP male, nestling and EP male genotypes had to match at all loci. We found the frequency of each allele and calculated the average exclusion probability at each locus and at all loci combined using CERVUS Version 3.03 (Marshall et al. 1998, Dolan et al. 2007, Kalinowski et al. 2007). Allele frequencies were used to assess deviations from Hardy-Weinberg equilibrium. We also assessed the probability of null alleles using CERVUS 3.03, which uses a Chi-square test with a Yates continuity correction when degrees of freedom were equal to 1. Calculated null allele frequencies were <0.05 in all cases, indicating a lack of deviation from Hardy-Weinberg equilibrium and that the microsatellite loci used in this study were probably not under selection.

Suboscine EPP Data Compilation and Comparison—We compared the percentage of young sired by extra-pair males in suboscine and oscine species. For suboscine EPP rates, we conducted a literature search in the following journals: *American Naturalist*, *Animal Behavior*, *Auk*, *Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Condor*, *Evolution*, *Ibis*, *Journal of Avian Biology*, *Journal of Field Ornithology*, *Molecular Ecology*, *Nature*, *Oikos*, *Proceedings of the Royal Society of London B*, and *Wilson Journal of Ornithology*. We supplemented searches with a general search using Google Scholar for every genus within the Tyranni suborder. We did this in an attempt to find articles in limited circulation journals, as well as to include data from theses and dissertations. When two or more values existed for a species, we used the weighted mean for all values for statistical analysis. In addition, we calculated confidence intervals around each suboscine EPP rate using the uncorrected score method (Newcombe 1998) to facilitate visual comparison among species. We did not attempt to conduct an exhaustive survey of the literature for oscine EPP rates, but instead used data summarized by Spottiswoode and Møller (2004) as our primary source.

Statistical Methods—We calculated the percentage of Scissor-tailed Flycatcher clutches with young fathered only by the social father (within-pair young; WPY only), clutches with young fathered only by extra-pair males (EPY only), and clutches with mixed paternity. If EPP was present, we calculated the proportion of EPY in each nest. We also calculated the proportion of young in all nests sampled that resulted from within-pair and extra-pair copulations to assess the genetic contribution that EPP made to the next generation of Scissor-tailed Flycatchers.

Data for all pairs were used to calculate summary statistics. When two birds re-paired with each other in successive nesting attempts, we only included data for the first pairing in statistical tests. We retained data for birds that were resampled but paired with different individuals in successive years because, while not completely independent, each new pairing represented a unique interaction. Inspection of the data revealed that males who paired with different females in successive attempts were not cuckolded in the same proportion each time, nor were males who had been cuckolded previously guaranteed to be cuckolded in successive nesting attempts (see below).

We compared the frequency of EPP across years and between our two study sites using *G*-tests, the proportion of EPY in nests across years using an ANOVA, and the arcsine square root transformed proportion of EPY in nests between sites using a

Student's *t*-test in SPSS 19 (IBM Corp. 2010). In the same manner, we compared the frequency of EPP in nests of Scissor-tailed Flycatchers and the frequency of EPY to the average frequency of EPP and EPY for Eastern Kingbird, the only congener for which data were available (61%; Rowe et al. 2001, Dolan et al. 2007) using *G*-tests. We used a *t*-test to compare suboscine and oscine EPP rates because these subfamilies are reciprocally monophyletic groupings.

RESULTS

EPP Rates of Scissor-tailed Flycatchers—We determined paternity for all young in 42 nests ($n = 168$ nestlings). Although the percentage of nests with EPY was high and varied from 50–88% among sites/years (Table 1), difference among years ($G_3 = 6.53$, $P = 0.11$) and sites (year combined) were not significant ($G_1 = 1.25$, $P = 0.26$). Similarly, there was no difference in the proportion of EPY in nests among years ($F_{3,38} = 0.5$, $P = 0.71$) or between sites ($t_{1,40} = 1.5$, $P = 0.15$). Neither the number of nests in which EPP occurred ($G_1 = 0.01$, $P = 0.9$; Figure 1) nor the proportion of EPY in nests ($G_1 = 0.4$, $P = 0.5$) differed between Scissor-tailed Flycatchers and Eastern Kingbirds. In both species 60–62% of nests contained EPY and 45–49% of young were the product of extra-pair copulations.

We identified extra-pair fathers for 35 of 82 EPY. Twelve males accounted for these extra-pair nestlings, with three males siring one EPY each, five males siring two EPY each, three males siring four EPY each, and one male siring ten EPY. Four males sired EPY in more than one nest. All young for each male were sired in the same year. We identified six males who sired young in their own nests as well as extra-pair young in the nests of other males. Of these six, only one experienced partial loss of paternity in his own nest.

We tracked paternity across nesting attempts, both within seasons and across years, for five males and three females. For two pairs that re-nested together in the same year, the nest of the first pair had no EPY in the first nest attempt and 67% EPY in the second attempt. Most of the young of the second pair were EP in both broods (83% first and 67% second year). Likewise, for the male we tracked that repaired with a different female, we found no EPY in the first nest and all young were extra-pair in the second attempt. We tracked three males and one female across years. The first male had 50%, 77%, and 100% EPY in nests in 2009, 2010, and 2011, respectively. The second also exhibited an increase from 50% EPY in 2009 to 80% EPY in 2010. Extra-pair young in the third male's nest decreased from 100% in 2008 and 2009 to 0% in 2010. Likewise, EPY in the female's nest decreased from 80% in 2008 to 50% in 2010. Although our sample size was too small to conduct statistical tests, we saw no clear pattern of increase or decrease in paternity within seasons or across years.

Comparison of EPP RATES between Oscines and Suboscines—Our literature search yielded EPP rates for 11 suboscine species, to which we added data for the Scissor-tailed Flycatcher (Fig. 1, Table 2). We compared these to the 83 oscine species reported in in Spottiswoode and Møller (2004). The distribution of EPP, as measured by the proportion of young that were sired by extra-pair males, was nearly as variable in the suboscines as oscines (Fig. 2). The proportion of species in which EPP accounted for ≤5% of young was virtually identical in suboscines (0.25 [3 of 12]) and oscines (0.24 [20 of 83]). Whereas a few oscines exhibited extremely high levels of EPP (Fig.

2), the proportion of species in which ≥30% of young were sired by extra-pair males included half of the suboscines species but only 22% of oscines. We view these as tentative results because the sample sizes of suboscines were small and our comparisons are not controlled phylogenetically, but the mean percentage of young sired by extra-pair males in this sample of suboscines (21.7, SD = 1.8, *n* = 12) and oscines (17.5, SD = 15.5, *n* = 83) did not differ (*t* = 1.2, *P* = 0.22).

DISCUSSION

EPP Rates of Scissor-tailed Flycatchers—The Scissor-tailed Flycatcher has among the highest reported frequency of EPP for a socially monogamous, non-colonial nesting passerine. Species with comparable rates include the Acadian Flycatcher (*Empidonax virescens*; Table 1, Hung et al. 2009), Common Reed Bunting (*Emberiza schoeniclus*; 86% of broods [*n* = 58 broods], Dixon et al. 1994), Tree Swallow (*Tachycineta bicolor*; 85% of broods [*n* = 25 broods], Barber et al. 1996), Rufous-collared Sparrow (*Zonotrichia capensis*; 60–64% of broods [*n* = 10, 11], Eikenaar et al. 2013), and Eastern Kingbird (60% of broods; Rowe et al. 2001 [*n* = 20], Dolan et al. 2007 [*n* = 89]). Rates of EPP in nests of Scissor-tailed Flycatchers were high in all years but exhibited a nearly 40% difference across years. The average proportion of EPY was more consistent, with <25% difference across years. Variation to this degree seems to be common among many passerines that typically exhibit high rates of EPP (Dunn et al. 1994, Yezerinac and Weatherhead 1997, Albrecht et al. 2007, Rubenstein 2007).

Dolan et al. (2007) found that 30% of male Eastern Kingbirds sired extra-pair young. We were unable to quantify the same statistic because a higher proportion of males were uncaptured at our study sites. Nonetheless, in both species it appeared that a few males disproportionately sired a large proportion of EPY. Importantly, the proportion of nests at which males lost all, some, or no paternity to EP males did not differ between Scissor-tailed Flycatchers (Table 1) and Eastern Kingbirds (Fig. 1; Dolan et al. 2007; $X^2 = 3.07$, df = 2, $P = 0.216$). Males in both species that sired extra-pair offspring were also less likely to be cuckolded by their own mates. Given the potential for monopolization of EPP by one or a few males and the ability of some males to secure both within- and extra-pair paternity, Scissor-tailed Flycatchers and Eastern Kingbirds seem to have comparable patterns of losses and gains of paternity and likely similar opportunities for sexual selection.

Extra-pair paternity rates in Scissor-tailed Flycatchers and Eastern Kingbirds were similar despite the more extreme plumage dimorphism of Scissor-tailed Flycatchers and the assumption that more intense sexual selection operating through extra-pair fertilizations would exist in the more dimorphic species (Lebigre et al. 2013). While our prediction of higher EPP rates in Scissor-tailed Flycatchers may seem unlikely given the already high EPP rate observed in Eastern Kingbirds, a small but diverse set of species exhibit rates of EPP exceeding 70% (e.g., Dixon et al. 1994, Barber et al. 1996, Rowe and Weatherhead 2007, Colombelli-Négrel et al. 2009). Many of these species are sexually dimorphic, with plumage a clear target of sexual selection (Petrie and Halliday 1994, Pryke and Andersson 2005, Olsen et al. 2008). However, other traits, for instance song (Searcy and Yasukawa 1996, MacDougall-Shackleton 1997, Riebel 2009), are equally likely to be the object of female choice of mates both within and outside social pair bonds. Song appears to influence female choice of extra-pair partners in the plumage monomorphic Eastern Kingbird (Murphy et al. 2008). Plumage, and especially tail length, would seem the object of female choice in Scissor-tailed Flycatchers, but more data are needed to test the role of morphology and behavior on the opportunity for sexual selection (sensu Webster et al. 1995) in this species. Equally important, additional study of other kingbirds, especially for those that breed in the tropics or are resident species, is needed to evaluate the extent to which high rates of EPP are characteristic of *Tyrannus* species in general, or associated with migratory behavior (Spottiswoode and Møller 2004, Stutchbury et al. 2007), breeding synchrony (Stutchbury and Morton 1995), breeding density (Westneat and Sherman 1997), food abundance (Hoi-Leitner et al. 1999), or abiotic factors (Hoset et al. 2014).

Comparison of EPP Rates between Oscines and Suboscines—Griffith et al. (2002) reported data for only two suboscines and Spottiswoode and Møller (2004) added one more in their comparative analysis of EPP and migratory strategy. Information on this mostly Neotropical group has been slow to grow, but data on the frequency of EPP now exists for species in eight genera, including three species in Thamnophilidae (typical antbirds) and eight in Tyrannidae (tyrant flycatchers). Two of the three antbirds displayed low EPP rates (2–26% of broods), but rates were more variable (8–86% of broods) in the flycatchers, with all species studied to date displaying EPP. Within this family, extra-pair paternity rates varied up to eight-fold among species pairs within the same genus and up to four-fold variation existed for the four species for which two or more parentage studies exist (Fig. 1, Table 2).

The average EPP rate for Scissor-tailed Flycatchers fell in the upper range of values for the suboscines (Fig. 1). Given that EPP is present in all but one of these 12 species, cryptic polygamy appears to be as widespread in suboscines as it is in oscines, although the frequency of EPP exhibits considerable variation among families (Griffith et al. 2002). The frequency of EPP varies with migratory distance (Spottiswoode and Møller 2004), and our sample of suboscines is dominated by long-distance migratory tyrannid flycatchers, which may account for much of the interspecific variability. Indeed, the lowest frequency of EPP among the North American breeding tyrant flycatchers occurred in the Eastern Phoebe (*Sayornis phoebe*), the only short-distance migrant.

The potential for future productive comparisons of extra-pair mating systems within the Tyrannidae is substantial given their wide distribution across northern and southern hemispheres and the existence of both migratory and resident species. We encourage further study of suboscines, and especially tyrannids in both temperate and tropical regions, because it is only with such phylogenetically controlled studies that we may elucidate mechanisms of EP mating systems that remain to be answered.

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TABLE 1. Proportion of nests of Scissor-tailed Flycatchers at each study site and year that contained young sired only by the social male (WPY only), young sired only by an extra-pair male (EPY only), broods with both social and extra-pair young (mixed paternity), and broods that contained any EPY (any EPY). Proportion of young that resulted from extra-pair paternity is reported for each site and year (proportion EPY).

		Proportion of Nests with					
Location	Nest *n*	WPY[a] Only	EPY[a] Only	Mixed Paternity	Any EPY[b]	Nestling *n*	Proportion EPY[a]
Fort Sill	29	0.28	0.24	0.48	0.72	110	0.55
Refuge	15	0.47	0.13	0.4	0.53	58	0.38
2008	5	0.4	0.2	0.4	0.6	17	0.35
2009	8	0.12	0.25	0.63	0.88	31	0.55
2010	13	0.23	0.15	0.62	0.77	51	0.59
2011	18	0.5	0.22	0.28	0.5	69	0.42
Average		0.36	0.18	0.46	0.64		0.49

[a] Abbreviations: WPY, within-pair young; EPY, extra-pair young.

[b] Any EPY refers to all nests that contained EPY (EPY only + mixed paternity) and indicates the overall rate of EPP.

TABLE 2. Frequency of extra-pair paternity is given for suboscine species for which EPP estimates are available. Estimates are rounded percentages of all sampled young that resulted from extra-pair copulations and percent of all sampled broods that contained extra-pair young. Numbers in parentheses are sample sizes given in each study.

	EPP Frequency		
Species	% Young (*n*)	% Broods (*n*)	Source
Cercomacra tyrannia	0 (15)	0 (12)	Fleischer et al. 1997
Stymphalornis acutirostris	13 (30)	29 (14)	Sobotka 2011
Thamnophilus atrinucha	3 (89)	2 (50)	Tarwater et al. 2013
Elaenia flavogaster	4 (24)	8 (13)	Stutchbury et al. 2007
Elaenia chiriquensis	37 (14)	67 (15)	Stutchbury et al. 2007
Empidonax minimus	39 (78)	62 (21)	Tarof et al. 2005
Empidonax minimus		33 (18)	Kasumovic et al. 2009
Empidonax traillii	14 (140)	23 (56)	Pearson et al. 2006
Empidonax virescens	41 (133)	58 (53)	Woolfenden et al. 2005
Empidonax virescens	14 (29)	25 (12)	Evans et al. 2009
Empidonax virescens	79 (14)	86 (7)	Hung et al. 2009
Pyrocephalus rubinus	33 (21)	44 (16)	Ríos-Chelén et al. 2008
Sayornis phoebe	5 (769)	9 (174)	Beheler et al. 2003
Sayornis phoebe	12 (76)	20 (20)	Conrad et al. 1998
Tyrannus tyrannus	42 (64)	60 (20)	Rowe et al. 2001
Tyrannus tyrannus	47 (257)	61 (89)	Dolan et al. 2007
Tyrannus forficatus	49 (168)	66 (44)	Current study

FIGURE 1. Weighted means and confidence intervals for the proportion of young of extra-pair origin (EPP young) and broods with extra-pair paternity (EPP brood) for 12 suboscine species. Confidence intervals were calculated using the uncorrected score method (Newcombe 1998).

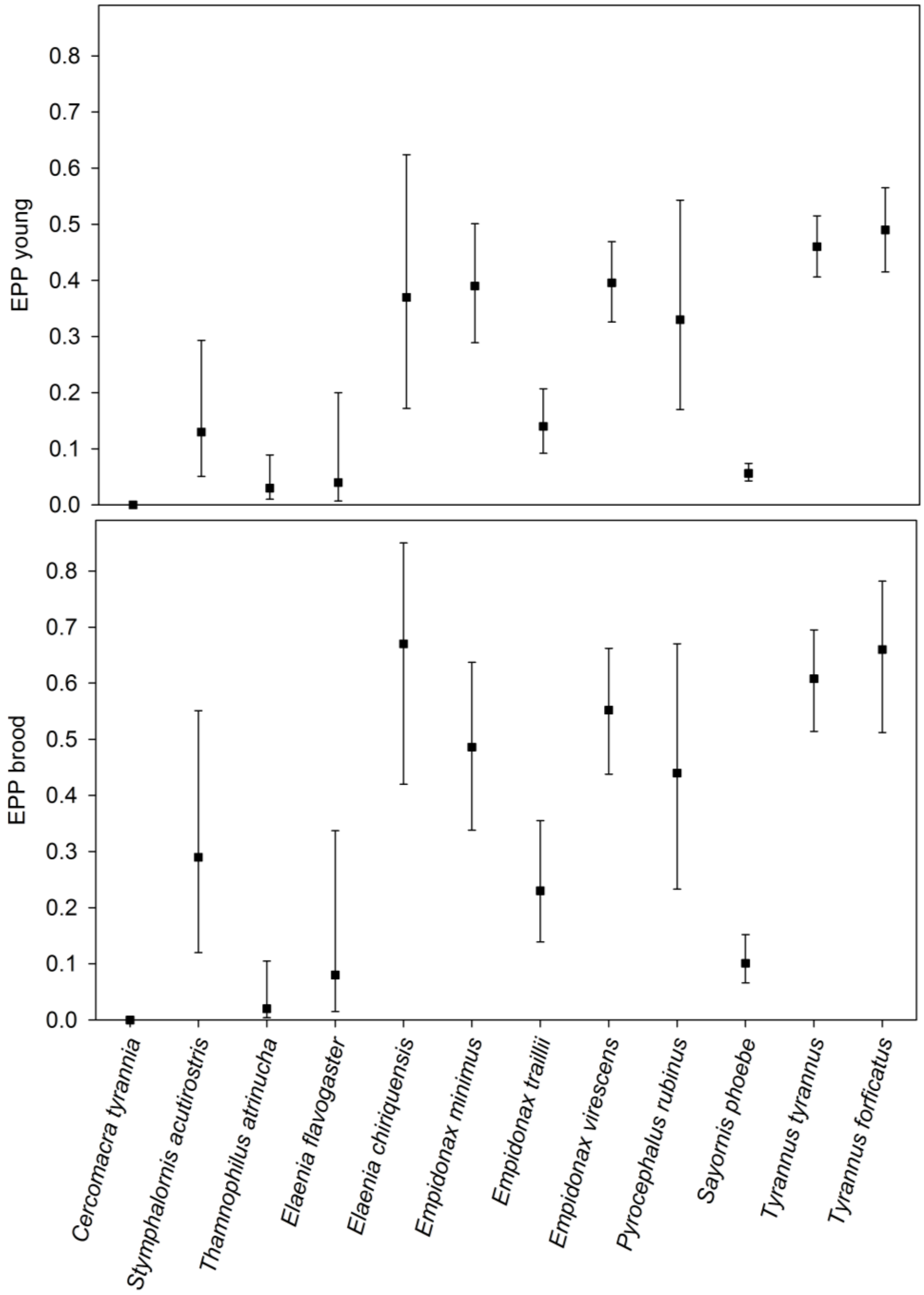
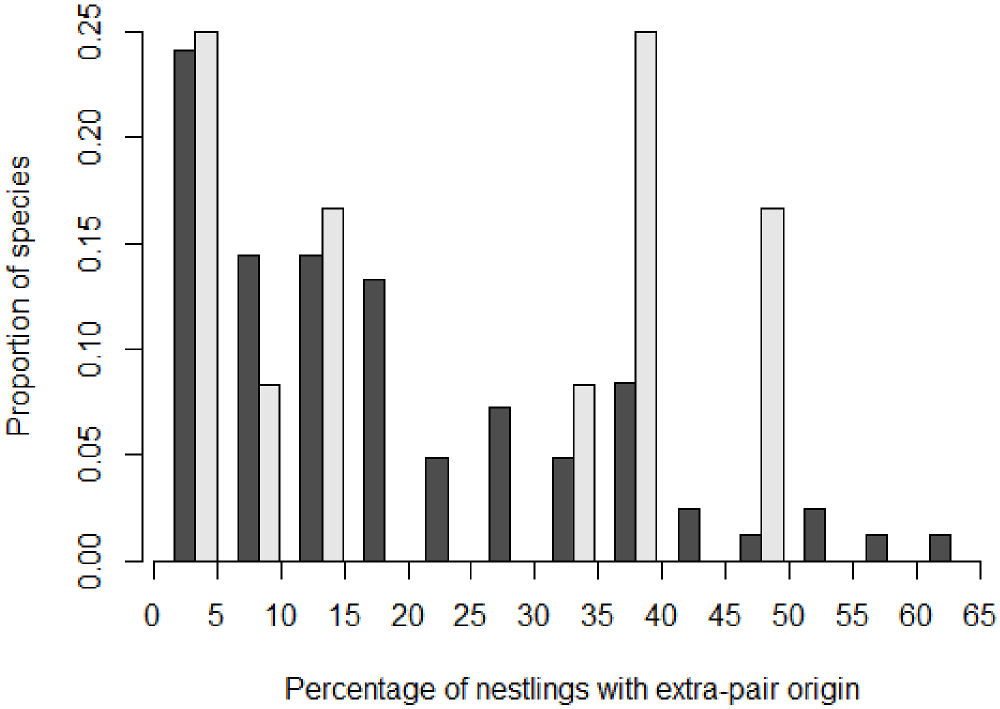


FIGURE 2. Histogram of the proportion of oscine (dark gray bars) and suboscine (light gray bars) passerine species with particular percentages of young from extra-pair origins. Weighted means are used when more than one estimate of EPP existed for a species. Data are from Spottiswoode and Møller (2004) and Table 2 of this paper.



CHAPTER TWO

ORNAMENTATION AND FLIGHT FEATHER MORPHOLOGY SHAPE EXTRA-PAIR PATERNITY IN A SEXUALLY DIMORPHIC PASSERINE

Diane V. Roeder[1],

Michael S. Husak[2], Michael T. Murphy[3], and Michael A. Patten[1]

[1] Department of Biology & Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019, USA

[2] Department of Biological Science, Cameron University, Lawton, OK 73505, USA

[3] Department of Biology, Portland State University, Portland, OR 97207, USA

ABSTRACT

Extra-pair paternity has been linked to increased variance in reproductive success of socially monogamous species. Morphology in sexually dimorphic species has been related to increasing opportunity for sexual selection when traits are variable and reflect individual quality. It is poorly understood how traits that are both ornamental and functional might interact to influence the distribution of paternity across individuals. We examined extra-pair paternity in the Scissor-tailed Flycatcher (*Tryannus forficatus*), a sexually dimorphic suboscine passerine, to not only determine how flight feather morphology and ornamental coloration were related to paternity for both males and females, but also whether morphologies that impacted paternity differed among birds with different flight performance. We assessed paternity at 140 nests across 7 years. We found that 73% of nests contained extra-pair young and that 59% of nestlings resulted from extra-pair fertilizations. Males that secured paternity with their social mate were in better body condition and had more symmetrical tails. In paired comparisons, males that were cuckolded were not different than their cuckolders. Long, symmetrical primary attenuations were also associated with greater maneuverability in flight (i.e. obstacle avoidance). Neither color nor female morphology was related to cuckoldry, but it may be important during initial mate choice. Our study demonstrates that males in better condition with larger, more symmetrical wing and tail morphologies were less likely to be cuckolded, but that these characteristics were not associated with female choice of extra-pair mates. Because wing features played a role in flight performance but not cuckoldry, our results suggest that males in good condition with symmetrical tails may maintain paternity through female faithfulness or via mate-guarding.

Keywords—Cuckoldry, mate choice, sexual selection, flight performance, tail length, asymmetry, color, Scissor-tailed Flycatcher, *Tyrannus forficatus*

INTRODUCTION

Sexual infidelity and extra-pair paternity (EPP) are common in socially monogamous birds, particularly in migratory passerines (Griffith et al. 2002, Westneat and Stewart 2003). EPP benefits some males via increased reproductive success, particularly when they can maintain paternity in their own nests (Dolan et al. 2007). Other males lose paternity in their own nests while being unable to secure extra-pair copulations (EPC), resulting in high variance in reproductive success within populations (Albrecht et al. 2007, Dolan et al. 2007, Lebigre et al. 2013). Benefits to females are difficult to assess. When females are not coerced into EPCs, benefits are attributed to fertility insurance (Sheldon 1994, Pizzari et al. 2004; *cf* Morrow et al. 2002), access to male-guarded resources (Griffith et al. 2002), or, indirectly, increased embryo survival (Kempenaers 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, Varian-Ramos and Webster 2012, Arct et al. 2015; *cf* Hsu et al. 2014, Kramer 2015). Females may 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 they have young in multiple nests (Eliassen and Jørgensen 2014).

Ultimate benefits aside, it has been shown 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, Potti and Merino 1996, Amundsen et al. 1997, Pryke and Griffith 2007, Moreno et al. 2015) to ensure that EPC attempts are worth the risk if multiple matings depletes sperm (Birkhead and Fletcher 1995) or of contracting either disease (Sheldon 1993, Westneat and Rambo 2000, Poiani 2010) or sustaining damage to sexual ornaments if 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 (Potti and Merino 1996, 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 and two opposing sets of traits for females that participate in EPCs, depending on whether they participate via coercion or choice.

If traits that help gain paternity are costly ornaments, then the traits are expected to serve as honest signals of quality and strength (Evans 1993, Pryke and Andersson 2005). Good body condition in birds with exaggerated ornaments may signal quality in both developmental and disease-resistance pathways (Balenger et al. 2015, Whittingham et al. 2015), as well as in foraging performance and predator evasion (Møller 1993, Brown and Brown 1998). 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 (Balmford and Read 1991, Pryke and Andersson 2005). Bilateral ornaments such as elongated tail feathers or sound-producing wing feathers must still function in flight, so we expect ornaments to be symmetrical (Evans 1993, Evans et al. 1995). 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 (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).

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 important in cuckoldry and flight performance, such as obstacle navigation success, in-flight collisions, and speed. We made four primary predictions: 1) males in poor condition and with dull coloration and relatively short or asymmetrical flight feathers will be cuckolded more often than brighter, more extravagant, and symmetrical males; 2) cuckolded males will be in poorer condition and have duller color and shorter or more asymmetrical flight feather characteristics than the extra-pair males that cuckold them; 3) females in poor condition and with dull coloration and short or asymmetrical wings and tails will cuckold social mates less often than those in better condition and with longer or more symmetrical flight feathers; and 4) morphology associated with cuckoldry and extra-pair mate selection, such as longer and more symmetrical flight feathers, will be associated with enhanced flight performance.

METHODS

Study Species—The Scissor-tailed Flycatcher is a suboscine passerine with high rates of EPP (Roeder et al. 2016). Adult males are marginally heavier and have brighter salmon-colored flanks and redder axillaries (underwing feathers) than females. Both sexes have forked tails, but males have longer wing and outer tail feathers (mean ± SD: wing 129.4 ± 3.8 mm; tail 216.8 ± 29.5 mm) than females (wing 114.3 ± 3.4 mm; tail 146.7 ± 20.5 mm; Regosin and Pruett-Jones 2001), although there is considerable variation in the morphology of each sex and tail length, plumage color, and mass of small males overlaps with that of large females (Pyle 1997). Wing feather and tail feather asymmetry is uncorrelated with tail length (Regosin and Pruett-Jones 2001). The outermost primary is attenuated on the trailing edge of the feather tip, with attenuation deeper in males (Pyle 1997) and probably functioning to fine-tune wing position during flight. Male 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 exaggerated primary attenuation (D. V. Landoll 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 on their own territories, although each will foray off-territory when resources are scarce (Regosin 2013). Females build nests and incubate eggs without male assistance, but both sexes provision young until several weeks post-fledging (Regosin 2013). Females often travel long distances unaccompanied by their social mates to search for soft material with which to line the nest.

Study Area—Data were collected from April to August of 2008–2014 at the Wichita Mountains Wildlife Refuge and the adjoining Fort Sill Artillery Base in Comanche County, Oklahoma. The refuge is primarily mixed-grass prairie broken by low-lying mountains and riparian corridors composed of oaks (*Quercus* spp.), American elms (*Ulmus americana*), and eastern red cedars (*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 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 travelled 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.

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 >6 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 2016). We collected blood samples from all captured birds (50 µL from adults and 25 µL 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.

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). Tarsus length can be difficult to accurately measure, so we measured tarsus length three times for a subset of 22 birds across seasons to estimate measurement error using a model II analysis of variance (Bailey and Byrnes 1990). Measurement error was relatively low at 2.5% ($s^2_{among} = 1.08$, $s^2_{within} = 0.03$), so we retained tarsus asymmetry in our analyses (see Marantz and Patten 2010). For each side of the body, feather measurements were taken with a wing rule to the nearest 0.5 mm and included flattened wing; 9th primary attenuation depth (from tip of primary to point on feather when the curve switches from angling towards the rachis to angling towards the feather tip); Kipp's distance, a measure of wing pointedness or primary projection (distance from the tip of the first secondary to the tip of the longest primary on a folded wing; Swaddle and Lockwood 2003); and each tail feather (from insertion to tip of each feather). We averaged both sides for character length except for the tail because individual feathers overlay to create a single visual signal when a bird is perched. Measurements from each side of the body were used to calculate trait asymmetry. Kipp's distance and primary attenuation asymmetry were measured starting in 2013. 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 2013-14. 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*).

Flight Measurements—To measure flight performance, we constructed a portable flight tunnel through which birds were flown (Bowlin and Winkler 2004; Fig. 1). The flight tunnel (1.2 m × 1.2 m × 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 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 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 µL with Type-It Microsatellite PCR Kits (Qiagen, Valencia; #206243). We used non-labelled reverse primers and forward primers labelled 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°C for 15 min; 25 cycles of 94°C for 30 s, 59°C for 90 s, and 72°C for 60 s; 15 cycles of 94°C for 30 s, 53°C for 90 s, and 72°C for 60 s; and a 60°C final extension for 30 min. Amplified PCR fragments were separated by capillary electrophoresis using an ABI 3130XL DNA Analyzer using Peak Scanner 2 (Applied Biosystems, Inc., Foster City, CA).

Parentage Assessment—We calculated allele frequencies and exclusionary probabilities for all loci using CERVUS v. 3.0.7 (Kalinowski et al 2007). Non-exclusionary probability over all loci was 0.0006 for the parent pair. Mean allele number per locus was 8.3 (range 3–17). All loci were in Hardy-Weinberg equilibrium, and the probability of null alleles was 0.

We assigned parentage with the maximum likelihood method in CERVUS (Kalinowski et al. 2007), which simulates paternity given the genetic dataset to generate a threshold logarithm of odds (LOD) score for parentage assignment. After mother/offspring genotype pairings are evaluated, CERVUS calculates a likelihood ratio for each candidate father/offspring pair across all evaluated loci. The most likely father is assigned paternity if the difference between his and the next most likely father's LOD score exceeds the threshold LOD value. We simulated 100000 offspring using the observed allele frequencies and an estimate of 0.99 loci typed and 0.01 mistyped. We set 60% of candidate fathers captured according to the mean capture rate of territorial males and the average number of males with abutting territories. No females mismatched nestlings in their nests at any loci. All males sampled or re-sighted in a population were included as potential fathers for paternity analysis (refuge, *n* = 101; Fort Sill *n* = 105).

When a nestling/social male pair had a negative LOD score, nestlings were considered extra-pair young (EPY), which was confirmed by nestlings mismatching social male genotype at a single locus or greater. If nestling/social male pairs had positive LOD scores and one or fewer mismatches, nestlings were considered within-pair young (WPY) because of the possibility of null alleles, mutations, or genotyping errors. This occurred only twice in our dataset. CERVUS provides paternity assignments at 80% and 95% confidence intervals. We assigned males as extra-pair sires only when they were flagged at the 95% confidence level and had no mismatches with the nestlings. Because we estimate that we captured around 60% of the males in the population, we used this conservative assignment criterial to avoid assigning the wrong male as genetic sire. 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 prevalence of EPP in nests and number of nestlings resulting from EPCs across years and between sites using *G*-tests (Gotelli and Ellison 2004). Morphological and flight variables were examined for symmetry, normality, and outliers and square-root or log-transformed when necessary for parametric tests. For clarity of interpretation, we present figures using untransformed data. All morphological comparisons were conducted using the statistical program R 2.3.2 (R Core Team 2013).

For males and for females, we constructed color scores for flank and axillary regions by combining L*, a*, and b* measures into a variate for each region using principal component analysis (PCA). The first principal component (PC1) accounted for a substantial amount of the variance in color for male axillary (85%) and flank (62%) color patches, as well as for female axillary (80%) and flank (59%) color patches. Red (a*) and yellow (b*) measurements had high loadings on each PC1 (Table 1) that corresponded to increasing intensity of crimson. Axillary PC1 for both males and females also corresponded to increasing darkness (L*) or deepness of color. L* loadings were weaker for both male and female flank PC1 (Table 1). We used axillary and flank PC1 scores to evaluate the relationship between color and morphology using Pearson's correlations and six morphological characters (body condition, tarsus length, wing chord, Kipp's distance, primary attenuation, and tail length). We report all correlation coefficients > 0.30. Flank and axillary color PCs were used in the analysis described below.

We examined differences in female and male morphology at nests where EPP was absent or present using logistic regression. For each sex, we ran two regression sets, the first with morphological variables measured for all birds across all years (body condition, tarsus length/asymmetry, flattened wing length/asymmetry, primary attenuation, tail length/asymmetry), the second with additional variables measured only in 2013–2104 (primary attenuation asymmetry, Kipp's distance/asymmetry, axillary coloration, flank coloration). Data were examined for multicollinearity using variance inflation factors (VIF > 4; Zuur et al. 2010). Flattened wing (VIF = 6.18) and body condition (VIF = 4.75) exceeded the VIF cutoff and were highly correlated ($r = 0.88$). When we removed flattened wing, all other variables had VIF < 4 and were retained. All morphological variables included in these models had low correlations ($r < 0.4$), with the exception of primary attenuation and tail length ($r = 0.54$). We used the MuMIn package to evaluate all possible combinations of morphological variables included in each regression data set. We evaluated model sets using the Akaike information criterion (AIC; Burnham and Anderson 2002) and ranked models from lowest to highest AIC. We presented models with informative parameters (Arnold 2010) within two AIC of the top model. Because our goal was to rank morphological predictors given their power to explain cuckoldry and flight performance, we summed Akaike weights (w_i) across all models in which a particular predictor was present to evaluate the relative contribution of that predictor to the probability of EPP (Arnold 2010). We interpreted morphological variables that had approximately twice the summed w_i than other variables in the model set. When there was evidence of strong predictors, we evaluated biologically meaningful interactions, although no interactions ranked higher than models in the additive sets. We used two-tailed paired *t*-tests to compare morphology between social males at a nest and males that cuckolded them.

We used the same approach to multimodel inference as above to compare flight morphology of birds that succeeded or failed to navigate the flight obstacle, as well as of birds with minor (wing or tail tip) or major hits (head, body, or wrist) on the obstacle. Flight morphology included body condition and all wing and tail measurements. Flattened wing (VIF = 11.6), Kipp's distance (VIF = 11.7), and primary attenuation (VIF = 8.8) were multicollinear, and all were highly correlated for birds in the flight dataset ($r > 0.89$). We thus removed wing length and Kipp's distance from the data set.

RESULTS

EPP Rates—We assessed parentage at 140 nests and for 547 nestlings. We identified mothers at 123 of these nests, captured social males at 119 nests, and identified 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 2). Males in our dataset sired 1-5 extra-pair young, generally spread across years. The most prolific males sired three EPY in a single year across three nests. Of the 24 nests at which we had paternity information for both the social and extra-pair males, half of the extra-pair males were cuckolded at their own nests. 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. A nest 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.

Color and Morphology—For both males and females, axillary and flank PC1 scores reflected increasing crimson and salmon color intensity, respectively, and deepness (Table 1). Male flank color was not correlated with any morphological character. By contrast, axillary coloration was positively correlated with primary attenuation length (r_{64} = 0.39; Fig. 2A), wing length (r_{64} = 0.33; Fig. 2B), and total tail length (r_{64} = 0.51; Fig. 2C). These scores reflect an increase in the intensity of crimson coloration in male axillary feathers as primary attenuation, wing chord, and tail length increased. For females, both axillary PC1 (r_{72} = 0.56; Fig. 2D) and flank PC1 (r_{72} = 0.33; Fig. 2E) were positively correlated with total tail length, meaning that females with longer tails had more intensely crimson axillary and flank feathers.

Male Morphology and Probability of Cuckoldry—Logistic regressions for the presence/absence of EPP in nests and male morphological characteristics measured in all birds (*n* = 200) resulted in five competing models <2 AIC of the “best” model (Table 3). The best model included body condition, total tail length asymmetry, and tarsus asymmetry. Body condition was present in four competing models and was the only single variable model in the set. Total tail length asymmetry was present in three competing models, as was tarsus asymmetry. When we summed w_i across all models in which a variable was present, these variables had sums twice those of all other variables (Table 4). When we used the subset of birds for which Kipp’s distance and asymmetry, primary attenuation asymmetry, and flank and axillary coloration had been measured (*n* = 123), the top logistic regression model set included a single model, Kipp's distance asymmetry (Table 3). Its Σw_i was greater than twice that of other variable weights (Table 4). Cuckolded males had poorer body condition and greater tail asymmetry than did males that were not cuckolded (Fig. 3). Contrary to expectations, these males had greater tarsus and Kipp's distance asymmetry (Fig. 3). We found no difference in morphology of social males and males that cuckolded them (Table 5).

Female Morphology and Probability of Cuckoldry—No female morphological characteristic or combination of female characteristics was related to either the presence or absence of EPP in nests (*n* = 123). Tarsus asymmetry was the only model better than the null (Table 3) and had the largest Σw_i (Table 4), but because it was not AIC > 2 better than the null model, we concluded that it did not have an important effect on cuckoldry.

Flight and Morphology—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. For success or failure at navigating the obstacle, two single variable models, primary attenuation and tail length, had AICc < 2 (Table 3), and primary attenuation Σw_i was larger than that of all other morphological variables (Table 4). For the degree of contact with the flight obstacle, primary attenuation asymmetry was the only model with AICc < 2 (Table 3), and its Σw_i was nearly double that of other variables (Table 4). Birds that successfully navigated the flight obstacle had longer primary attenuation (Fig. 4A), while birds with greater primary attenuation asymmetry were more likely to have major contact with the obstacle (Fig. 4B).

DISCUSSION

The objective of our study was to determine whether the incidence of cuckoldry was related to feather morphology and flight performance in a species with exaggerated sexual dimorphism (Regosin and Pruett-Jones 2001) and high rates of EPP (Roeder et al. 2016). We documented a highly promiscuous system in which females did not appear to exhibit strong extra-pair selection, but also did not cuckold high-quality social males. For nests that contained EPY, social mates and extra-pair mates did not differ in body condition, color, or morphology, suggesting that some males were unsuccessful at maintaining paternity not because of flight performance or morphology, but for other reasons, perhaps lack of experience or lower aggressiveness (Hoi et al. 2013). Reasons for female participation in EPCs remains unclear, despite years of research, as most adaptive scenarios have weak support (Akçay and Roughgarden 2007). Female extra-pair behavior may have no adaptive basis, but may be a product of sexual conflict and strong selection on males to obtain extra-pair fertilizations (Arnqvist and Kirkpatrick 2005). Alternately, females may engage in EPP to encourage a “cooperative neighborhood” in which paternity uncertainty promotes a neighborhood response to predation threats (Eliassen and Jørgensen 2014).

Scissor-tailed Flycatchers in this 7-year study had one of the highest rates of EPP recorded for socially monogamous passerines (Spottiswode and Møller 2004, Roeder et al. 2016), with 73% of nests containing EPY and 59% of nestlings resulting from EPCs. We could not calculate the total within- and extra-pair contributions to reproductive success of males because we were unable to sample every nest in the population. Nevertheless, an average of 62% of males maintained at least partial paternity in their own nests, and no males were disproportionately successful in siring EPY. In fact, 50% of males that sired young through EP fertilizations and for whom we also had data from their own nest lost paternity to other males.

When we assessed whether the probability of EPP was related to individual social female characteristics, we found that no morphological trait was related to the probability of a female cuckolding her social mate, even though female color and size varied considerably and axillary and flank color intensity was greater in longer-tailed females. Similarly, Bradely et al. (2014) failed to find a relationship between female morphology and reproductive performance in the sexually dimorphic Barn Swallow (*Hiruno rustica*), which also has elongated tail feathers. Although we found no evidence that males targeted females in poor condition for EPCs or that large females in good condition escaped mate-guarding, if both occurred then we would expect no pattern, as seen here. It is possible that female condition and color helps to initiate social mate selection (female-female aggression) or signals a female’s ability to defend her nest (Hill 1993, Amundsen et al. 1997, Cain and Ketterson 2012, Jacobs et al. 2014). Alternatively, female coloration may be a correlated response to selection on male coloration (Hill 1993, Bradley et al. 2014), or females paired to high quality or genetically compatible males, regardless of their own phenotype, may invest more to avoid EPCs than do females paired to low quality males (Eliassen and Kokki 2008).

Cuckoldry was related to body condition and tail ornament symmetry of the social male. Males not cuckolded were in better body condition and had lower tail asymmetry than cuckolded males. We found no evidence that tail asymmetry and length were linked, thus indicating that tail asymmetry was neither promoted nor constrained by increasing length (Evans 1993). Tail asymmetry may reflect natal developmental stability (Evans 1993, Greico 2003) or seasonal developmental stability during feather molt (Møller 1996), both of which may be influenced by stress, food availability, and environmental conditions (Swaddle and Witter 1994, Møller 1996, Greico 2003). Male condition and ornament quality has been related to both mate and territory quality in some species (Keyser and Hill 1998, Wolfenbarger 1999), and high territory quality could reduce cuckoldry in several ways. If there is a tradeoff between foraging time and time spent mate guarding, males in good condition may be able to secure WPP by investing more in mate guarding (Hoi et al. 2013) and may be more successful at repelling intruding males (Olsen et al. 2008). Social mates of these males may be less inclined to copulate outside of the pair bond if condition and ornament quality were good cues of overall male quality (Podmokła et al. 2015, Whittingham et al. 2015).

Contrary to expectations, Kipp’s distance asymmetry and tarsus asymmetry were greater in male Scissor-tailed Flycatchers that were not cuckolded. 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 (Dawideit et al. 2009, Leisler and Winkler 2003). The shape and symmetry of wingtips is particularly important during take-off or when upward thrust is needed (Lockwood et al. 1998), such as during foraging, territorial contests, or flight displays. We expected that Kipp's distance asymmetry would be related to a greater probability of cuckoldry but found the opposite pattern. This result was counterintuitive and may have been a result of measurement error, as wear on wing feather edges may have resulted in greater asymmetry than in fresh feathers. Still, if Kipp's distance asymmetry resulted in greater drag on one side of the body, asymmetrical males may have an advantage during their sideways, zig-zag flight displays. It is possible that asymmetry resulted in sharper changes in direction at the top and bottom of each maneuver, rendering displays of such males more attractive and lowering their probability of being cuckolded. Confirmation would require careful observation of the right versus left directionality of each display.

We unexpectedly found that tarsus asymmetry was greater in males that maintained complete paternity in their own nests. This trait has been used as a measure of developmental stability, and thus quality, in many studies (Watson and Thornhill 1994, Rowe et al. 1997). Experimental work suggests that tarsus asymmetry can result from brief periods of stress during nestling development without affecting any other aspect of morphology or post-fledging survival (Talloen et al. 2010), and thus it may not relate directly to fitness (Palmer 1999, Gangestad and Thornhill 2003). We posit that tarsus asymmetry was not under direct sexual selection pressure, but was related to nestling resource allocation and developmental tradeoffs with other features such as tail asymmetry, particularly when environmental conditions are unfavorable (Andersson et al. 2002, Talloen et al. 2010). Whereas the two were only weakly negatively correlated (r = - 0.20), birds with the most symmetrical tails also had the most asymmetrical tarsi and vice versa, suggesting a constraint relationship in which resources allocated to even tail growth negatively impact tarsus symmetry.

Male body condition and tail symmetry may be signals of genetic or developmental quality (Evans 1993, Greico 2003), but these traits do not predict flight performance. Only primary attenuation length and asymmetry were related to coarse-scale measures of flight performance. These results agree with the relationship between primary feather length and symmetry in European Starlings (*Sturnus vulgaris*), for which individuals with shorter, more asymmetrical primary feathers had reduced flight performance (Swaddle et al. 1996). Additionally, flight models of fork-tailed birds (Thomas 1993) suggest that asymmetry in wing surfaces that provide lift and thrust, such as primary feathers, should have a greater effect on flight than asymmetry in tail surfaces, particularly those that are primarily ornamental, such as the outer two tail feathers of the Scissor-tailed Flycatcher. Axillary and flank coloration, which are displayed during male flight displays and were correlated with measures of body size, were not related to the probability of cuckoldry. It is likely that females did not evaluate potential extra-pair partners on the basis of their flight displays, nor was flight performance measured at this scale related to a male's ability to maintain paternity. Flight displays instead may be used in initial mate choice and in the maintenance of territory boundaries, as displays continue throughout the season. Similar relationships are present in males of the Red-collared Widowbird (*Euplectes ardens*), in which red color badges are involved in male-male competition but not in female choice (Pryke et al. 2001, Pryke and Andersson 2003), and in the Superb Fairy-wren (*Malurus cyaneus*), in which displays continued throughout the season but were not related to paternity (Green et al. 2000).

The relationship between cuckoldry, body condition, and tail asymmetry likely reflects female faithfulness to social partners of good genetic or developmental quality rather than female choice for extra-pair partners with particular qualities. Direct comparison of social males with the extra-pair males to whom they lost paternity revealed no difference in morphology, body size, or condition, unlike patterns seen in the congeneric Eastern Kingbird (*T. tyrannus*; Dolan et al. 2007) and other species (Bitton et al. 2007, Dias et al. 2014, Moreno et al. 2015, Olsen et al. 2008). Taken together, our results suggest that male-male competition was not a driver of EPP in this system, nor was female choice for extra-pair mates with exaggerated morphology or better flight performance. We posit that cuckoldry was driven by a combination of male mate-guarding and female faithfulness to high quality social mates.

Why is extra-pair paternity so high in this system if it is not driven by strong inter- or intra-sexual selection on exaggerated male plumage or displays? We hypothesize two reasons that EPP was high during our study. First, our observations suggest that Scissor-tailed Flycatcher nestlings require care from both females and males to fledge; females alone cannot feed nestlings at a high enough rate or successfully drive off predators (Landoll 2011). We never saw a case of divorce during a nesting attempt, despite detailed tracking of >800 nests across 7 years; instead, partners were lost because of death, and all losses resulted in either nest abandonment or nestling starvation (Landoll 2011, D. V. Landoll personal observation). Males of some species reduce care in response to perceived cuckoldry (Perlut et al. 2012, Matysioková and Remeš 2013), but the cost of withdrawing care is high (i.e., total nest failure) for male Scissor-tailed Flycatchers. Because most males retained at least some WPP, nest failure would result in complete loss of within-pair success (Whittingham et al. 1993), which is the largest component of reproductive success (Lebigre et al. 2012). Likewise, if males do not directly observe EPCs, they may not be able to assess paternity loss and may not reduce nestling care, as has been shown for the congeneric Eastern Kingbird (Chutter et al. 2016) and other species (Varian-Ramos et al. 2012). As a result, female Scissor-tailed Flycatchers may not suffer high male-imposed costs for engaging in EPCs (Hoi et al. 2013).

A second hypothesis relates to an idea by Eliassen and Jørgensen (2014), who suggested a more immediate benefit beyond male quality to explain why females might engage heavily in EPP when nest predation rates are high, as they were during our study (68% total and 11% partial nestling loss). By mating multiply, females create paternity uncertainty for males breeding nearby, behavior that creates a “cooperative neighborhood” in which many males invest to protect their own social nest and other nests in their neighborhood because they are sires at multiple nests. Males in good condition and capable of protecting their nests without help should be cuckolded less often, while females cuckold poorer quality males to gain extra protection for their nestlings. These predictions match the high EPP rates we recorded and fit the relationship between body condition, tail asymmetry, and the probability of cuckoldry. Notably, we caught multiple males at over a third (~35%) of nests at which we used predator decoys, and additional males that we failed to capture were present at many more, implying that males respond to threats at nearby nests, not just at their own nests.

Whether such a response toward presence of predators within visual range is ingrained or is geared towards protecting EPY remains to be explored.

In summary, we found evidence that male Scissor-tailed Flycatchers in good condition and with symmetric tails were less likely to be cuckolded than asymmetrical males in poor condition, yet cuckolded males did not differ morphologically from their cuckolders. Likewise, morphological characters important to flight performance were not associated with extra-pair paternity. We conclude that it is unlikely females choose extra-pair mates on the basis of an assessment of morphology or flight, whether independent of, or relative to, the social mate. We found no evidence of extra-pair selection on female morphology, so we infer it is unlikely that mutual choice or male coercion was a primary driver of cuckoldry, although we cannot rule out simultaneous targeting of small females in poor condition for forced copulations while large females in good condition escaped mate-guarding and engaged in mutual choice. Even so, we suggest that females were faithful to males in good condition and with symmetrical tails because such birds are better at mate-guarding and nest defense. Recruitment of young from sampled nests was low at our study site because of high dispersal distance (Becker 2016), so we were unable to determine if EPP was adaptive for females. Future research on juvenile recruitment and reproduction, individual quality and flight performance, and on the cooperative neighborhood hypothesis are needed if we are to understand the costs and benefits of EPP and its distribution across populations.

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TABLE 1. Color loadings on principal component 1 for a principal component analysis used to construct a single measure of color of both the wing axillary and flank color patches of male and female Scissor-tailed Flycatchers captured in Comanche County, Oklahoma, from 2012–2014. The color scale is represented by light-to-dark (L*), green-to-red (a*), and blue-to-yellow (b*) axes. High positive loadings corresponded to colors that were deeper and more red and yellow.

	Loadings		
	L*	a*	b*
Male			
Flank	-0.45	0.87	0.82
Axillary	-0.95	0.99	0.7
Female			
Flank	-0.31	0.7	0.94
Axillary	-0.79	0.98	0.86

TABLE 2. Summary of the proportion of Scissor-tailed Flycatcher broods with extra-pair paternity (EPP) present and nestlings resulting from extra-pair copulations between sites and across years. Broods could contain within-pair young only (WPP only), extra-pair young only (EPP only), or mixed paternity. The proportion of broods containing one or more extra-pair young are given in the Any EPP column. Nestlings were either of within-pair (WPY) or extra-pair (EPY) origin.

	Broods					Nestlings		
Location	*N*	WPP Only	EPP Only	Mixed Paternity	Any EPP	*N*	WPY	EPY
Fort Sill	74	0.26	0.35	0.39	0.74	293	0.42	0.58
Refuge	66	0.29	0.41	0.30	0.71	254	0.41	0.59
2008	4	0.50	0.25	0.25	0.50	14	0.71	0.29
2009	8	0.13	0.25	0.62	0.87	31	0.45	0.55
2010	13	0.23	0.39	0.38	0.77	52	0.33	0.67
2011	21	0.57	0.19	0.24	0.43	71	0.68	0.32
2012	21	0.19	0.48	0.33	0.81	84	0.32	0.68
2013	37	0.24	0.38	0.38	0.76	144	0.47	0.53
2014	36	0.20	0.47	0.33	0.81	151	0.28	0.72
Totals	140	0.27	0.38	0.35	0.73	547	0.41	0.59

TABLE 3. Best logistic regression models (ΔAICc < 2) and model weights (w_i) for differences in morphology between Scissor-tailed Flycatcher males that were or were not cuckolded, for females that did or did not cuckold their mates, for birds that succeeded or failed to navigate the flight obstacle, and for birds with minor versus major head, body, or wrist hits on the obstacle. All males/females refers to models run with morphological characters measured in all years (2008-2014). Subset males/females refers to models run with morphological characters measured only in 2013-2014

TABLE 3.

Model Set	AIC_c	ΔAIC_c	w_i
Cuckoldry - All Males			
Body Condition + Tail Asym + Tarsus Asym	147.3	0.00	0.029
Body Condition + Tail Asym	147.7	0.42	0.023
Body Condition + Tarsus Asym	148.3	1.00	0.017
Tail Asym + Tarsus Asym + Primary Attenuation	148.5	1.21	0.016
Body Condition	149.1	1.79	0.012
Cuckoldry - Subset Males			
Kipp's Distance Asym	80.60	0.00	0.19
Cuckoldry - All Females			
Tarsus Asym	147.70	0.00	0.03
Null	148.90	1.24	0.01
Cuckoldry - Subset Females			
Null	79.30	0.00	0.17
Primary Attenuation Asym	80.60	1.25	0.09
Flank Coloration PC	80.70	1.36	0.09
Kipp's Distance	81.10	1.78	0.07
Axillary Coloration PC	81.20	1.89	0.07
Kipp's Distance Asym	81.30	1.94	0.07
Obstacle Navigation			
Primary Attenuation	57.90	0.00	0.05
Tail Length	58.90	0.96	0.03
Hits on Obstacle			
Primary Attenuation Asym	68.50	0.00	0.05

TABLE 4. Weight of evidence, given as summed Akaike weights ($\Sigma\ w_i$) across all models containing a particular variable, for each morphological character in logistic regressions between morphology and cuckoldry, obstacle navigation, and obstacle hits for Scissor-tailed Flycatchers. Weights were summed within each model set for the presence or absence of EPP in nests and morphology measured for males and females and for differences in morphology for birds that succeeded or failed to navigate the flight obstacle and for birds with minor brushes versus major head, body, or wrist hits on the obstacle. Weights in bold were well above competing variables and were considered for interpretation. No weights are indicated for interpretation for the female dataset because the null model was within 2 AIC of the top model.

TABLE 4.

	Cuckoldry		Obstacle	
	Male	Female	Navigation	Hits
Morphological Character	$\Sigma\ w_i$	$\Sigma\ w_i$	$\Sigma\ w_i$	$\Sigma\ w_i$
All Individuals				
Body Condition	0.65	0.34	0.25	0.27
Tarsus Length	0.30	0.26	-	-
Tarsus Asymmetry	0.62	0.68	-	-
Wing Chord Asymmetry	0.26	0.35	0.26	0.29
Primary Attenuation	0.37	0.26	0.67	0.25
Functional Tail Length	0.32	0.32	0.30	0.37
Functional Tail Asymmetry	0.26	0.37	0.25	0.25
Tail Length	0.33	0.29	0.41	0.25
Tail Asymmetry	0.63	0.43	0.25	0.44
Subset				
Primary Attenuation Asymmetry	0.38	0.33	0.32	0.75
Kipp's Distance	0.25	0.27	-	-
Kipp's Distance Asymmetry	0.76	0.27	0.25	0.24
Axillary Coloration PC	0.25	0.27	-	-
Flank Coloration PC	0.29	0.30	-	-

TABLE 5. Estimates (mean ± SE) of Scissor-tailed Flycatcher body condition, morphology, and coloration for cuckolded social males and their cuckolders in Comanche County, OK. All data were collected from 2008-14, except for primary attenuation asymmetry, Kipp's distance and asymmetry, and axially and flank coloration, which were collected from 2012-14. Birds were compared using paired *t* tests.

Variable	Social Mean ± SE	Cuckolder Mean ± SE	t	df	p
Body Condition	1.40 ± 0.34	0.84 ± 0.37	1.28	76	0.20
Tarsus Length	18.78 ± 0.07	18.67 ± 0.09	-0.82	76	0.42
Tarsus Asymmetry	0.20 ± 0.02	0.26 ± 0.02	-0.82	76	0.42
Primary Attenuation	20.30 ± 0.21	19.82 ± 0.24	1.61	76	0.11
Primary Attenuation Asymmetry	0.51 ± 0.07	0.69 ± 0.13	-1.30	43	0.20
Kipp's Distance	45.11 ± 0.56	44.93 ± 0.44	0.22	43	0.82
Kipp's Distance Asymmetry	1.62 ± 0.19	1.57 ± 0.21	1.28	43	0.21
Wing Chord	122.12 ± 0.37	121.81 ± 0.41	0.71	76	0.48
Wing Chord Asymmetry	1.67 ± 0.18	1.35 ± 0.15	1.38	76	0.17
Tail Length	221.09 ± 3.41	215.67 ± 4.12	1.03	76	0.31
Tail Asymmetry	5.56 ± 0.96	6.57 ± 0.98	1.68	76	0.10
Axillary Coloration PC	-3.02 ± 1.76	-3.68 ± 0.60	-1.72	43	0.09
Flank Coloration PC	1.08 ± 1.04	0.97 ± 0.75	0.09	43	0.93

FIGURE 1. Schematic diagram of the flight tube 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.

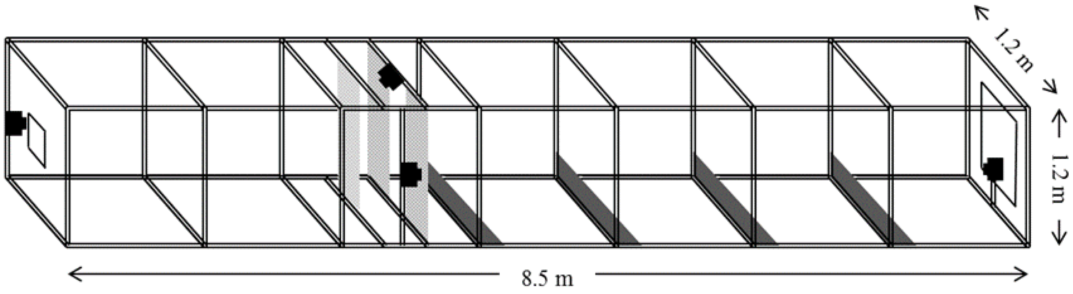


FIGURE 2. Correlations between axillary and flank color and morphological characteristics for males (A-C) and females (D-E). Correlations shown had *r* > 0.30. Increasing wing and flank PCs for both males and females represent decreasing lightness and increasing red and yellow intensity, indicating an increase in the deepness and intensity of the crimson axillary and salmon flank patches.

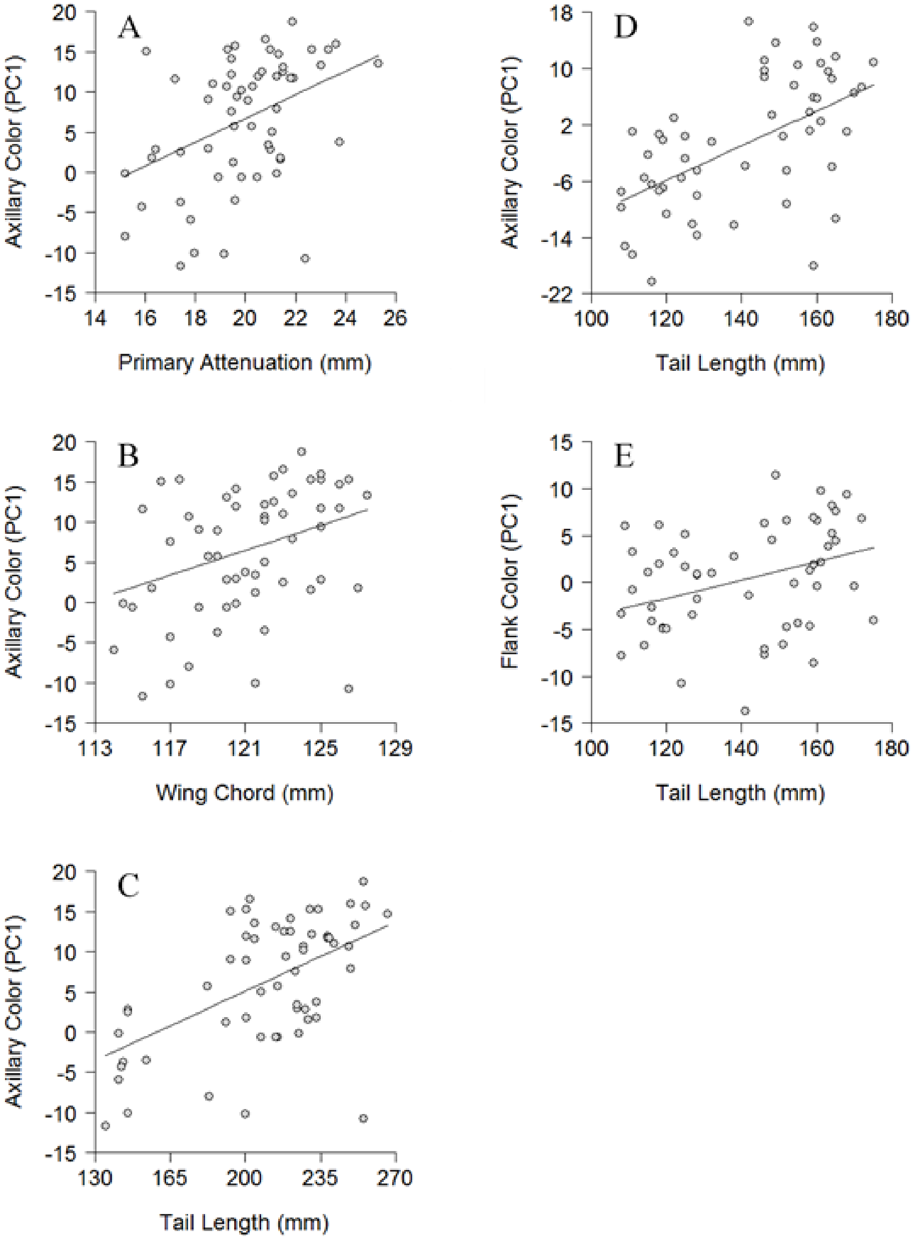


FIGURE 3. Body Condition (A), tail asymmetry (B), Kipp's distance asymmetry (C), and tarsus asymmetry (D) of male Scissor-tailed Flycatchers that were and were not cuckolded by their social mate. Body condition is the residuals of a mass/wing chord regression and indicates increasing residual mass when wing chord is taken into account. Values are means with 84% confidence interval error bars.

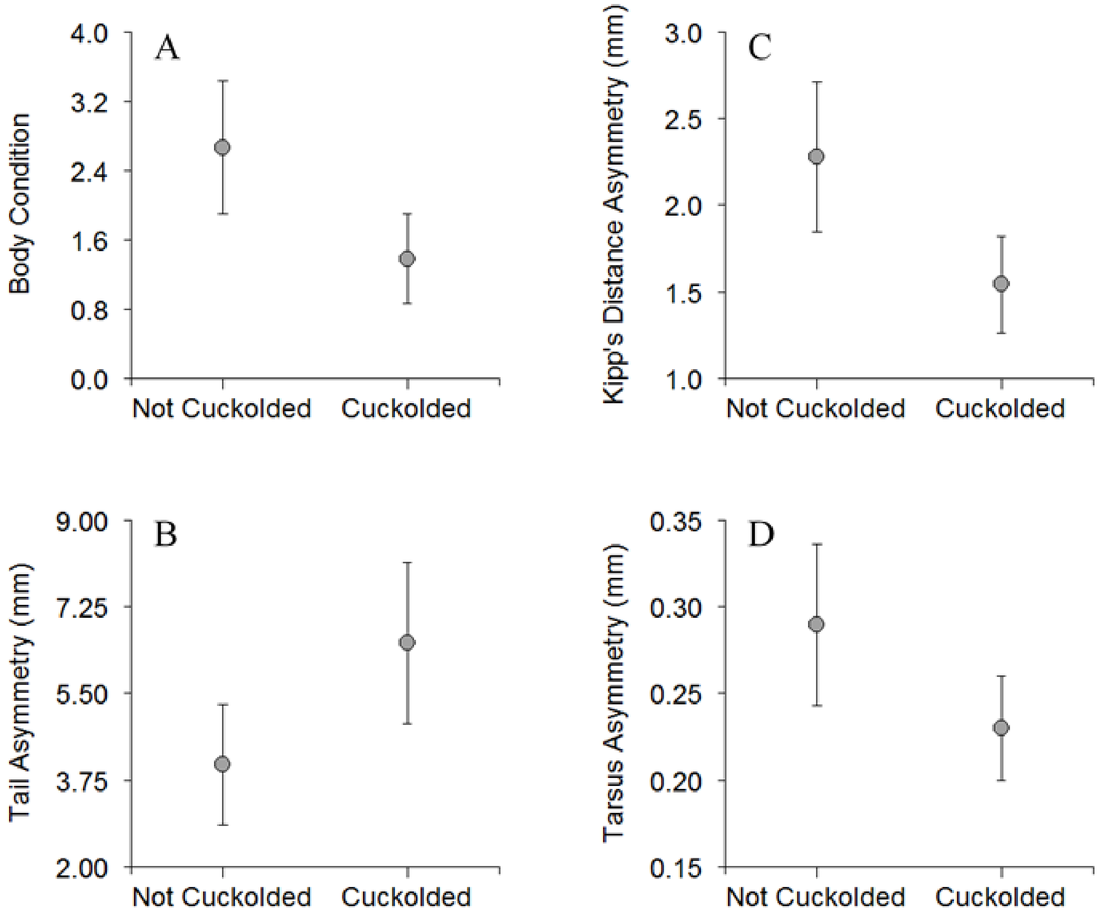
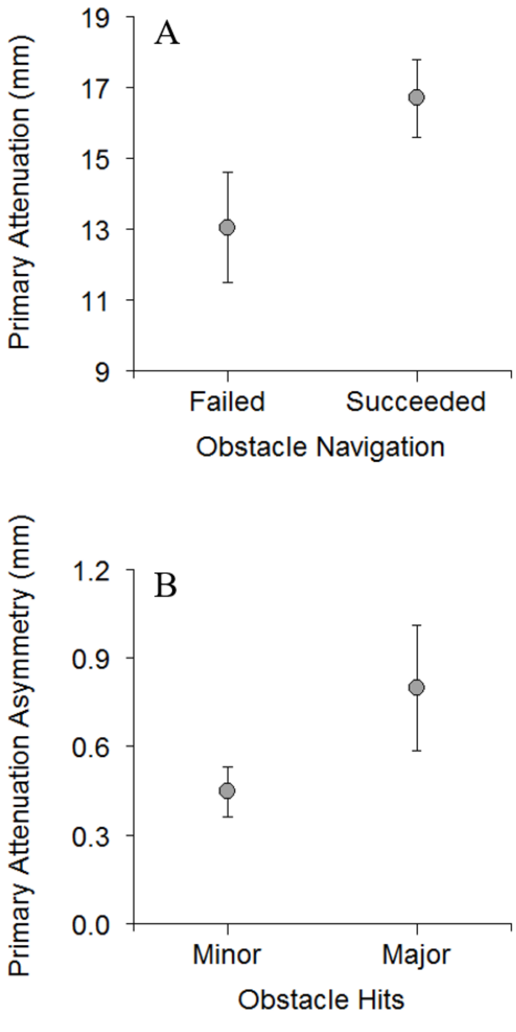


FIGURE 4. Primary attenuation length of birds that failed or succeeded in navigating the flight obstacle (A) and primary attenuation asymmetry of birds with minor or major body, wing, or tail hits on the obstacle (B). Values are means with 84% confidence interval error bars.



CHAPTER THREE

SPATIAL DISTRIBUTION AND SYNCHRONY OF NESTS IMPACT EXTRA-PAIR PATERNITY INDEPENDENT OF HABITAT STRUCTURE

Diane V. Landoll[1],
Michael S. Husak[2], Michael T. Murphy[3], and Michael A. Patten[1]

[1] Department of Biology & Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019, USA
[2] Department of Biological Science, Cameron University, Lawton, OK 73505, USA
[3] Department of Biology, Portland State University, Portland, OR 97207, USA

ABSTRACT

Although social monogamy is one of the most common mating systems in birds, over three-quarters of passerine species regularly engage in extra-pair copulations (EPC) that result in extra-pair paternity (EPP). EPP has been linked to increased variance in reproductive success, but is still poorly understood because correlates are variable across species. Spatial distribution of nests and breeding synchrony at both a local and population level are hypothesized to influence the occurrence of EPP in breeding birds in one of two ways. Short neighbor distances, high density, and high synchrony should increase individual interactions, causing either: 1) an increase in EPP as extra-pair mate availability and ease of comparisons with social mates increases, or 2) a decrease in EPP as social males increase the effort they invest in paternity assurance behaviors, such as mate guarding. Visual occlusion due to vertical habitat structuring on breeding territories may allow extra-territorial forays to go unnoticed because dense vegetation provides covered sites for EPCs. Using multimodel inference, we assessed these hypotheses with the Scissor-tailed Flycatcher (*Tyrannus forficatus*). EPP rates were high during our seven-year study, with 73% of nests containing EPY and 59% of nestlings resulting from EPCs. Few identified cuckolders (4 of 37) had mates that were concurrently fertile with cuckolded males' mates. Breeding synchrony best predicted cuckoldry, but only when distance between nesting pairs was taken into account. When synchronous pairs nested close together and when population synchrony was high and nearest neighbor distance was low, the probability of EPP in a nest was also low. These results suggest that when neighboring males had mates that were simultaneously fertile, they invested heavily in mate guarding, potentially at the cost of pursuing EPCs. The effect of breeding synchrony and distance between neighbors on EPP was independent of the effect of habitat structure. The probability of cuckoldry was low on territories with high woody vegetation cover but few trees and increased as the number of trees increased. This was likely because, while shrubs provide perches from which males can be vigilant against extra-pair forays, trees reduced visibility across the territory and may have provide cover for EPCs. Cuckoldry was also more likely as fence length increased. Fences were used as foraging perches for birds from neighboring territories, as well as by floater males. Fences may have brought together birds that would normally not have interacted, therefore increasing interaction rates between asynchronous individuals. Our study confirms that breeding synchrony and distance between synchronous neighbors influences the probability of EPP. We provide the first evidence that habitat structure on individual territories is a strong predictor of paternity and acts independently of breeding density or synchrony at our scale of measurement. We suggest further investigation into how synchrony, neighbor distance, and habitat structure might interact to influence cuckoldry within a population.

Keywords—cuckoldry, mate guarding, nearest neighbor distance, density, fence length, visual occlusion, Scissor-tailed Flycatcher, *Tyrannus forficatus*.

INTRODUCTION

Monogamy was once thought to be the most common bird mating system (Lack 1968). In fact, genetic polygamy is the norm (Westneat and Stewart 2003) and fewer than 25% of socially monogamous passerine species actually feature true genetic monogamy (Griffith et al. 2002). Genetic polygamy in socially monogamous species usually occurs in the form of extra-pair paternity (EPP), in which copulations between a female and a male that is not her social mate results in fertilization (Griffith et al. 2002). Thus, paternity can be divided into two categories, within-pair paternity (WPP) and EPP. Paternity patterns of monogamous passerines have been explored extensively, but we are still far from understanding what features of individuals, nesting populations, and landscapes drive extra-pair paternity (Griffith et al. 2002), in part because of flexible sexual selection and mate choice across populations, habitats, and environmental conditions (Chaine and Lyon 2008). Characteristics of breeding populations in particular have been predicted to affect EPP by influencing rates of individual interactions (Westneat et al. 1990). The occurrence and frequency of extra-pair paternity may depend on nest initiation date, nearest neighbor distance, breeding density, and breeding synchrony (Griffith et al. 2002). A factor little explored as a potential driver of EPP is habitat structure. Habitat structure may interact with nest spacing and density to influence EPP by providing more nesting or foraging habitat. Rates of cuckoldry may also be related to habitat structure within a territory because of its effect on mate guarding via visual occlusion (Blomqvist et al. 2006, Sherman and Morton 1988).

Extra-pair paternity rates vary across time and space in many species. Variation in cuckoldry across a season may be linked to arrival and pairing dates on the breeding grounds under two conditions (Spottiswoode and Moller 2004). First, if high quality birds arrive early in the season and are less likely to be cuckolded, then EPP should be low at the start of nesting and increase across the season (Spottiswoode and Moller 2004). Second, if hasty pairings result in an inability to accurately assess partner quality, then high rates of EPP are expected early in the season when many birds have recently arrived and newly paired (Spottiswoode and Moller 2004, Weatherhead and Yezerinac 1998). As nests fail and birds with breeding experience either stay with the same mate or pair with a new partner, EPP should decline. However, EPP may not be related to nest timing and clutch initiation dates if nest failure rates are high and the number of nesting individuals does not decline throughout the season (Krokene and Lifjeld 2000).

The spatial distribution of nests in a population may also have an impact on the occurrence of EPP. The density hypothesis posits that increasing nest density, and thus the proximity of individuals, will increase the encounter rate (Birkhead 1978, Taff et al. 2013), thereby reducing the cost of searching for extra-pair partners and increasing rates of EPCs and EPFs (Charmantier and Perret 2004). As a result, there should be a negative relationship between nearest neighbor distance and EPP rates but a positive relationship between nesting density and EPP rates both within and across populations (Stewart et al. 2010, Mayer and Pasinelli 2013).

Breeding synchrony combines both nest timing and spatial distribution (Stutchbury and Morton 1995, Weatherhead 1997) and refers to the degree to which the fertile period of breeding females overlaps. It can be measured between females at local and population levels. Synchrony is predicted to influence EPP rates in several conflicting ways. The synchrony hypothesis posits that increasing synchrony should result in higher rates of EPP under two conditions (Stutchbury and Morton 1995, Arlt et al. 2004). First, if females control EPCs and select the highest quality mate of those that are available, then increasing synchrony should lead to higher EPP rates because it facilitates comparisons among a greater number of potential extra-pair males (Kempenaers et al. 1992). Second, under high synchrony conditions, EPP may increase because males will have a greater opportunity to seek EPCs as more females become fertile simultaneously (Stutchbury and Morton 1995). The synchrony hypothesis has been supported both across species (Stutchbury 1998) and across populations (Dunn et al. 1994) and at both the population (Stewart et al. 2010, Wang and Lu 2014) and local level (Chuang et al. 1999, Stewart et al. 2010, Wang and Lu 2014).

Alternately, the asynchrony hypothesis (Neudorf 2004) suggests that increased synchrony can lower EPP rates if increasing neighbor proximity leads to enhanced mate guarding by a female’s social mate (i.e. the mate guarding hypothesis of Westneat et al. [1990] and guarding constraint hypothesis of Arlt et al. [2004]). This relationship is expected when males face a trade-off between time invested in paternity assurance activities (e.g. repeated copulations and mate guarding) and time spent pursuing EPCs (Birkhead and Biggins 1987, Thusius et al. 2001). This hypothesis has only been formalized for synchrony, but its reasoning also holds true for the spatial distribution of nests. If mate guarding increases with increased neighbor proximity, EPP should decrease as inter-nest distance decreases and density increases.

The spatial distribution of nests and its interaction with the timing of fertility may have strong impacts on EPP rates, but these effects might not be independent of the habitat in which they occur (Sherman and Morton 1988). Spatial distribution and synchrony can vary by habitat type, which may reflect availability of nest sites or differential nest settlement in territories of different quality (Barber et al. 1996, Thusius et al. 2001). However, studies that have simultaneously examined EPP, spatial distribution, synchrony, and habitat have focused on habitat types, as opposed to finer-scale measurements of habitat structure at the nest and in a pair's territory (Dunn et al. 1994, Thusius et al. 2001, Westneat and Mays 2005). Such fine-scale measures of habitat structure may better reflect nesting opportunities, as well as provide insight into how habitat structure affects cuckoldry (Sherman and Morton 1988). Habitat structure is expected to influence EPP by influencing movements of both territory holders and extra-pair individuals in several ways (Sherman and Morton 1988, Mays and Ritchison 2004). If habitat complexity and vertical vegetation structuring increase visual occlusion, then territorial males may not be able to mate guard as efficiently on territories with denser and taller vegetation (Blomqvist et al. 2006), as tall, dense vegetation may provide cover for extra-territorial forays for both males and females and provide hidden sites for EPCs (Mays and Ritchison 2004, Tryjanowski et al. 2007). If habitat influences resource availability within a territory, then males in high-quality territories may be able to devote less time to foraging and more time to mate guarding. Likewise, females may have lower neighbor encounter rates if they do not have to forage at the boundaries of or off their own territories. Both of these scenarios would result in lower EPP rates for habitats with higher resource availability (Westneat et al. 1990).

In this study, our goal was to investigate simultaneously how breeding population characteristics, such as timing, spacing, density, and synchrony of nests, and habitat characteristics on nesting territories interact to influence rates of EPP of a suboscine passerine, the Scissor-tailed Flycatcher (*Tyrannus forficatus*). This species is socially monogamous but has high rates of EPP (73% of nests and 59% of nestlings; Roeder et al. 2016). Males perform aerial displays that are visible from a distance and are thought to both attract mates and reinforce territory boundaries (Regosin 2013). Both members of a pair aggressively defend their territory from conspecifics and predators (Regosin 2013), and mate guarding has been suggested as a constraint on EPP (Chapter 2). Scissor-tailed Flycatchers nest in scattered trees in mesquite/oak savannah where habitat heterogeneity is high and suitable nesting sites can be either clumped or widely spaced. The species suffers from high depredation rates (32% average success rate; Landoll 2011), which results in variable breeding density and synchrony, making the species ideal to investigate the relationship between cuckoldry, nest spatial distribution and synchrony, and habitat structure.

We predicted that cuckoldry would be less likely in focal nests with nearer neighbor distances. If males invest more time mate guarding as the number of neighbors increases, then focal nests should have a lower probability of EPP when neighbor density is higher. Likewise, EPP should rarely occur when synchrony is high, both at the local and population scale. We also predicted that greater visual occlusion should lead to higher EPP rates and that greater foraging area in a territory should lead to lower EPP. We also expected that visual obstruction should interact with the density of neighbors such that territories with greater vertical structuring and higher neighbor density should have a greater probability of EPP. We evaluated these hypotheses for two estimates of female fertile period drawn from the literature reflecting the peak of copulations (Dunn et al. 1994, Stewart et al. 2010) versus the time span over which all copulations and sperm storage might occur (Weatherhead 1997, Krokene and Lifjeld 2000, Hammers et al. 2009). We also examined these hypotheses at two spatial scales that reflected habitat structure directly surrounding nest trees and habitat structure of the territory as a whole.

METHODS

Study duration and location—We collected data from April to August of 2009-2014 at the Wichita Mountains National Wildlife Refuge and the adjoining Fort Sill Artillery Base in Comanche County, Oklahoma. These sites are contiguous within the mixed-grass prairie ecoregion of the Great Plains and all contain oak (*Quercus* sp.) or mesquite (*Prosopis* sp.) savannah broken by low-lying mountains. The Fort Sill artillery range experiences greater human disturbance than does the refuge. It is divided into mile sections by gravel or paved roads and fences, whereas both of these are present in lower numbers on the refuge.

Field methods—We located Scissor-tailed Flycatcher nests by searching trees in areas of suitable habitat and trailing adults carrying nest material or food to nests. Nest locations were marked with a Garmin 60CSX GPS unit and were checked every 2-3 days to track nest stage and fate (Ralph et al. 1993). We captured adults visiting their nests when nestlings were >5 days of age by mist netting at the nest tree with predator or conspecific models or playback calls as lures. Adults were fitted with an aluminum United States Fish and Wildlife Service (USFWS) band and a unique combination of three colored Darvic leg bands, with a total of two bands per leg, for individual identification from a distance. Nestlings were removed from the nest by hand and given only a USFWS band. We sexed all adults in the field at the time of capture using the length of the 9th primary attenuation (Pyle 1997). We collected blood samples (50 µL from adults and 25 µL from nestlings) from all captured birds by puncturing the underside of the brachial vein of the wing with a 22-gauge sterile, disposable needle and collecting blood into heparinized capillary tubes. Blood was transferred into Eppendorf tubes containing 1.5 mL Longmire's buffer (Longmire et al. 1997), placed in a cooler in the field, and later stored at 4ºC. Nestlings were then placed back in the nest and monitored from a distance for a short time to ensure that they remained in the nest. Adults were released and later re-sighted to confirm their association with the nest.

Genetic sex determination and microsatellite paternity analysis—We isolated DNA from blood samples (QIAGEN DNeasy extraction kit, Valencia, CA: #69504) and genetically confirmed the sex of all individuals using 22550F/2718R primers to amplify the CHD|W and CHD|Z gene (following Fridoflsson and Ellegren 1999). We used eight polymorphic microsatellite loci in parentage analysis (Roeder et al. 2016). Forward microsatellite loci primers were labeled with a universal M13(-21) tail to which we could attach different dyes for multiplexing reactions during PCR (Schuelke 2000). PCR fragments were amplified in 25 µL reactions following the conditions given in Roeder et al. (2016). We separated amplified fragments using capillary electrophoresis and visualization on an ABI 3130 XL DNA Sequencer (Applied Biosystems, Inc., Foster City, CA). We used Peak Scanner 2 (Applied Biosystems, Inc., Foster City, CA) to determine the size (in base pairs) of each allele and used these data to construct allele profiles for each bird. The number of alleles per locus ranged from 3 – 17 with a mean of 8.3. All loci were in Hardy-Weinberg equilibrium, and null allele probability was 0.

We assessed paternity using the maximum likelihood method in CERVUS 3.0.7 (Kalinowski et al. 2007). We used CERVUS to simulate paternity with the given allele database to calculate a threshold logarithm of odds (LOD) score for parentage assignment. For this simulation, we set n = 100000, 0.99 loci typed, 0.01 loci mistyped, and 60% of potential fathers captured (according to mean capture rate and number of territories abutting a focal pair's territory). We included all captured males as potential fathers in the population where they were located (refuge = 101, Fort Sill = 105). No females mismatched their offspring at any locus. After mother/offspring pairs were evaluated, all candidate father/offspring pairs were given a likelihood of paternity. A candidate father was assigned paternity if the difference between his and the next most likely father's LOD score exceeded a threshold LOD value. If a nestling/social father pair had a negative LOD score, then that nestling was considered to be of extra-pair origin. Such pairs also all had ≥ 1 allele mismatches. CERVUS provided paternity assignments at both an 80% and 95% confidence interval. Because we captured ~ 60% of the males in the population, we used the conservative 95% CI to assign males as extra-pair sires to avoid assigning the wrong male as genetic sire. At this level, no extra-pair sire mismatched his putative offspring at any locus.

Nest timing, spacing, and synchrony—We used clutch initiation date as a measure of nesting seasonality. We standardized Julian dates by setting the first date of egg-laying in each year as day one. Clutch initiation dates were then recorded as the standardized date the first egg of a clutch appeared in each nest. We used two different estimates of female fertile period to calculate nearest neighbor distance, breeding density, and breeding synchrony. The 4-day fertile period estimate encompassed data from the time-frame just before egg-laying commenced in which the highest intensity of copulations, and therefore peak fertility, has been shown to occur (Dunn et al. 1994, Stewart et al 2010). This period started three days before egg-laying and ended on the date the first egg was laid. Scissor-tailed Flycatchers typically have 5-egg clutches, with a single egg laid each day (Regosin 2013). To account for the possibility of short-term sperm storage from fertilizations prior to peak fertility and for fertilizations during egg-laying (Weatherhead 1997, Krokene and Lifjeld 2000, Hammers et al. 2009), we expanded the fertile window to encompass a 10-day period ending on the day the penultimate egg was laid.

We measured nearest and average neighbor distances as our estimate of spatial distribution of nests (Mayer and Pasinelli 2013). We calculated nearest neighbor distance (m) for each nest as the straight line distance from the focal nest to the closest adjacent nest. We also measured the distance to the nearest synchronous neighbor (Mayer and Pasinelli 2013), where synchrony was defined as any nest that was concurrently fertile with the focal female. We estimated the average distance to available extra-pair mates by calculating the average distance to nests that were active at the same time as each focal female was in her fertile period, as well as to nests that were synchronous with focal nests, within a 700 m radius circle around each nest. This area was about three times the average nearest neighbor distance during this study and from previous accounts (Regosin and Pruett-Jones 1995) and when extreme distances were removed, was the average distance to the nest of identified extra-pair sires (following Mayer and Pasinelli 2013). Thus, it represents the distance at which most interactions with potential extra-pair mates should occur.

To estimate nest density, we counted the number of nests active when a focal female was in her fertile period, as well as the number of nests that were synchronous with focal females, within 700 m of each focal female's nest. We calculated synchrony among nests using Kempenaers (1993) synchrony index (SI). This index gives the average proportion of females fertile on each day across each focal female's fertile period. It ranges from 0 when her fertile period does not overlap with any other fertile period to 1 when her fertile period overlaps with all other female fertile periods (Kempenaers 1993). We calculated a local SI for focal nests and neighbors within the 700m radius circle around each nest (Dunn et al. 1994, Wang and Lu 2014), as well as a population SI for all females at each site (Kempenaers 1993).

Habitat structure—We measured habitat structure at two scales for each focal nest. As a measure of fine-scale habitat structuring directly surrounding each nest, we visually estimated the proportion of ground covered (to the nearest 5%) in an 11.3 m radius plot centered on the focal nest tree by the following categories: flat ground (including dirt, pavement, and leaf litter), short grass (< 0.5 m tall), tall grass (> 0.5 m tall), forb, and woody vegetation (including shrubs and trees). We did not split forbs into short and tall categories because the majority of forbs at our sites were < 0.5 m tall.

In addition, we counted the number of shrubs/saplings (hereafter shrubs) and trees in 11.3 m plots at each focal nest. We classified woody vegetation as shrubs or trees based on height (shrubs < 1.5 m, trees > 1.5 m tall) because we were interested in how the structure of vegetation influenced EPP and not in the identity of woody species. The nest tree was not included in woody vegetation cover or in the tree count.

We also measured coarse-scale habitat structure in a 57 m radius plot (one-hectare area) centered on the nest tree, corresponding to the core territory in which breeding pairs foraged and which they defended from conspecifics and predators (Landoll 2011, Fitch 1950). Coarse-scale measurements included proportional ground cover of flat ground, short vegetation (< 0.5 m tall), tall vegetation (> 0.5 m tall), shrubs, and trees. Because Scissor-tailed Flycatchers regularly forage on warm road surfaces and use fences as perches (Regosin 2013), we measured the total linear length of roads and fences within the 57 m radius plots.

Statistical analysis—All analyses were carried out in program R (R Development Core Team). Comparisons of population parameters between sites using *t*-tests yielded only a single difference (average distance to neighbors; $t_{109} = 2.49$, $p = 0.01$). Because of this and the similarity in frequency of EPP in nests and the proportion of young sired by EPCs across sites and years (Chapter 2), we grouped all data for the following analyses.

We used general linear models (GLM) with binomial errors (presence/absence of EPP in nests) and logit links (logistic regression) to evaluate the relationship between EPP and variables in each dataset: 4-day fertile period nest timing, spacing, and synchrony variables; 10-day fertile period nest timing, spacing, and synchrony variables; 11.3 m habitat structure; and 57 m habitat structure. Proportion variables were arcsine square root transformed and counts square root transformed before inclusion in this analysis, but these variables are presented in the original units in figures for ease of interpretation. For each dataset, we ran models for all combinations of variables using the MuMIn package, then ranked models from smallest to largest using the Akaike Information Criterion corrected for small sample size (AICc). We calculated ΔAICc and Akaike weights (w_i) for each model to evaluate model fit, where higher values represent better model fit (Burnham and Anderson 2002), and interpreted models < 2 AIC from the best model. Inclusion of the null model in this set meant that none of the models were different from random and we did not interpret them.

Because most model sets had a large number of competing models, we summed Akaike weights across all models in which each predictor was present to evaluate its relative contribution across all models. We interpreted predictors only when Σw_i for the top predictor was approaching twice the magnitude of the next highest Σw_i. We ran all two variable interaction models but did not include these in Σw_i. We included them in presented model sets only if they fell within 2 AIC of the top model. If an interaction model was > 2 AIC higher than the next best model, that interaction model was interpreted as the best model. All models in the top sets were compared to the null model using the likelihood ratio test and all had significantly better fit.

Because of the possibility of additive or interaction effects between habitat structure and nest spacing or density variables, we combined variables with the highest Σw_i from each data set into a final model selection analysis. We followed the procedure described above to evaluate models and determine the relative importance of variables across all scales for predicting the probability of cuckoldry.

RESULTS

As reported in Chapter 2 of this dissertation, Scissor-tailed Flycatcher EPP was high across all years of the study and ranged from 43-87% of nests across years ($\bar{x}$ = 73%), with 29-72% ($\bar{x}$ = 59%) of nestlings resulting from EPFs. Rates of EPP were similar between the refuge ($\bar{x}$ = 71% of nests, 59% of nestlings) and Fort Sill ($\bar{x}$ = 74% of nests, 58% of nestlings) and 38% of sampled males lost all paternity in their own nests (Chapter 2). We measured nest population and habitat parameters for 124 nests for which we had EPP data from 2009-14, including 65 nests from Fort Sill and 59 nests from the refuge.

Cuckolded males versus their cuckolders—We were able to identify both the social and extra-pair sire at 37 nests and assign 27 extra-pair males to their social nests. For these 27 males, we identified the stage of nesting that the extra-pair sire's mate was in when he cuckolded the other male. In only 4 cases were mates of extra-pair sires fertile during the cuckolding female's 10-day estimate of fertile period. In all other cases, mates of extra-pair males were non-fertile (i.e. nest-building [n = 3], incubating [n = 5], brooding [n = 6], feeding fledglings [n = 1], or post-nest failure [n = 8]) or extra-pair males had no social nest identified and were probable floaters in the population (Figure 1 – inset). The mean distance between nests with extra-pair young and nests of their extra-pair sires was 1034.5 m ± 336.2 SE. Over half of all cuckolders (15 of 27) nested < 700 m from cuckolded males' nests, while roughly a third nested ≥ 1 km away (Figure 1). We did not compare nearest neighbor distance, density, synchrony or habitat structure of extra-pair males to the males they cuckolded because so few were concurrently fertile.

Nest timing, spacing, and synchrony—For both the 4-day and 10-day fertile period model sets, the best model involved a measure of synchrony combined with a measure of nest spacing. Logistic regressions for the presence/absence of EPP in nests and nest population characteristics measured for the 4-day focal female fertile period resulted in 7 competing models within two AIC of the top model (Table 1). No interaction models were better than models appearing in the top model set. Nearest synchronous neighbor distance was present in all top models and had a summed Akaike weight (Σwi = 0.94) nearly double that of all other variables in the model set (Table 2). EPP was less likely to occur in a nest when it was close to the nearest synchronous neighbor (Figure 2A).

We found a similar relationship when we used a 10-day fertile period to calculate spacing and synchrony. No additive logistic regression model was 2 AICc less than the null model and no summed Akaike weight was double that of the next highest (Table 2). However, the interaction model between population SI and nearest neighbor distance performed better than all additive models and was 9.1 AICc less than the null model (AICc=148.0; Table 1). The interaction model indicated that as population SI increased (i.e. increasing proportion of the population that was synchronous with the focal fertile female), the probability of EPP occurring in her nest decreased (Figure 2B). When neighbors were very distant (> 800 m), the probability of EPP was similar across population SI values. However, as nearest neighbor distance decreased, the probability of EPP increased as population SI decreased. The opposite was true when population SI was low, but this effect was of a much lower magnitude. This indicates that males retained paternity more often when more females were breeding synchronously and when neighbors were close.

Interestingly, we found a negative correlation between population SI and clutch initiation date (R = -0.67; Figure 2C), where population synchrony increased quickly as nesting began and hovered above the population mean for the first third of the season. Synchrony then declined as the season progressed until it was very low at the end of the season. The lowest probability of EPP occurred during the high synchrony phase at the start of nesting, with the switch from increasing to decreasing probability of EPP with decreasing nearest neighbor distance occurring near the mean population SI (Figure 2B, C). Once the population rose above mean synchrony, the probability of EPP in focal nests decreased for close neighbors.

Habitat Structure—The probability of EPP at the 11.3 m radius plot scale was best predicted by the proportion of the plot covered by woody vegetation and the number of trees on plots (Table 1). These variables also had the highest summed Akaike weights (Table 3), and no other model was within 2 AICc of this model. At low proportions of woody vegetation cover, most of the woody vegetation was trees and the probability of EPP was always high (Figure 3A). For the probability of EPP to remain high as the proportion of woody vegetation on a plot increased, the number of trees also had to continue to increase. Consequently, nests with the lowest probability of EPP were found on sites with high woody cover but few trees (Figure 3A), indicating that they had high shrub cover. At the 57 m radius scale, wire length (fence and powerline) was present in both top models (Table 1) and was the only variable with a high summed Akaike weight (Table 3). Nests at which males were cuckolded had higher wire lengths than did those where males were not cuckolded (Figure 3B).

Combined Models—Territory-scale habitat variables appeared to be independent of any measure of nest spacing, density, or synchrony, as there were no strong correlations ($r < 0.20$) between these and any habitat structure variable. This lack of correlation indicates that our territory-scale habitat predictors were not reflective of nesting opportunities beyond the focal territory. No interaction model between number of neighbors, distance, or synchrony and any habitat variable had a lower AIC than did additive models. When we examined additive models with nest spacing, synchrony, and habitat variables that were important predictors in each dataset, nearest neighbor distance and population synchrony during the 10-day fertile period were the only variables not included in all of the top models (Table 1). We found that EPP was best predicted by nearest synchronous neighbor distance during the 4-day fertile period, woody cover and number of trees in an 11 m radius plot, and total wire length in the 57 m radius plot (Table 4).

DISCUSSION

Our study demonstrated that the spacing and synchrony of individuals during breeding had a strong effect on extra-pair paternity that was independent of the effect of habitat structure. Our results support the guarding-constraint hypothesis (Birkhead and Biggins 1987), which suggests that cuckoldry decreases with increasing breeding synchrony, but only after accounting for distance to synchronous nests. In addition, our study is the first to examine the effect of nest site and territory habitat structure on cuckoldry since it was suggested as a potential driver of EPP nearly 30 years ago (Sherman and Morton 1988). We found that increasing vertical habitat structure (i.e. visual occlusion) led to a higher probability of cuckoldry.

Nest timing, spacing, and synchrony—We found support for the guarding constraint hypothesis primarily in the context of the distance between focal nests and nearest synchronous neighbors (Thusius et al. 2001). When synchrony was low and fertile neighbors were distant, the probability of cuckoldry was high. It is likely that fewer males were engaged in mate guarding and instead were free to invest time in pursuing EPCs (Neudorf 2004, Westneat et al. 1990). When neighboring males were distant, it may have been harder for males guarding fertile mates to keep track of where their neighbors were, thus lowering the effectiveness of mate guarding.

When synchrony was high and fertile neighbors were close, the probability of cuckoldry decreased. When both focal and nearby males were simultaneously guarding fertile mates, the probability of EPP was lower likely because most males in the area were mate guarding instead of pursuing EPCs. Indeed, if most males were engaged in mate guarding as opposed to extra-territorial forays in search of EPCs, EPC opportunities may have been less available to females on their own territories. Females of some species pursue EPCs through extra-territorial forays of their own (Houtman 1992). Scissor-tailed Flycatchers may do the same, but territorial females aggressively defend their territories from intruding females (Regosin 2013), potentially lowering the effectiveness of such forays. Alternately, if pairs breeding earlier in the season, when nesting attempts were more synchronous, were of better quality than those breeding later, as some studies have shown (Spottiswoode and Moller 2004), females may have been less likely to attempt to cuckold their mates (Thusius et al. 2001).

We found a stronger effect of distance to synchronous nests at a local than population scale. Population synchrony, calculated as the overlap of female fertile periods across the entire population, is likely too broad a measure to reflect what happens at individual nests when most extra-pair sires were from nests < 1 km distant. Indeed, most studies have shown that extra-pair partners are within a two territory distance from one another (Dunn et al. 1994, Chuang et al. 1999, *cf* Dolan et al. 2007). At the local level, there is some support for a relationship between synchrony and EPP (Thusius et al. 2001, *cf* Chuang et al. 1999, Stewart et al. 2010, Wang and Lu 2014). However, some authors have suggested that even local synchrony is too course a measure of fertile period overlap, and instead recommend that the synchrony between a focal female and the female of her extra-pair mate, or individual-level synchrony, be evaluated (Wang and Lu 2014). We found that the relationship between individual-level synchrony and cuckoldry reflected results at both the local and population level. During our study, cuckolders rarely had fertile mates at the same time as the males they cuckolded. Similarly, Pied Flycatcher (*Ficedula hypoleuca*) males gained EPFs only after their mate started laying her eggs and after the peak of her fertile period (Canal et al. 2012). Cuckolding Scissor-tailed Flycatcher males most often originated from nearby when not concurrently synchronous with a focal pair, as seen in other studies (Mayer and Pasinelli 2013, Thusius et al. 2001). This was also reflected in our population synchrony by nearest neighbor distance interaction result, where the probability of EPP was high when nests had low synchrony and neighbors were nearby.

We found no support for the encounter rate hypothesis as the probability of EPP was unrelated to the density of neighboring pairs. Other studies have also failed to find such a relationship (Dunn et al. 1994, Barber et al. 1996, Sundberg and Dixon 1996, Tarof et al. 1998, Chuang et al. 1999, Moore et al. 1999), although a density/EPP relationship may be complicated by the actual origin of extra-pair fathers. Extra-pair fathers often originate on neighboring nest territories (Gibbs et al. 1990, Westneat 1993, Stutchbury et al. 1994, Mayer and Pasinelli 2013), but in some species they also originate at a lower frequency from farther away (Charmantier and Perret 2004, Canal et al. 2012, Mayer and Pasinelli 2013). When this happens, as in our study, a relationship between the probability of EPP and neighbor density surrounding a focal nest is unlikely. Additionally, mate guarding at high nesting densities may compensate for what would otherwise be an increase in the presence or proportion of EPP in nests (Komdeur 2001, Kokko and Rankin 2006). We provide some evidence for this notion, in that when fertile neighbors were nearer to each other, the probability of EPP decreased, likely due to increased mate guarding.

Habitat structure—As predicted by Sherman and Morton’s (1988) habitat structure hypothesis (see also Mays and Ritchison 2004), we found that structural habitat characteristics associated with nest success predicted the probability of cuckoldry. Shrub cover in this population of Scissor-tailed Flycatchers is an important predictor of Scissor-tailed Flycatcher nest success (Landoll 2011), probably because shrubs provide perches above grass and forbs from which both males and females can be vigilant for airborne avian predators (Foreman 1978). Such perches may also allow males to be vigilant against forays onto their territories by extra-pair males. We found that when the number of trees on a territory increased in conjunction with shrub cover, the probability of EPP increased. In this savannah system, trees obscured the view of the airspace within a territory. High shrub cover in combination with visual occlusion from trees may have allowed extra-pair males less contested access to females on such territories by allowing them cover to approach females and solicit EPCs (Mays and Ritchison 2004). Alternately, it may have been harder for males on these territories to continually accompany their mates, who would have been freer to foray around or off their own territories without male accompaniment (Westneat and Sherman 1997). Dense vegetation may allow cover for EPCs in either scenario. Few studies have examined the location of EPCs because they are difficult to observe in most species. However, Tryjanowski et al. (2007) found that WPCs took place in open habitat, while EPCs took place in dense vegetation.

We did not find a link between the proportion of short grass or forbs on a territory and EPP. Both of these land cover types are associated with higher food abundance and easier foraging in this system (Foreman 1978, Landoll 2011, Teather 1992), so visual occlusion as opposed to trade-offs between foraging and mate-guarding (Westneat 1994) are probably responsible for the habitat effect on EPP rates.

Interestingly, we found that the probability of cuckoldry increased with an important habitat feature - perching structures. The probability of cuckoldry was greater with increasing fence and powerline length. Scissor-tailed Flycatchers often use fences and powerlines as foraging perches, sometimes to the exclusion of other suitable perches (Foreman 1978, Tatschl 1973). The use of fences, which can span or border many territories, as foraging perches may put birds in greater contact than when perches are discrete plants located within the borders of defended territories. Because not all of these foragers will be synchronously breeding, there may be a greater opportunity for EPCs in such a situation (Dunn et al. 1994, Reyer et al. 1997, Hammers et al. 2009). Fences may also attract floater males that might be more difficult for territorial males to repel because of the transitory and unpredictable nature of their visits (Tarof et al. 1998, Ewen et al. 1999). However, the effect of transitory visits on EPP are not well known (Westneat et al. 1990).

Combined models—We expected that breeding density and nearest neighbor distance would increase the likelihood of EPP in visually occluded territories, as more and closer males should have better access to females on those territories (Sherman and Morton 1988). However, we found no interactive effects of habitat structure and nearest neighbor distance, density, or synchrony when we combined the best predictors of cuckoldry from each dataset in additive and interaction models. Habitat structure around nests and in core foraging territories was not correlated with nest spacing, density, or synchrony and therefore was not indicative of nesting opportunities across the landscape. Instead, it appears likely that if nearest neighbors were the strongest competitors for paternity, dense vegetation simply allowed those males better opportunities to obtain EPCs. In fact, this was represented in the variables that ranked highest from the combined data set. Population synchrony and its interaction with nearest neighbor distance were far less important predictors of EPP than were the additive effect of nearest synchronous neighbor distance, woody cover, number of trees, and wire length.

Conclusions—Our results emphasize the importance of breeding synchrony in the context of the spatial distribution of nesting pairs in a population. Synchrony alone was not a strong predictor of EPP, but when we evaluated distance to synchronous neighbors, we found that nests with close, synchronous neighbors were less likely to contain EPY. We suggest this was because when nearby neighbors were synchronous simultaneously, both the social and neighboring males put more effort into mate guarding and little effort into seeking EPCs. Likewise, greater fence and powerline length was associated with an increased probability of EPP. Linear man-made structures such as fences and powerlines may alter foraging behavior and therefore interactions between potential extra-pair partners that might lead to EPCs. Our study also provides support for the hypothesis that visual complexity due to increasing vertical habitat structure may provide opportunities for EPCs, regardless of the spatial distribution, density, or synchrony of breeding pairs; indeed, deception may require cover. In species where density or synchrony alone are more important for predicting EPP, interaction between habitat structure and breeding population characteristics may be of greater importance in determining EPP rates. Alternately, habitat structure that results in visual occlusion may present only brief opportunities for interactions, as males are likely to regularly patrol their territories. If this is the case, then neighbors that are close enough to quickly take advantage of short periods where males are not in visual contact with their mates may be the only birds to benefit from increased vegetation structuring on a territory. Further research into how habitat structure promotes or constrains EPP is needed, as it may play as important a role as other factors such as nest spatial distribution and breeding density.

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TABLE 1. Best logistic regression models (ΔAICc < 2) and model weights (w_i) for differences in 1) 4-day fertile period estimates of nest timing, spatial distribution, and synchrony, 2) 10-day fertile period estimates, 3) 11.3 m habitat structure measurements, 4) 57 m habitat structure measurements, and 5) combinations of top 4- and 10-day fertile period and 11.3 m and 57 m habitat structure variables between nests with (n = 90) and without (n = 34) extra-pair paternity. No w_i was calculated for interaction models.

TABLE 1.

Model Set	AICc	ΔAICc	w_i
4-day Fertile Period Estimate			
Nearest Sync Neighbor Dist + Mean Neighbor Dist + Local SI	141.30	0.00	0.03
Nearest Sync Neighbor Dist + Mean Neighbor Dist	141.40	0.10	0.03
Nearest Sync Neighbor Dist + Mean Sync Neighbor Dist	141.70	0.40	0.03
Nearest Sync Neighbor Dist + Local SI	142.00	0.70	0.02
Nearest Sync Neighbor Dist + Density	142.50	1.20	0.02
Nearest Sync Neighbor Dist + Nearest Neighbor Dist	142.60	1.30	0.02
Nearest Sync Neighbor Dist	142.70	1.40	0.02
10-day Fertile Period Estimate			
Population SI * Nearest Neighbor Dist	138.90	0.00	-
11.3 m Habitat Structure Plot			
Woody Cover + Number Trees	143.10	0.00	0.18
57 m Habitat Structure Plot			
Wire Length + Road Length + Short Vegetation Cover	142.90	0.00	0.08
Wire Length	144.00	1.10	0.05
Top Ranked Fertile Period and Habitat Structure Variables			
11.3m Woody Cover + 11.3m Number Trees + 57m Wire Length + 4-day Nearest Sync Neighbor Dist + 10-day Nearest Neighbor Dist	130.00	0.00	0.26
11.3m Woody Cover + 11.3m Number Trees + 57m Wire Length + 4-day Nearest Sync Neighbor Dist	130.70	0.70	0.18

TABLE 2. Weight of evidence for each variable in additive logistic regressions for differences in 4- and 10-day fertile period estimates of nest timing, spacing, and synchrony between nests with and without extra-pair paternity, given as summed Akaike weights ($\Sigma\ w_i$) across all models. Weights in bold were well above competing variables and were considered for interpretation.

	4-day Fertile Period	10-day Fertile Period
Variables	$\Sigma\ w_i$	$\Sigma\ w_i$
Clutch Initiation Date	0.32	0.31
Density	0.36	0.47
Nearest Neighbor Distance	0.38	0.29†
Average Neighbor Distance	0.47	0.39
Nearest Sync Neighbor Distance	**0.94**	0.3
Average Sync Neighbor Distance	0.41	0.39
Local SI	0.49	0.27
Population SI	0.28	0.58†

† denotes variables not important in additive logistic regression models but appearing in high scoring interaction models.

TABLE 3. Weight of evidence for each variable in additive logistic regressions for differences in 11.3 m and 57 m habitat structure plots between nests with and without extra-pair paternity, given as summed Akaike weights ($\Sigma\ w_i$) across all models. Weights in bold were well above competing variables and were considered for interpretation.

Variable	$\Sigma\ w_i$
11.3 m plot	
Number Shrubs	0.32
Number Trees	**0.75**
Flat Ground Cover	0.26
Forb Cover	0.26
Short Grass Cover	0.34
Woody Vegetation Cover	**0.88**
57 m plot	
Flat Ground Cover	0.31
Short Vegetation Cover	0.51
Tall Vegetation Cover	0.44
Shrub Cover	0.32
Tree Cover	0.32
Road Length	0.52
Wire Length	**0.89**

TABLE 4. Weight of evidence, given as summed Akaike weights (Σw_i) across all models, for each variable in additive logistic regressions when top ranking variables for 4- and 10-day fertile period estimates of nest timing, spatial distribution, and synchrony and 11.3 m and 57 m habitat structure variables were combined. Weights in bold were well above competing variables and were considered for interpretation.

Variables	Σw_i
11.3m Woody Cover	**0.96**
11.3m Number Trees	**0.90**
57m Wire Length	**0.89**
4-day Nearest Synchronous Neighbor Distance	**0.87**
10-day Nearest Neighbor Distance	0.55
10-day Population SI	0.39

FIGURE 1. Histogram of the distance (km) between the nests of cuckolded males and their cuckolders. Light gray bars represent the distribution of all social male-cuckolder distances. Dark gray bars represent cuckolders whose mates were in their fertile period when cuckoldry occurred. Inset: total number of cuckolders who had fertile or non-fertile mates at the time of cuckoldry, as well as males that were probable floaters (i.e. not identified as fathers at any nest).

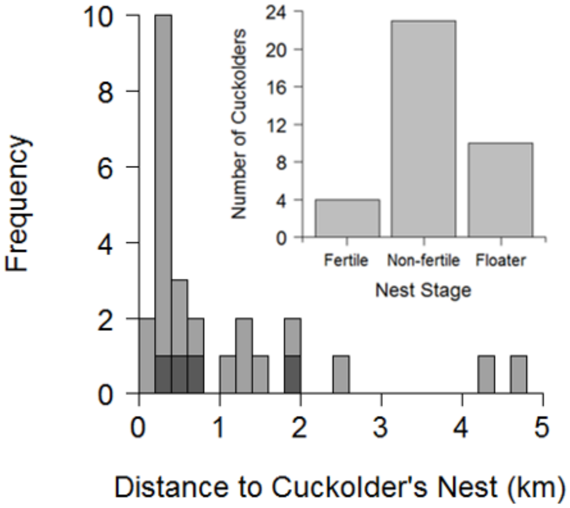


FIGURE 2. Best nest distribution and timing predictors of the probability of EPP in Scissor-tailed Flycatcher nests during estimated 4-day (A) and 10-day (B, C) female fertile period in Comanche County, OK. A) Difference in nearest synchronous neighbor distance between nests where extra-pair paternity was absent versus present. B) Interaction between population synchrony (SI) and nearest neighbor distance (m). Lines represent distance to the nearest neighbor from 0 m (darkest line) progressing in 100 m intervals to 800 m (lightest line). C) Relationship between population synchrony (SI) and clutch initiation date (standardized by setting first egg date each season to day 0). The dotted line in panels B and C shows the mean for population synchrony.

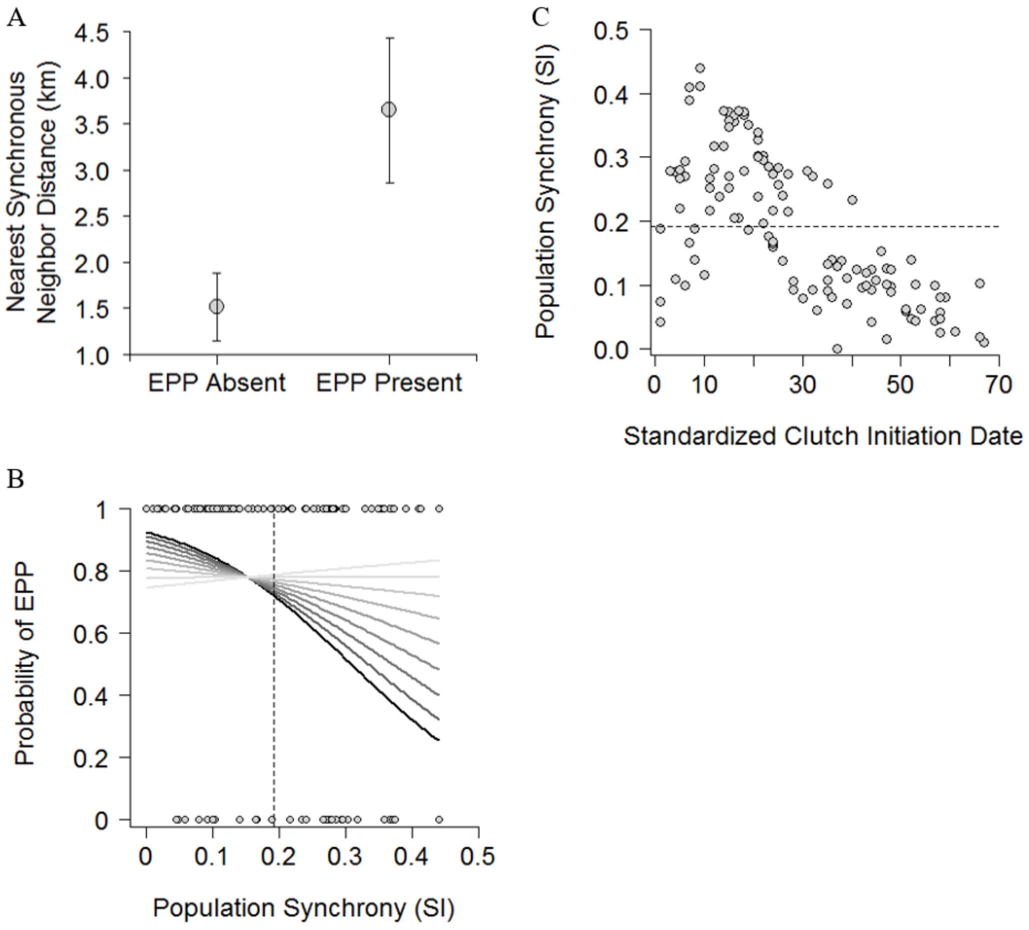
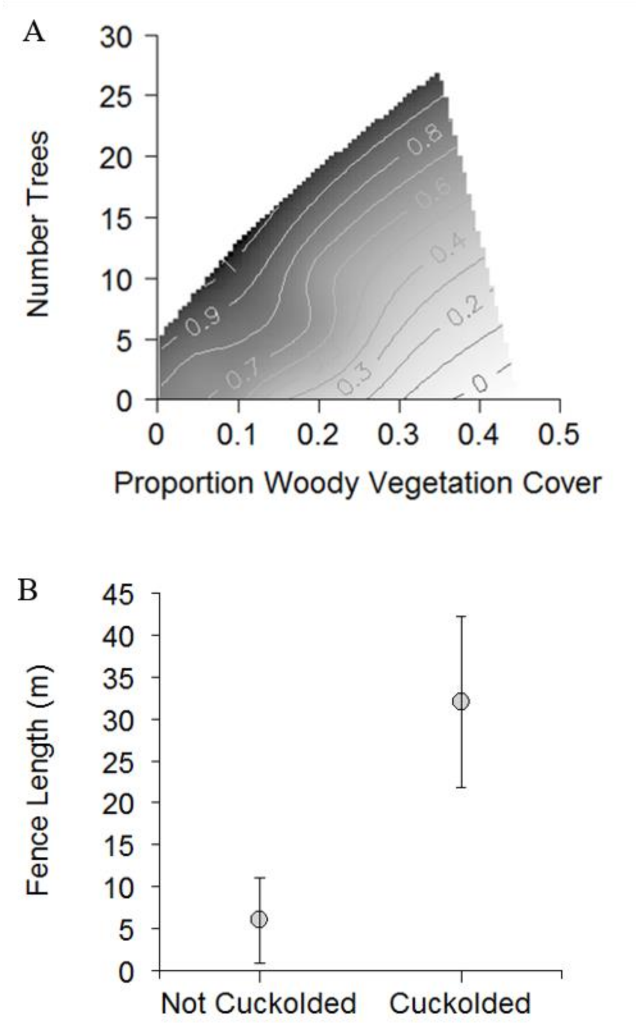


FIGURE 3. Best habitat predictors of the probability of EPP in nests of Scissor-tailed Flycatchers at two plot sizes centered on the nest tree: directly surrounding the nest tree (11.3m radius plot) and within the home territory (57m radius plot). A) Response surface of predicted EPP probabilities depended on the number of trees and proportion of woody vegetation cover at 11.3m plots. B) Fence length means ± 84% CI for nests without (Not Cuckolded) and with (Cuckolded) EPP at 57m plots.



CHAPTER FOUR

ENVIRONMENTAL CONSTRAINTS ON EXTRA-PAIR PATERNITY IN A SOCIALLY MONOGAMOUS PASSERINE

Diane V. Roeder[1],
Michael S. Husak[2], Michael T. Murphy[3], and Michael A. Patten[1]

[1] Department of Biology & Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019, USA
[2] Department of Biological Science, Cameron University, Lawton, OK 73505, USA
[3] Department of Biology, Portland State University, Portland, OR 97207, USA

ABSTRACT

Extra-pair paternity (EPP) is common in socially monogamous birds, but its frequency varies within and across species. Local environmental factors, such as ambient weather conditions, can affect reproductive behavior and may therefore influence the chance that individuals engage in extra-pair copulations (EPCs). We investigated the effect of weather conditions and predictability during the female fertile period on the probability of cuckoldry in nests of Scissor-tailed Flycatchers (*Tyrannus forficatus*). The Scissor-tailed Flycatcher is a sexually dimorphic, socially monogamous passerine with high levels of EPP. In our seven-year study, we found that 73% of nests contain EPP and 59% of offspring result from EPCs. We found that low vapor pressure deficit, a measure of the dryness of the air, and daily minimum temperature variability during the fertile period were associated with a higher probability of cuckoldry. Evaporative heat loss, and therefore thermoregulation, was more difficult with lower vapor pressure deficits. While fertile females must continue to forage in order to acquire energy for egg-laying, males may choose to seek out shade during challenging conditions and not accompany their mates, resulting in a higher chance of encounters with extra-pair males. Unpredictable low temperatures, however, should affect all birds in an area equally, such that most birds will need to invest more in self-maintenance than extra-pair behavior. Weather conditions during fertility, therefore, drive trade-offs between mate-guarding, extra-pair behavior, and self-maintenance in socially monogamous birds.

Keywords—Scissor-tailed Flycatcher, *Tyrannus forficatus*, cuckoldry, weather, vapor pressure deficit, temperature.

INTRODUCTION

Extra-pair paternity (EPP) is widespread in passerines, with <14% of all passerine species and <25% of socially monogamous passerines exhibiting true genetic monogamy (Griffith et al. 2002). In most species with EPP, rates vary greatly among years, particularly those species with high rates of EPP (Dunn et al. 1994, Suter et al. 2007, Varian-Ramos et al. 2012). Specific factors that control extra-pair behaviors have been debated for 30 years (Westneat and Stewart 2003), with the focus of investigation primarily on traits at the level of the individual (age, experience, morphology, song, and genetic quality) and population (nesting density and synchrony). Supporting evidence for a given factor is equivocal across species (Griffith et al. 2002), in part because sexual selection and mate choice may be flexible across environmental conditions (Chaine and Lyon 2008). This environmental effect has been demonstrated across species for divorce and EPP (Botero and Rubenstein 2012), but may also hold within species during a breeding season, particularly when environmental conditions, such as weather, exhibit short-term temporal variation before and during breeding (Johnsen and Lifjeld 2003).

Weather should affect passerine paternity in two key ways. First, weather patterns during the growing season drive food availability (Hawkins and Holyoak 1998, Huberty and Denno 2004), which has been shown to influence body condition and reproductive effort of birds (Bolger et al. 2005, Studds and Mara 2007). Because precipitation drives ecosystem productivity (Tanaka et al. 1982, Grant et al. 2000), it may also drive the time allocated to foraging behaviors and self-maintenance relative to mating effort and pursuit of extra-pair copulation (Blanckenhorn et al. 1995). The "constrained female" hypothesis (Gowaty 1996, Petrie and Kempenaers 1998, Hoi-Leitner et al. 1999) suggests that extra-pair paternity should be higher on territories with abundant food resources because females on these territories will be better able to resist male control of copulations, either because females that control these territories are of high quality or because they are in better condition when they have access to more food resources.

This hypothesis has some support (Hoi-Leitner et al. 1999), yet there is support for the idea that access to more abundant food resources should lower the occurrence of extra-pair paternity in nests (Westneat 1994, Gray 1997, Václav et al. 2003, Rubenstein 2007). The probability of EPP may be lower if birds forage off-territory less often when food is abundant on-territory. Westneat (1994) showed that male and female Red-winged Blackbirds (*Agelaius phoeniceus*) left their territories less often when supplemented with food, which allowed the pair to spend more time in close proximity. When males were experimentally removed from the territory, extra-pair copulations (EPC) and fertilizations (EPF) increased as a result of extra-territorial male intrusion. These results indicated that the probability of EPP is lowered when males accompany their mates during fertility. Similar results were found by Václav et al. (2003) when they supplemented House Sparrows (*Passer domesticus*) with food. Additionally, if females can gain access to resource-rich territories by cooperating with EPCs (Gray 1997) or if females are exposed to more EPC attempts when foraging alone off-territory or when their mates are absent (Westneat 1994, Rubenstein 2007), EPP should increase when on-territory resources are poor, but decrease when abundant on-territory resources lower the necessity of off-territory foraging (Gray 1997).

Second, ambient weather conditions during a female's fertile period can influence extra-pair paternity by constraining time available for extra-pair pursuits (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006). Temperature, humidity, rainfall, and wind speeds can influence energy expenditure and resulting time budgets (Bryant and Westerterp 1983, Redpath et al. 2002). During cold or rainy weather, birds must prioritize thermoregulation and self-maintenance (Gass et al. 1999) and may increase foraging activity to generate heat (Webster and Weathers 1990); hence, foraging to maintain body condition and restore energy reserves should take precedence over seeking EPCs (Jorde et al. 1984), particularly as insect activity is low in such weather (Redpath et al. 2002, Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006). Rainfall and high wind speeds should restrict off-territory forays because flight during these conditions can be energetically costly and physically challenging (Grubb 1978, Gabrielsen et al. 1987, Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006). Vapor pressure deficit may affect time budgets because it affects thermoregulation and evaporative heat loss (Wolf 2000). Low vapor pressure deficits, which result from high water saturation of the air and make evaporative heat loss difficult, may impose similar constraints if birds find shade to avoid overheating (Wolf and Walsberg 1996, Wolf 2000), although wind may help alleviate the metabolic stress of high temperature (Wolf and Walsberg 1996). Birds should spend less time engaged in non-essential activities that boost metabolic rates when thermoregulation is difficult, such as extra-territorial flights searching for EPCs. If both males and females are equally affected by the increased need to mediate physiologically challenging conditions at the cost of seeking EPCs, then EPP should be lower under adverse conditions; however, if one sex is disproportionately affected or must maintain activity regardless of ambient conditions, EPP may be higher in challenging conditions.

Unpredictability of ambient weather conditions might affect patterns of paternity across species (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011, Botero and Rubenstein 2012), although this idea has yet to be tested within a species. When weather is unpredictable, birds may be less inclined to invest energy to obtain EPCs. This is particularly important if activity in current fair conditions is hedged against energy needed to maintain body condition when weather conditions turn poor.

In this study, we examined the relationship between cuckoldry and weather conditions, as well as a longer-term measure of precipitation, during the fertile period of Scissor-tailed Flycatchers (*Tyrannus forficatus*). The species breeds in the south-central United States and northeast Mexico and contends with hot, windy weather with varying degrees of humidity and rainfall, both yearly and within a breeding season (Regosin 2013). Because high plant productivity and insect abundance are tied directly to water availability (Murphy 1986, Blancher and Robertson 1987), we predicted that: 1) greater cumulative rainfall in the months leading to clutch initiation would result in cuckoldry because birds could access food more easily and thus have more time to pursue EPCs. For ambient weather conditions during the female fertile period, we predicted that trade-offs among pursing EPCs and self-maintenance would result in a lower probability of cuckoldry at nests experiencing, 2) low daily minimum temperatures as more time was spent on self-maintenance, 3) high daily maximum wind speed, which might impose physical constraints on flight, 4) low vapor pressure deficit which would increase heat stress, 5) high variability and lower predictability of any of these measures, and 6) increasing cumulative precipitation leading to higher food availability.

METHODS

Study Species—The Scissor-tailed Flycatcher is a sexually dimorphic (Regosin and Pruett-Jones 2001), socially monogamous passerine species with frequent EPP (64% of nests and 49% of young; Roeder et al. 2016). Scissor-tailed Flycatchers are aerial insectivores that forage primarily in their own territories during breeding (Teather 1992), but often wander once a breeding attempt has concluded (Regosin 2013). Ambient weather conditions affect foraging strategies, with shorter foraging flights in high winds and cold weather, as well as foraging on or near the ground during cold or rainy conditions (Teather 1992). Pairs defend their territories from conspecifics and predators (Regosin 2013). Females build nests and incubate eggs without male help, although they are often escorted on nest material gathering and foraging trips. Both parents feed nestlings and fledglings (Regosin and Pruett-Jones 1995). Females usually lay a 5-egg clutch, with one egg laid per day, and incubation lasts an average of 14.7 days (Regosin and Pruett-Jones 1995, Regosin 2013)

Study Site—We collected data for this study from April to August of 2008–2014 in Comanche County in southwestern Oklahoma, U.S.A. We tracked Scissor-tailed Flycatcher breeding pairs on Fort Sill Artillery Base, which is primarily mesquite savannah maintained by prescribed fire and manual tree clearing, and on the adjoining Wichita Mountains Wildlife Refuge (WMWR), which is composed of low-lying mountains broken by riparian areas, oak savannah, and mixed-grass prairie. Weather in this prairie/savannah region is highly variable and can be quiet extreme, particularly in terms of temperature and wind speeds (Table1). Rainfall and temperature variation likely drives arthropod abundance through its impact on vegetation (Studds and Marra 2007, Bang et al. 2012) and arthropod development (Marcandier and Khachatourians 1987, Hagstrum and Milliken 1988, Carruthers et al. 1992).

Field Methods—We searched suitable habitat daily for Scissor-tailed Flycatcher nests and recorded locations with a Garmin 60CSX GPS unit. We visited nests every 2–3 days to record clutch initiation, hatching, and fledging date, as well as clutch and brood size and number fledged (Ralph et al. 1993). When nests were found after eggs had been laid, we back-calculated clutch initiation date based on an average incubation period and assuming one egg laid per day (Regosin and Pruett-Jones 1995). We attempted to capture parents with mist nets placed around nest trees, often with the aid of predator models and playback calls, when nestlings were ≥ 6 days old. We removed nestlings from the nest by hand for banding. We banded adults with an aluminum United States Fish and Wildlife Service band and a unique combination of three colored Darvic leg bands. We observed adults attending the nest after banding and used color bands to identify them as social parents or as visitors. We collected blood samples from all captured birds (50 µL from adults and 25 µL from nestlings) by puncturing the brachial vein on the underside of the wing with a 22-gauge sterile, disposable needle and collected blood into heparinized capillary tubes. Blood was transferred into Eppendorf tubes containing 1.5 mL of buffer (Longmire et al. 1988) and refrigerated until processing. Nestlings were placed back in the nest and monitored from a distance for a short time to ensure that they remained in the nest.

Molecular Methods—DNA was isolated from blood samples with a QIAGEN DNeasy extraction kit (Qiagen, Valencia, CA: #69504). We tentatively sexed all adults in the field at the time of capture and later genetically confirmed sex in the lab (following Fridolsson and Ellegren 1999). We used eight polymorphic microsatellite loci in parentage analysis (Roeder et al. 2016). We amplified loci in 25 μL PCR reactions (Roeder et al. 2016) using Type-It Microsatellite PCR kits (Qiagen, Valenci, CA: #206243), unlabeled reverse primers, and forward primers labelled with a universal M13(-21) tail. The M13(-21) tail allowed us to incorporate different fluorescent dyes when multiplexing reactions (Schuelke 2000). Amplified microsatellite fragments were separated by capillary electrophoresis and visualized on an ABI 3130XL DNA Analyzer (Applied Biosystems, Inc., Foster City, CA). We determined fragment size using Peak Scanner 2 (Applied Biosystems, Inc., Foster City, CA), after which fragments were binned into consistent sizes and a microsatellite profile compiled for each bird.

Paternity Analysis—Allele frequency, exclusionary probabilities, and parentage were evaluated using CERVUS v. 3.0.7 (Kalinowski et al. 2007). All loci were in Hardy-Weinberg equilibrium and the probability of null alleles was 0. The number of alleles per locus ranged from 3–17 with an average of 8.3. Non-exclusionary probability over all loci was 0.0006 for the parent pair. We used maximum likelihood in CERVUS to simulate paternity with the given genetic dataset and to generate a threshold logarithm of odds (LOD) score for parentage assignment (Kalinowski et al. 2007). CERVUS calculates a likelihood ratio for each offspring and candidate father after the mother/offspring pair is evaluated. It then assigns paternity to the most likely father if the difference between his and the next most likely father's LOD score exceeds the threshold LOD value. We simulated 1000000 offspring using observed allele frequencies, an estimate of 0.99 loci successfully typed and 0.01 loci mistyped, and 60% of candidate fathers captured (mean capture rate of territorial males). All female/offspring pairs matched at all microsatellite loci, so final parentage analysis was between candidate father/offspring pairs. All males sampled or re-sighted were included as potential fathers in the study site at which they were located in the final analysis (refuge = 101, Fort Sill = 105).

Nestlings were considered extra-pair young (EPY) when the social male/offspring pair had a negative LOD score and mismatched at ≥ 1 loci. Nestlings that had no mismatches and positive social male/offspring LOC scores were considered within-pair young (WPY). We assigned paternity to extra-pair males when CERVUS assigned them as genetic fathers with 95% confidence and when they did not mismatch candidate sires. We used these conservative criteria to avoid assigning the wrong male as genetic sire because we only captured around 60% of males in the population. Based on paternity of each nestling, we classified nests as either containing only WPY (cuckoldry absent) or at least one EPY (cuckoldry present).

Weather Data—We downloaded weather data from the Oklahoma Mesonet database (www.mesonet.org; Brock et al. 1995, McPherson et al. 2007). One hundred and twenty Mesonet weather stations around the state continuously collect weather measurements at a local scale and condense them into five-minute intervals that are verified by the Oklahoma Climatological Survey. We used weather records from the Medicine Park station, which was centrally located among our nest sites (< 20 km from any nest), to examine how one longer-term precipitation variable and several measures of ambient weather conditions during female fertility related to the probability of cuckoldry. Because of the potential for food limitation via rainfall variation for this insectivorous, prairie species, we included in our analysis cumulative rainfall in the three months leading to clutch initiation for each nest (Patten and Rotenberry 1999) as a surrogate for food abundance (Saino et al. 2004).

We calculated ambient fertile period weather conditions for two estimates of female fertile period. First, we used the methodology of Johnsen and Lifjeld (2003) and Bouwman and Komdeur (2006) so our results could be compared to theirs. These studies defined the period of peak female fertility as a 4-day period from three days prior to clutch initiation until the day the first egg is laid, when the majority of fertilizations are thought to occur in many passerine species (O'Malley 1993, Krokene et al. 1996, Lifjeld et al. 1997, Sheldon and Ellegren 1998, Komdeur et al. 1999). For the 4-day fertile period estimate, we calculated the mean daily vapor pressure deficit (kPa), minimum daily temperature (ºC), maximum daily temperature (ºC), and maximum daily wind speed (km/hr). We also calculated cumulative rainfall (cm) and rainfall duration (minutes) during this period.

Second, because Scissor-tailed Flycatchers have a longer egg-laying period and lay more eggs than the species in the previous studies (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006), we also used a 10-day time-frame ending the day the penultimate egg was laid in each clutch. This longer fertile period estimate sampled greater variability in weather conditions and probably more completely encompassed any possible short-term sperm storage (Bouwman and Komdeur 2006). Because we were interested in how the predictability of weather conditions can affect EPP, we used ambient weather conditions during this period to calculate standard deviation (SD) of vapor pressure deficit (kPa), minimum daily temperature (ºC), maximum daily temperature (ºC), and maximum daily wind speed as a measure of the variability of ambient weather conditions during female fertility.

Statistical Methods—We used logistic regression (R Development Core Team) to evaluate the relationship between the probability of cuckoldry and fertile period ambient weather conditions and 90-day cumulative precipitation. We excluded multicollinear variables, as determined by the variance inflation factor (VIF > 4; Zuur et al. 2010). Mean minimum (VIF = 5.2, $r = 0.7$) and maximum (VIF = 4.6, r = 0.9) daily temperature exceeded the VIF cutoff and both were strongly correlated with mean vapor pressure deficit. Maximum daily temperature SD also exceeded the VIF cutoff (VIF = 5.6) and varied closely with minimum daily temperature SD ($r = 0.7$). Finally, rainfall duration (VIF = 6.9) was multicollinear with rainfall amount (VIF = 6.8), which we retained in our analysis. We retained mean vapor pressure deficit, as it is likely a more biologically meaningful predictor of a bird's ability to thermoregulate. We also retained both measures of minimum daily temperature, as copulations occur more frequently in the morning hours in other species (Birkhead et al. 1987). We evaluated all possible additive combinations of retained variables using the package MuMIn. Model fits were ranked using corrected Akaike Information Criterion (AICc) scores (Burnham and Anderson 2002). We calculated ΔAIC for each model and Akaike weights (w_i) to evaluate model fit, where higher w_i values represent better model fit (Burnham and Anderson 2002). We interpreted all models < 2 AIC from the top model as plausible. Because we were interested in determining which variables had the greatest effect on the probability of cuckoldry, we summed Akaike weights across models in which each predictor was present to evaluate its relative contribution across all models. We interpreted predictors only when Σw_i for the top predictors approached twice the magnitude of Σw_i of other predictors. We ran all two-variable interaction models but did not include these in Σw_i. If an interaction model was > 2 AIC lower than the next best model, that interaction model was interpreted as the better model. All models in the top sets were compared to the null model using the likelihood ratio test and all had significantly better fit.

RESULTS

Scissor-tailed Flycatcher EPP rates were high in our study population (Chapter 2). Across the 7-year study, the percentage of nests with EPY ranged from 43-87% ($\bar{x}$ = 73%, n = 140) and 29-72% of nestlings ($\bar{x}$ = 59%, n = 547) resulted from EPCs. Rates of EPP were similar between Fort Sill ($\bar{x}$ = 74% of nests, 58% of nestlings) and the refuge ($\bar{x}$ = 71% of nests, 59% of nestlings). Because EPP rates did not differ between sites ($G_1 = 0.1$, $P = 0.2$) or across years ($G_6 = 6.2$, $P = 0.6$), we combined paternity data for statistical analysis.

Our multimodel inference examination of all possible additive models of differences in weather conditions between nests with and without EPP yielded only two models in the top set. The best model included mean vapor pressure deficit, vapor pressure deficit SD, and minimum temperature SD (AICc = 154.4, $w_i = 0.10$), whereas the second best model was a subset of this and included mean vapor pressure deficit and minimum temperature SD (AICc = 155.3, w_i = 0.06). When we summed Akaike weights across all models in which they were present, vapor pressure deficit (Σw_i = 0. 89) and mean daily minimum temperature SD (Σw_i = 0.83) were the best predictors of cuckoldry in sampled nests (Table 2). Both mean vapor pressure deficit (Figure 1A) and minimum daily temperature variability (Figure 1B) were higher in nests that were not cuckolded.

DISCUSSION

Two measures of ambient weather conditions during female fertility were predictive of cuckoldry in nests of Scissor-tailed Flycatchers. The first, vapor pressure deficit, was a measure of average conditions during the estimated 4-day fertile period, whereas the second, standard deviation of minimum daily temperature, was a measure of the variability of conditions during the estimated 10-day fertile period. Both variables likely affected the probability of cuckoldry by modifying individual time-budgets and promoting or constraining the ability of males to accompany their mates either when foraging or collecting nest material.

Mean vapor pressure deficit during the 4-day estimate of female fertile period was higher for nests without EPP. Temperature has been investigated in past studies (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006, Hoset et al. 2014), but we instead used vapor pressure deficit, a metric that combines information on temperature, atmospheric pressure, and humidity, because it is more indicative of the ability of individuals to thermoregulate effectively (Wolf 2000, Smit et al. 2013). At a low vapor pressure deficit, air contains more water vapor than at a high vapor pressure deficit.

The drier the air, the easier it is for organisms to shed excess heat through evaporative cooling during periods of high activity, such as during foraging, mate-guarding, or flight (Smit et al. 2013, Smit and McKechnie2015). Low vapor pressure deficits in our system also likely negatively affected arthropod activity (Kingsolver 1983, Shipp et al. 1987, Peng et al. 1992, Bestelmeyer and Wiens 2003). We suggest that at high vapor pressure deficits, members of a fertile pair must forage separately because of lower activity, and thus availability, of arthropod prey (Kingsolver 1983, Shipp et al. 1987, Peng et al. 1992), leading to a trade-off between foraging and mate-guarding (Bryant and Westerterp 1983, Redpath et al. 2002).

Fertile females forage at a higher rate than their mates because they must support the greater metabolic activity associated with breeding, growth of reproductive tissues, and production of eggs (Jones 1987, Askenmo et al. 1992). Social males, on the other hand, may opt to reduce their heat loads when thermoregulation is difficult by spending more time in the shade and less time accompanying their foraging mates. This could result in a higher probability of cuckoldry if physical distance makes it more difficult for the social male to respond quickly to intrusions by extra-pair males (Westneat 1994, Vaclav et al. 2003). Indeed, we have shown previously that the probability of EPP was higher on Scissor-tailed Flycatcher territories that had more trees and thus, more shaded areas (Chapter 3). We suggest that either social males spent more time in the shade when thermoregulation is difficult (Wolf 2000), thus leaving their mates unaccompanied, or that extra-pair males used shaded areas to approach foraging females. Extra-pair males whose mates were not concurrently fertile may not have been as strongly affected by low vapor pressure deficits as social males because they were free to forage or remain in the shade without the constraints of mate guarding. Prior work with Scissor-tailed Flycatchers supports this idea, in that most extra-pair sires either had mates that were not concurrently fertile with extra-pair mates or were unpaired (Chapter 3).

In addition to average ambient weather conditions, we investigated how predictability of weather patterns during fertility affected the probability of cuckoldry. We found that lower variability of minimum daily temperature during female fertility correlated with an increased probability of cuckoldry. When minimum temperatures were variable, arthropod activity was likely variable as well (Hodkinson et al. 1996, Redpath et al. 2002, Johnsen and Lifjeld 2003), necessitating more time spent foraging after cold nights to restore energy reserves and maintain body condition (Webster and Weathers 1990, Gass et al. 1999, Hilton et al. 1999, Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006). Unlike vapor pressure deficit, temperature variability resulting in unpredictable arthropod availability should impact males and females similarly because both sexes must capture enough prey to fuel thermoregulation. We posit that foraging takes priority over extra-pair behavior when minimum daily temperatures are unpredictable (Jorde et al. 1984, Dawson and O’Connor 1996, Johnsen and Lifjeld 2003, Hoset et al. 2014). Likewise, when temperature is low, birds often forage closer to the ground (Grubb 1987, Teather 1992) and make shorter foraging flights (Murphy 1987, Teather 1992), decreasing their visibility to extra-pair birds.

Along with ambient weather conditions during the fertile period, resource abundance likely plays an important role in extra-pair behavior (Hoi-Leitner et al. 1999, Václav et al. 2003, Rubenstein 2007). Most studies that have documented an effect of food abundance on EPP have relied on sampling arthropod abundance on territories or supplementing food to breeding birds (Westneat 1994, Hoi-Leitner et al. 1999). Precipitation is a driver of primary productivity and arthropod abundance in many systems (Kirchner 1977, Boyer et al. 2003) and has been linked with vegetation growth and sexual selection (Saino et al. 2004). Because we were unable to directly sample arthropod abundance, we used three-month cumulative precipitation as a proxy for food resource abundance. We expected to see a strong effect of our longer-term measure of precipitation on EPP, particularly because of the temporal heterogeneity in precipitation during our study. Contrary to our expectations, cumulative precipitation in the three months leading to clutch initiation was not a good predictor of the presence of EPP when compared to other predictors. It may be that in savannah systems, arthropod populations increase in response to greater rainfall and plant productivity (Kirchner 1977), but some taxa on which Scissor-tailed Flycatchers rely for a large portion of their diet, such as grasshoppers (Beal 1912), either decrease in diversity and abundance during high rainfall years (Kirchner 1977) or when plant biomass is high (Joern 2005), or their population dynamics are unrelated to rainfall (Pinheiro et al. 2002). Because our study species preys upon taxa abundant in both low and high rainfall conditions, resource abundance may not have been variable enough to affect rates of EPP.

We found no effect of maximum daily wind speed or predictability on EPP, nor did we find an effect of fertile period precipitation. While wind speeds can be quite high and variable in our system, they are typically highest during mid-day. If the majority of copulations occur prior to mid-day, as they do in other species (Briskie 1992, Pinxten and Eens 1997), maximum wind speed may not have been a good indicator of physical constraints on movement. Likewise, our savannah system received relatively low rainfall during each breeding season (Table 1) and it generally did not occur in multi-day stretches. As with wind speed, it may not provide a strong enough constraint on movement to depress extra-pair behavior (Johnsen and Lifjeld 2003).

The results of our population-level investigation are contrary to results of an across-species study that found high EPP rates for species in environments with high within-year variance in temperature (Botero and Rubenstein 2012). Botero and Rubenstein (2012) suggested that when the conditions that offspring will experience are unpredictable, greater genetic diversity among offspring resulting from EPP could improve the long-term fitness of females. We suggest that while climatic variability may be positively associated with EPP at the species level, the consequences of variability during fertility within a population may result in a lower probability of cuckoldry at the nests of individuals that must cope physiologically with unpredictable conditions on a daily basis.

In this study, we demonstrated that ambient weather conditions during female fertility have an effect on extra-pair paternity. Our results are similar to those of the few other studies that examined how weather conditions during female fertility influenced EPP (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006, Hoset et al. 2014), supporting the role of time budget trade-offs with and physiological constraints on mate-guarding behavior and extra-pair pursuits. We found no support for a link between EPP and three-month cumulative precipitation prior to clutch initiation, our proxy for long-term variation in food abundance. However, our proxy may not have been closely linked to arthropod abundance because of the differential response of grasshoppers to rainfall (Joern 2005), one of the primary prey taxa for Scissor-tailed Flycatchers. Studies such as ours are necessary to provide insight into the relationship between climate and EPP. To understand fully the drivers of extra-pair behavior, the field must progress to behavioral studies that link foraging, mate-guarding, and extra-territorial intrusions with individual, breeding population, and environmental characteristics (Griffith et al. 2002). Seeking an integrative method for exploring the causes and consequences of EPP will help us not only better understand patterns of paternity but also the potential impacts of climate change and altered environmental landscapes on the evolutionary future of many passerine species.

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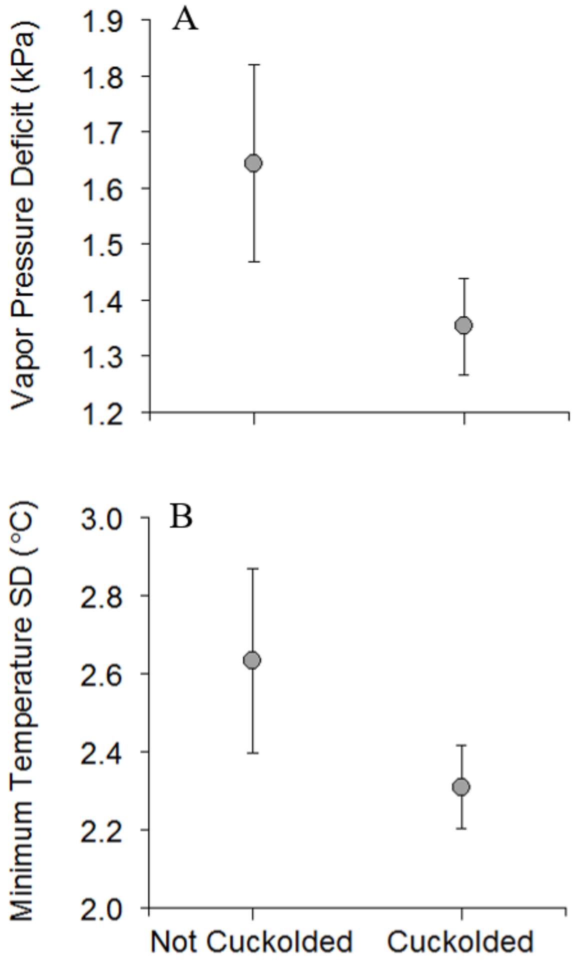
TABLE 1. Daily ambient weather conditions during the Scissor-tailed Flycatcher breeding season (May–August) in Comanche County, Oklahoma, from 2008-2014. Cumulative breeding season rainfall was averaged across years and the range represents the lowest and highest yearly cumulative rainfall measure. Other weather measurements represent long-term averages and lowest and highest measurements across all breeding season months and years. Data were summarized from the Oklahoma Mesonet weather station in Medicine Park, Oklahoma.

	Average	Range
Cumulative rainfall (cm)	26.5	14.0–37.9
Daily minimum temperature (ºC)	20.2	2.9–29.5
Daily maximum temperature (ºC)	32.8	11.5–44.2
Daily maximum wind speed (km/hr)	34.4	15.0–78.0
Relative humidity (%)	56.7	18.0–98.3
Vapor pressure deficit (kPa)	17.7	0.3–48.5

TABLE 2. Weight of evidence, given as summed Akaike weights (Σw_i) across all models containing a particular variable, for each ambient weather variable in logistic regressions between weather and cuckoldry. Means and cumulative rainfall were calculated for the 4-day fertile estimate and standard deviations (SD) were calculated for the 10-day fertile estimate for Scissor-tailed Flycatchers in Comanche County, Oklahoma, from 2008–2014. Weights in bold were well above competing variables and were considered for interpretation.

Variables	Σw_i
Cumulative 90-day Precipitation	0.41
Daily Minimum Temperature SD	**0.83**
Mean Vapor Pressure Deficit	**0.89**
Vapor Pressure Deficit SD	0.54
Mean Maximum Wind Speed	0.26
Maximum Wind Speed SD	0.33
Rainfall	0.41

FIGURE 1. Best weather predictors of the probability of EPP in Scissor-tailed Flycatcher nests in Comanche County, Oklahoma from 2008-2014. A) Mean daily vapor pressure deficit for female 4-day fertile period estimates. B) minimum daily temperature standard deviation (SD) for 10-day fertile period estimates. Values are means (± 84% CI) for nests at which males were not or were cuckolded.



CHAPTER FIVE

TOWARDS A HOLISTIC VIEW OF THE CAUSES AND CONSEQUENCES OF EXTRA-PAIR PATERNITY

Diane V. Roeder[1],

Michael S. Husak[2], Michael T. Murphy[3], and Michael A. Patten[1]

[1] Department of Biology & Oklahoma Biological Survey, University of Oklahoma,
Norman, OK 73019, USA

[2] Department of Biological Science, Cameron University, Lawton, OK 73505, USA

[3] Department of Biology, Portland State University, Portland, OR 97207, USA

ABSTRACT

Fitness and reproductive success of individuals is influenced by the number of young an individual can produce. In birds with socially monogamous mating systems, an important component of reproductive success is extra-pair paternity (EPP), when offspring in a nest are sired by males outside of the social pairing. Given that EPP is prevalent in passerine birds, it is important that we understand how individual, ecological, and environmental factors drive or constrain the opportunity for EPP, and thus sexual selection. We compiled data from four datasets used in previous studies to examine the effect of morphology, nest spacing and synchrony, habitat structure, and weather conditions on the probability of EPP in nests of Scissor-tailed Flycatchers in Comanche County, Oklahoma from 2009-2014. We used path analysis to examine the relative influence of direct predictors from each dataset, as well as the strength of effect of indirect predictors on EPP via related direct predictors. We found that the direct predictors important in our morphology path analysis (body condition and tail asymmetry) and vegetation structure around a nest (woody vegetation cover and number of trees and shrubs) had little effect when combined with ambient weather predictors (vapor pressure deficit and variability of minimum daily temperature), nearest synchronous neighbor distance, and a human-influenced structural component of habitat, fence length. Other predictors unimportant in our initial studies as direct influences on the probability of cuckoldry were indirect predictors with strong effects in our final global path analysis. In particular, average maximum wind speed and variability had moderate effects on EPP by influencing temperature variability and vapor pressure deficit. Likewise, local neighbor density increased and local synchrony decreased the probability of cuckoldry via their influence on nearest neighbor distance. These indirect effects were as strong as some direct predictors. Our compilation of measurements across multiple levels of biological organization, multiple years, and within one population revealed the importance of examining individual characteristics in the context in which they occur. Sexual selection on morphology may be flexible across ecological and environmental conditions, explaining their weak effect in many studies. Breeding synchrony, ambient weather conditions, and their correlates, all of which influence the time individuals must devote to mate-guarding and self-maintenance, strongly constrain time-tradeoffs between foraging, accompanying fertile mates, and seeking extra-pair copulations.

Keywords—cuckoldry, density, habitat structure, mate-guarding, morphology, path analysis, Scissor-tailed Flycatcher, synchrony, *Tyrannus forficatus*, weather

INTRODUCTION

Fitness measures the reproductive success of an individual in relation to that of other individuals (Emlen and Oring 1977). Because not all individuals will be able to reproduce, there should be strong competition to contribute genetically to the next generation. This is particularly true when some individuals are able to dominate mating opportunities, resulting in increased intrasexual competition for access to mates and more intense sexual selection (Emlen and Oring 1977). Competition for mates, and thus sexual selection, is particularly high among males in promiscuous and polygamous mating systems because many males fail to secure mating opportunities (Bennett and Owens 2002). In contrast, most individuals of monogamous species have the opportunity to pair and raise young, leading to substantially lower sexual selection pressure and more evenly distributed reproductive success (Bennett and Owens 2002). However, sexual selection and variance in reproductive success can still be relatively high in socially monogamous species when some individuals can monopolize copulations both within and outside of the pair bond (Webster et al. 1995, Yezerinac et al. 1995, Griffith 2007). Thus it is important that we understand how social and extra-pair reproductive behaviors affecting fitness are shaped by the social and ecological environment in which they take place.

Most passerine birds have socially monogamous mating systems in which a male and female pair for a breeding attempt and work together to raise their young. However, the genetic underpinnings of mating systems often do not reflect social pairings (Griffith et al. 2002, Westneat and Stewart 2003). Birds often engage in extra-pair copulations (EPC), or copulations outside of the pair. When these matings result in fertilizations, the result is extra-pair paternity (EPP; Griffith et al. 2002). EPP is common in some groups of birds, including passerines in which >86% of all species and >75% of socially monogamous species exhibiting genetic polygamy (Griffith et al. 2002, Westneat and Stewart 2003).

The causes and correlates of extra-pair behaviors in birds have been debated since the discovery of widespread EPP (Griffith et al. 2002, Westneat and Stewart 2003). Yet, we still know very little about how different factors interact to shape reproductive behaviors (Westneat and Stewart 2003). Individual traits, such as age, experience, morphology, song, and genetic quality, influence sexual selection or the ability of individuals to secure copulations (Griffith et al. 2002, Westneat and Stewart 2003, Açkay and Roughgarden 2007, Cleasby and Nakagawa 2012). Characteristics of breeding populations, including spatial distribution and synchrony of fertile pairs, influence interaction rates between individuals (Westneat et al. 1990, Stewart et al. 2010, Mayer and Pasinelli 2013). Habitat structure may act to provide cover for EPCS and may mediate the effects of poor weather, which may physically constrain movement about a territory (Sherman and Morton 1988, Blomqvist et al. 2006) or act on an individual's ability to forage effectively (Murphy 1987) or thermoregulate (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006, Botero and Rubenstein 2012). The search to explain variation in EPP rates across passerine populations and species has progressed from a focus on each of these sets of factors to a realization that EPP may be the outcome of interactions across all of these (Westneat and Stewart 2003). Comprehensive approaches that examine how individual characteristics, population dynamics, and the environment both directly and indirectly influence reproductive and extra-pair behavior may also help us understand why characteristics important in predicting EPP and reproductive success for some species do not appear to be important in others (Griffith et al. 2002, Westneat and Stewart 2003, Wan et al. 2013). However, few such studies are available because of the substantial time investment necessary to collect data across such a large variety of variables in the same population.

In this study, we synthesized data simultaneously collected during a six year, multipart study of EPP rates in a population of Scissor-tailed Flycatchers (*Tyrannus forficatus*) using a path analytic approach. Data included measurements of individual morphology (Chapter 2); timing of nesting, spatial distribution of nests, and breeding synchrony (Chapter 3); habitat structure (Chapter 3); and local climate (Chapter 4). We had three primary goals for this study: 1) determine the direct effects of variables in each data set on the probability of cuckoldry, 2) evaluate the relative influence of each data set on EPP when combined into a single analysis, and 3) assess possible pathways leading to differences between variables of importance.

We expected that variables related to a male's ability to mate guard or a female's ability to escape guarding would have the strongest direct influence on the probability of EPP. These variables included: 1) vapor pressure deficit and temperature variability, which are related to trade-offs between mate-guarding and thermoregulatory demands (Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006, Botero and Rubenstein 2012, Chapter 4); 2) woody vegetation and tree cover on territories, which may act to provide shade for heat-stressed males, thereby separating them from their mates, and to provide visual obstruction that may allow extra-pair males to approach females without the social male's knowledge (Chapter 3); and 3) the spatial distribution of synchronous neighbors, which may influence interaction rates between fertile pairs (Chapter 3). We expected that morphological characteristics important in cuckoldry, such as body condition and tail symmetry, would have a lower relative influence on EPP because of the likelihood that sexual selection on morphology is flexible across social and ecological conditions (Chaine and Lyon 2008) and because it seems to only have a weak influence on paternity rates across species (Hsu et al. 2015). Additionally, we expected that strong indirect effects of climatic factors, such as growing-season rainfall, would have indirect effects on EPP through its influence on vegetation structure or body condition of individual birds. Likewise, vegetation structuring should influence the spatial distribution of pairs and potentially the body condition of birds in those habitats, which likely influences paternity.

METHODS

Study Species—The Scissor-tailed Flycatcher is a sexually dimorphic (Regosin and Pruett-Jones 2001), socially monogamous passerine species that engages often in EPP (73% of nests and 59% of young; Roeder et al. 2016). Adult males are heavier, more brightly colored, and have longer wing and outer tail feathers than females (Regosin and Pruett-Jones 2001). The outermost primary is attenuated on the trailing edge of the feather tip, with attenuation deeper in males (Pyle 1997). This feature is important for flight performance of both sexes (Chapter 2). There is a considerable degree of asymmetry in most flight feathers, and asymmetry is unrelated to feather length (Regosin and Pruett-Jones 2001).

Scissor-tailed Flycatchers nest in scattered trees in mesquite/oak savannah (Regosin 2013). The species suffers from high depredation rates (32% average success rate; Landoll 2011), which results in variable breeding density and synchrony (Chapter 3). Both males and females defend their territories from conspecifics and predators (Regosin 2013). Females build nests and incubate eggs without male help, but both parents feed nestlings and fledglings (Regosin and Pruett-Jones 1995). Scissor-tailed Flycatchers are aerial insectivores that forage primarily in their own territories during breeding (Teather 1992), but often wander once a breeding attempt has concluded (Regosin 2013). Ambient weather conditions affect foraging strategies (Teather 1992) and influence the probability of cuckoldry, potentially by making mate-guarding more difficult (Chapter 4).

Study Duration and Location—We collected data used in this study from April to August of 2008–2014 in Comanche County, Oklahoma. Scissor-tailed Flycatchers were captured and their nests observed at the Wichita Mountains Wildlife Refuge and on the adjoining Fort Sill Artillery Base. These sites are within the mixed-grass prairie ecoregion of the Great Plains and all contain either oak (*Quercus* spp.) or mesquite (*Prosopis glandulosa*) savannah broken by low-lying mountains and riparian woods. Both contain stretches of roads and fences, although Fort Sill experiences heavier human impacts via army maneuvers, hunting, and maintenance than does the refuge. This prairie/savannah region has variable ambient weather conditions during breeding and is characterized by low rainfall, high temperature, and high wind speed (Table 1 in Chapter 4).

Data Sources and Variables—Prior to this study, we investigated the effect of variables in four datasets on the probability of cuckoldry (social male morphology – Chapter 2; nest spacing, density and synchrony – Chapter 3; habitat structure – Chapter 3; weather conditions – Chapter 4). We used the variables from these datasets (Table 1) in the current study to construct paths to elucidate direct and indirect effects of variables on the probability of EPP. Social male morphology variables included body condition (residuals of mass by wing chord regression), tarsus length and asymmetry, wing chord asymmetry, primary attenuation length, and tail length and asymmetry.

Statistical analysis—To explore direct and indirect effects of morphology, breeding population characteristics, habitat structure, and weather conditions on the probability of cuckoldry, we used a directed separation path modeling framework (Shipley 2000, Shipley 2009). Path modeling can easily accommodate both the normal distribution of our predictor variables and the non-normal distribution of our response variable, the presence/absence of EPP in nests (Shipley 2000, Shipley 2009). It allows the user to draw stronger inferences from correlational data than linear models (LM) and generalized linear models (GLM) do on their own (Shipley 2000, Shipley 2009). This approach allowed us to conceptualize and assess both direct and indirect effects of predictors on the probability of EPP (Shipley 2000, Shipley 2009). We constructed our global path model based on previous knowledge of how individual, breeding population, and weather characteristics are believed to influence the probability of cuckoldry. The fit of the model was evaluated through directed separation (d-sep) tests (Shipley 2009). D-sep tests work on the basis that, for each path model, there is a set of independence tests that must be true if the hypothesized causal structure of the model matches the correlational structure of the data. The global model fit was evaluated using Fisher's C statistic: $C = -2 \sum \ln (p)$, which follows a chi-squared distribution with $2*k$ df, where p is the null probability of each d-sep test between predictors in each path ($n = k$; Shipley 2009). If the C value was significant at $\alpha < 0.05$), we rejected the model due to poor model fit. Variables were dropped from each path if d-sep tests indicated that they were not independent of other variables in that path (i.e. multicollinearity). We fit paths and calculated relative path coefficients (i.e. standardized partial regression coefficients) for all direct predictors on EPP with multiple logistic regression and for relationships between indirect predictors and direct predictors with multiple linear regression. With the exception of our response variable, presence/absence of EPP, we standardized each variable using z-score scaling (V–mean of V/standard deviation of V) to put variables on the same scale (Provencher et al. 2016). Total effect sizes for a given variable, where appropriate, were calculated by summing the direct effect and the products of the indirect effect sizes (Shipley 2000). We calculated error for regressions as the model square root * $(1 - r^2)$ (Shipley 2000). All data were analyzed using R 2.3.2 statistical software (R Development Core Team 2013). All statistical tests were evaluated at $\alpha=0.05$ and means are presented ± standard deviations (SD).

RESULTS

EPP Rates and Sample Size—From 2008-2014, we determined the prevalence of EPP in 140 Scissor-tailed Flycatcher nests. EPP rates were high across all years of the study (Table 1; Chapter 2), averaging 73% of nests and 59% of nestlings from 2008-2014. We collected morphology, breeding population, habitat structure, and weather conditions for 106 of these nests (67.9% of nests contained EPP). Data for these nests were used to parameterize our path models. We present results of path analysis for each data set, followed by results for the relative influence of direct predictors on the probability of EPP and any across-data set indirect effects for our global path model. A number of variables were highly correlated with each other and d-sep tests indicated that their effect was not independent of the effect of the correlated variable. These were dropped from final paths for each dataset and for the global path (Table 1).

Morphology—Our final morphology path model included direct effects important in our previous study of the effect of morphology on EPP (Chapter 2). As before, tarsus asymmetry and body condition were higher in nests without EPP (tarsus asymmetry: 0.30 mm ± 0.20, body condition: 2.62 ± 3.49) than in nests with EPP (tarsus asymmetry: 0.23 mm ± 0.20, body condition: 1.37 ± 3.33), while decreasing tail asymmetry was associated with lower cuckoldry (cuckolded: 6.46 mm ± 10.37, not cuckolded: 4.36 mm ± 5.48; Figure 1A; Figure 3 in Chapter 2). Inclusion of a path between tarsus length and asymmetry, as well as tail length and asymmetry, was consistent with the correlational structure of our data (Fisher's C statistic = 6.40, df = 4, p =0.17). However, these indirect effects were not significantly related to either direct predictor (tarsus asymmetry: t = -0.78, p = 0.44; tail asymmetry: t = 0.70, p = 0.49) and thus had little effect on EPP.

Nest Timing, Distribution, and Synchrony—In our final breeding population path model (Fisher’s C statistic = 7.93, df = 6, p = 0.25), the only predictor with a direct effect on the probability of EPP was nearest synchronous neighbor distance during the 4-day fertile period estimate. Synchronous neighbors were closer when EPP was absent

(1.51 km ± 1.53) than when present (3.69 km ± 5.31), as in our previous study (Figure 2a in Chapter 3). Three predictors acted on EPP indirectly via their impacts on nearest synchronous neighbor distance: nearest synchronous neighbor distance decreased as the number of neighbors at the local scale ($t = -2.20$, $p = 0.03$), local synchrony index ($t = -3.18$, $p = 0.00$), and population synchrony index ($t = -4.47$, $p = 0.00$) increased (Figure 1B).

Habitat structure—As in our prior study of the effect of habitat on probability of EPP, proportion of woody vegetation cover in the 11.5 m radius circle surrounding each nest tree was higher and fence length in the 57 m radius constituting the core of defended territory surrounding each nest was shorter on territories with no EPP (woody cover: 0.10 ± 0.11; fence length: 5.94 m ± 21.20) than with EPP (woody cover: 0.06 ± 0.07; fence length: 38.01 m ± 75.01; Figure 3 in Chapter 3). In our habitat structure path model (Fisher's C statistic = 6.87, df = 6, $p = 0.33$), both number of trees ($t = 6.28$, $p < 0.00$) and shrubs ($t = 5.66$, $p < 0.00$) had indirect effects on the probability of EPP as a result of their positive relationship with the proportion of woody cover (Figure 1C). Our hypothesized path was also consistent with an indirect effect of short vegetation cover in the 57m radius territory surrounding each nest and EPP, mediated through fence length. However, the relationship between short vegetation cover and fence length was not significant ($t = -053$, $p = 0.60$; Figure 1C).

Weather Conditions—Our final weather path model (Fisher's C statistic = 4.08, df = 4, $p = 0.40$) included the direct effects of average vapor pressure deficit and variability of minimum daily temperature during female fertility on probability of EPP (Figure 1D). As in our prior study, when EPP was absent, average vapor pressure deficit (1.63 ± 0.79) and daily minimum temperature SD (2.74 ± 1.00) were high, while both were low when EPP was present (vapor pressure deficit: 1.27 ± 0.57; minimum temperature SD: 2.34 ± 0.88; Figure 1 in Chapter 4). Increasing variability in maximum wind speed indirectly affected the probability of EPP by lowering vapor pressure deficit ($t = -6.28$, $p < 0.00$). Likewise, increasing average maximum wind speed was related to decreasing variability of minimum daily temperature ($t = 0.35$, $p < 0.00$).

Global Model Fit—Our final global model was consistent with the correlational structure of the data and indicated the independence of predictors (Fisher's C statistic = 9.65, df = 10, $p = 0.47$). Several variables that were important in individual data sets were not important when all data sets were combined. All direct morphological predictors dropped out of significance when we examined direct predictors from each data set using multiple logistic regression (body condition: $z = -1.06$, $p = 0.29$; tarsus asymmetry: $z = -1.40$, $p = 0.16$, tail asymmetry: $z = 1.24$, $p = 0.22$). Morphological variables also had no indirect effects on the probability of EPP through other predictors in the global model (Figure 2). Nearest synchronous neighbor distance remained a significant direct predictor of the probability of EPP in nests in our final global model ($z = 2.52$, $p = 0.01$, effect size = 1.68). Population synchrony dropped from our final path model as an indirect predictor, and it was not related to any other predictor in our complete dataset. Both local synchrony index ($t = -3.04$, $p < 0.00$, effect size = 1.21) and local neighbor density ($t = -2.02$, $p = 0.05$, effect size = 1.36) remained important indirect predictors of EPP, acting through nearest synchronous neighbor distance. The direct effect of woody vegetation cover dropped out of significance ($z = -1.24$, $p =$

0.22), with only fence length remaining as a predictor directly influencing the probability of EPP ($z = 1.96$, $p = 0.05$, effect size = 1.08; Figure 2). Both of the direct predictors in our weather path model remained important in our final global model (vapor pressure deficit: $z = -3.45$, $p < 0.00$, effect size = -1.15; minimum temperature SD: $z = -2.04$, $p = 0.04$, effect size = -0.60). Maximum wind speed variability indirectly affected the probability of EPP through vapor pressure deficit ($t = 3.83$, $p < 0.00$, effect size = -0.63) and average maximum wind speed ($t = -6.28$, $p <0.00$, effect size = -0.77) through minimum temperature variability, as in the weather path model. Clutch initiation date ($t = -5.45$, $p < 0.00$, effect size = 0.35) was an important indirect predictor of EPP in our final global path model and was a significant predictor of minimum temperature variability with maximum wind speed ($t = 3.70$, $p < 0.00$).

DISCUSSION

Extra-pair paternity has been examined in a range of bird species, leading to a number of hypotheses explaining why some individuals, populations, or species may be more or less prone to extra-pair behavior (Griffith et al. 2002, Westneat and Stewart 2003). In this study, we used paternity data from Scissor-tailed Flycatcher nests sampled across six years to investigate the relative influence of individual, ecological, and environmental predictors on the probability of cuckoldry. Because we were able to use data collected at the same time on morphology, nest spacing and synchrony, habitat structure, and ambient weather conditions, we were able to determine how each directly and indirectly influenced EPP. We suggest that mate-guarding may be the primary way by which Scissor-tailed Flycatcher males maintain paternity in their own nests, but that mate-guarding can be constrained by trade-offs in time spent engaged in self-maintenance activities.

Direct Predictors of Cuckoldry—When we built path models for morphology, breeding population, habitat structure, and weather datasets individually, variables with direct effects were the same as those important from multimodel inference during each initial study. However, when we combined variables with a direct influence on the probability of cuckoldry from all datasets, we found that the relative importance of some predictors was much lower than that of others. In particular, all direct morphological predictors (body condition, tarsus asymmetry, tail asymmetry) and the combined effect of woody vegetation cover and number of trees had negligible effects on cuckoldry compared to nearest synchronous neighbor distance, fence length, average vapor pressure deficit, and variability in minimum daily temperature in the final global model.

In our initial study of the effect of morphology on the probability of cuckoldry, males in good condition and with symmetrical tails were less likely to be cuckolded (Chapter 2). These characteristics were likely related to a male's ability to mate-guard, as well as female faithfulness to a high quality mate (Komdeur 2001). However, sexual selection on morphology can be variable across years and varied with male traits that predicted female reproductive success (Chaine and Lyon 2008). We suggest that sexual selection on social male morphology is a relatively weak predictor of cuckoldry across years because of the potential for adaptive plasticity in female mate selection (Chaine and Lyon 2008). Studies examining more than one set of variables simultaneously may therefore be less likely to detect an effect of morphology on cuckoldry due to variable sexual selection pressure on male morphology occurring on a local level and encompassing a female's response to breeding population, habitat, and weather conditions (Chaine and Lyon 2008, Hsu et al. 2015).

The effect of woody vegetation cover and its associated indirect predictors, number of trees and shrubs, also became non-significant in the final global path model. As in our prior study, the probability of cuckoldry decreased when woody vegetation cover was primarily composed of shrubs, likely because males on these territories were better able to survey their territories from perches raised above grass and forb level (Chapter 3; Foreman 1987). Visual obstruction of territories increased as the composition of woody cover became more tree-biased, likely providing opportunities for extra-territorial forays by females or intrusions by extra-pair males (Mays and Ritchison 2004, Tryjanowski et al. 2007). Additionally, fertile females forage at a higher rate and for a long duration than their mates because they must build energy reserves to invest in egg production (Jones 1987, Askenmo et al. 1992), potentially making foraging necessary during periods of thermal stress. Their social mates, however, may have been able to cease foraging and reduce their heat loads by taking cover in trees, which provide shade. If time spent on decreasing heat load results in less time spent accompanying their foraging mates, this could result in a higher probability of cuckoldry as it would then be more difficult for the social male to respond quickly to intrusions by extra-pair males (Westneat 1994, Vaclav et al. 2003).

However, this path did not significantly affect the probability of EPP in our final global model. We suspect this was because vapor pressure deficit and variability of minimum temperature during female fertility were more direct measurements of the drivers of thermoregulation-imposed trade-offs between time spent foraging, self-maintenance, and mate-guarding than was woody vegetation (Bryant and Westerterp 1983, Redpath et al. 2002, Johnsen and Lifjeld 2003, Bouwman and Komdeur 2006). Likewise, nearest synchronous neighbor distance, which was the direct predictor with the strongest effect, was a strong predictor of the need to mate-guard. Although woody vegetation cover and nearest synchronous neighbor distance were not directly related, there seemed to be a constraint relationship between the two. Distance between nearest synchronous neighbors was only very high when there was little woody vegetation, while nearest neighbor distances were low across a range of woody vegetation cover. Because the probability of EPP was lowest when nearest synchronous neighbor distance was low and woody vegetation cover on a territory was high, but distances were low across a range of woody cover, the weaker effect of woody vegetation on EPP was likely confounded.

Fence length continued to have a strong direct effect on EPP (Chapter 3). This effect may have persisted in the final global model because it likely indicated the degree to which non-synchronous neighbors came into contact. Scissor-tailed Flycatchers often use fences as foraging perches to the exclusion of other suitable perches (Tatschl 1973, Foreman 1987, Teather 1992). Fences can span many territories and may thus put birds in greater contact than when perches are plants within the borders of defended territories. Many males in such situations may not be guarding fertile mates, making it more difficult for territorial males to guard their own fertile mates and increasing the opportunity for EPCs (Dunn et al. 1994, Tarof et al. 1998, Ewen et al. 1999, Hammers et al. 2009). Birds may be subject to greater EPC pressure when fences are abundant, such as on rural residences and farm land where fences are used to divide property. An abundance of fencing provides foraging perches in high quality foraging areas on which many birds can congregate, potentially leading to a human-mediated increase in levels of EPP.

Indirect Predictors of Cuckoldry—Several predictors had indirect effects on the probability of EPP via their effects on direct predictors in our global path model. Local neighbor density and local synchrony index had a strong indirect effect on EPP via their negative relationship with nearest synchronous neighbor distance. When a focal pair had many neighbors (high neighbor density) and when more of those neighbors were concurrently fertile (higher local synchrony), the distance from a focal nest to its nearest synchronous neighbor was likely to be low. Because males with fertile mates were engaged in mate-guarding, they and their mate-guarding neighbors spent less time pursuing EPCs, as has been documented in a number of studies (Birkhead and Biggins 1987, Westneat et al. 1990, Thusius et al. 2001), an effect similar to that in our initial analysis of nest spacing and synchrony (Figure 2B in Chapter 3). The need for mate-guarding, therefore, likely constrained interactions between individuals (Charmantier and Perret 2004, Stewart et al. 2010) and was exacerbated by increasing the synchrony and closeness of neighbors (García-Navas 2014).

Another variable potentially related to both nest synchrony and weather conditions is timing of nesting, measured here as clutch initiation date. Nest timing had only a small impact on cuckoldry via its influence on minimum temperature variability. As the nesting season progressed, minimum daily temperatures continually warmed and became less variable, and less variable temperature was associated with higher rates of

EPP. Seasonality, therefore, had little impact on EPP via nest spacing or average ambient conditions during breeding, but did have a small influence by decreasing variability in ambient conditions. The lack of direct effect is consistent with the findings of prior studies of EPP and nesting date (Yezerinac et al. 1995, Møller and Ninni 1998).

Several ambient weather conditions also acted as indirect predictors of the probability of cuckoldry by influencing temperature variability and vapor pressure deficit. Average maximum daily wind speed and its variability, both of which had no effect in our initial analysis of ambient weather conditions (Chapter 4), moderately depressed the occurrence of cuckoldry. Minimum daily temperature variability increased with maximum daily wind speed. Because we found no direct effect of average wind speed or its variability on cuckoldry, its indirect effect was unlikely to have been due to the physical constraints on movement (as proposed in Chapter 4). Instead, high wind speeds may have exerted further thermoregulatory constraints on pairs fertile during days when minimum temperature was variable via additional cooling (Steadman 1979). These birds may have experienced even greater trade-offs between pursuing EPCs and foraging to maintain body fuel reserves (Bouwman and Komdeur 2006, Hoset et al. 2014). Similarly, we found that as variability in maximum wind speed decreased, vapor pressure deficit increased and the probability of EPP decreased. Variability in maximum wind speed may have influenced the way in which breeding birds experienced the effects of vapor pressure deficit. High winds contribute to more effective evaporative cooling (Steadman 1979), magnifying the advantage of breeding when vapor pressure deficit is high. Males nesting in these conditions may face a less severe trade-off between time spent mate-guarding versus engaging in thermoregulation behavior, such a seeking shade.

Conclusions—Our study emphasizes the importance of examining multiple predictors of EPP simultaneously to better understand how individual, ecological, and environmental characteristics contribute to EPP (Arnold and Owens 2002, Bennett and Owens 2002, Griffith et al. 2002). We found no effect of morphology when we examined body condition and tail asymmetry in the context of the population and environment in which EPP occurs. It is likely that these predictors were important when considered in isolation, but their relative effect was much lower than the effects of breeding synchrony, fence length, and both temperature and vapor pressure deficit. Morphology may have been under variable selection pressures as nest spacing, synchrony, and weather conditions changed, leading to an apparent lack of effect if average patterns were not strong (Jennions and Petrie 1997, Chaine and Lyon 2008). Additionally, female selection on extra-pair male morphology may have been constrained by a social male's ability to guard his mate (Petrie and Kempenaers 1998, Akçay and Roughgarden 2007), which was likely due only in part to male morphology.

In contrast, the importance of nest timing, synchrony, fence length, and ambient weather conditions, which influenced the ability of breeding birds to interact with extra-pair individuals or to effectively mate-guard, suggests that time trade-offs between self-maintenance, mate-guarding, and seeking EPCs were the primary drivers of EPP for Scissor-tailed Flycatchers during our study and in other studies (Johnsen and Lifjeld 2003, Garcia-Navas et al. 2014). Indeed, it seems as if the ability of males to effectively control interactions between their fertile mates and extra-pair males may have been a particularly important driver of EPP in our system, and has been suggested as such for passerines in general (Johnsen and Lifjeld 2003, Westneat and Stewart 2003). Time trade-offs such as those suggested here may be a much more universal problem facing all individuals, overriding weak or variables patterns of extra-pair sexual selection on morphology (Garcia-Navas et al. 2014).

Our results suggested that EPP was driven by variation in ecological and environmental factors (Griffith et al. 2002, Johnsen and Lifjeld 2003). We recommend additional studies such as ours to further clarify the role of extra-pair sexual selection on individuals versus that of trade-offs between self-maintenance, mate-guarding, and pursuit of EPCs. Understanding how different levels of biological organization combine to influence EPP and reproductive success in large-scale, single-species studies will allow us to begin to understand the relative constraints on mate fidelity, cuckoldry, and sexual selection in ways not possible by examining correlates of EPP at a single level of organization.

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TABLE 1. Variables and their effect in individual dataset path analysis (dataset path) and in the final global model (global path). Dashes indicate no significant effect on EPP or variables that were dropped because they were non-independent in d-sep tests, while the effect of significant predictors is indicated as direct or indirect. Effect sizes are partial regression coefficients calculated as direct path coefficient + (direct*indirect coefficient), where coefficients are partial regression coefficient.

TABLE 1.

	Effect of variable on EPP				
	Dataset	Effect	Global	Effect	
Variable	path	size	path	size	Variable Description
Morphology					
Body condition [a]	direct	-0.46	-	-	Residuals of mass by wing chord regression
Tarsus length	indirect	-0.30	-	-	Intertarsal joint to distal end of last tarsus scale
Tarsus asymmetry	direct	-0.31	-	-	Absolute value of difference between body sides
Primary attenuation length	-	-	-	-	Length of attenuated tip of primary feather
Tail length	indirect	0.46	-	-	Outermost feather from tip to body insertion point
Tail asymmetry [a]	direct	0.43	-	-	Absolute value of difference between body sides
Timing of nesting					
Clutch initiation date	-	-	indirect	0.35	Date of first egg in nest
Breeding population					
Neighbor density [b]	indirect	0.80	indirect	1.36	Number of neighbors
Nearest neighbor distance [b]	-	-	-	-	Distance to nearest neighbor
Nearest synchronous neighbor distance [a]	direct	0.95	direct	1.68	Distance to nearest synchronous neighbor
Local synchrony index [b]	indirect	0.76	indirect	1.21	Proportion of local females fertile on each day of focal female's fertile period
Population synchrony index	indirect	0.64	-	-	Proportion of fertile females in the population on each day of female's fertile period

TABLE 1. Continued

Habitat structure					
Grass cover (11.3 m) [c]	-	-	-	-	Visually estimated proportion
Forb cover (11.3 m) [e]	-	-	-	-	Visually estimated proportion
Woody vegetation cover (11.3 m) [a,c]	direct	-0.49	-	-	Visually estimated proportion
Number shrubs (11.3 m) [c]	indirect	-0.69	-	-	Count
Number trees (11.3 m) [a,e]	indirect	-0.73	-	-	Count
Short vegetation cover (57m) [d]	indirect	1.06	-	-	Visually estimated proportion
Shrub cover (57m) [d]	indirect	-	-	-	Visually estimated proportion
Tree cover (57m) [d]	indirect	-	-	-	Visually estimated proportion
Fence length (57m) [a,d]	direct	1.00	direct	1.08	Linear measurement
Climate					
3-month cumulative precipitation	-	-	-	-	Three-month precipitation preceding clutch initiation
Fertile period weather					
Vapor pressure deficit [a,e]	direct	-0.72	direct	-1.15	Average (kPa)
Vapor pressure deficit SD [f]	-	-	-	-	Standard deviation (kPa)
Minimum daily temperature [e]	-	-	-	-	Average (ºC)
Minimum daily temperature SD [a,f]	direct	-0.63	direct	-0.60	Standard deviation (ºC)
Maximum daily wind speed [e]	indirect	-0.85	indirect	-0.77	Average (km/h)
Maximum daily wind speed SD [f]	indirect	-0.35	indirect	-0.63	Standard deviation (km/h)
Cumulative precipitation [e]	-	-	-	-	Summed daily precipitation

[a] indicates variables important in prior analysis of individual datasets

[b] 700 m radius circle around focal nests represents the average distance to nests of identified extra-pair sires

[c] 11.3 m radius circle around focal nests encompasses the vegetation directly surround the nest tree

[d] 57 m radius circle around focal nests represents the average core territory size (D.V. Landoll, unpublished data)

[e] 4-day female fertile period estimate encompasses the core of fertility and likely has more stable weather conditions, calculated from Medicine Park Oklahoma Mesonet weather station records

[f] 10-day female fertile period estimate encompasses the majority of fertilizations and allows variability in weather conditions, calculated from Medicine Park Oklahoma Mesonet weather station records

FIGURE 1. Path model of the influence of indirect (light gray) and direct (medium gray) predictor variables on the probability of EPP (dark gray) in nests of Scissor-tailed Flycatchers in Comanche County, Oklahoma from 2009-2014. Models are for morphology (A), breeding population (B), habitat structure (C), and weather (D) datasets. Black arrows indicate significant paths and path coefficients are linear or logistic regression coefficients or partial multiple regression coefficients when more than two predictors were present. Non-significant relationships are indicated as ns. Solid arrows represent a positive relationship between variables, while dashed lines indicate negative relationships. Arrows are proportional in size to the strength of each coefficient. Gray arrows indicate error calculated as square root * $(1 – r^2)$ from each regression. Total effects for indirect predictors are given in Table 1.

FIGURE 1.

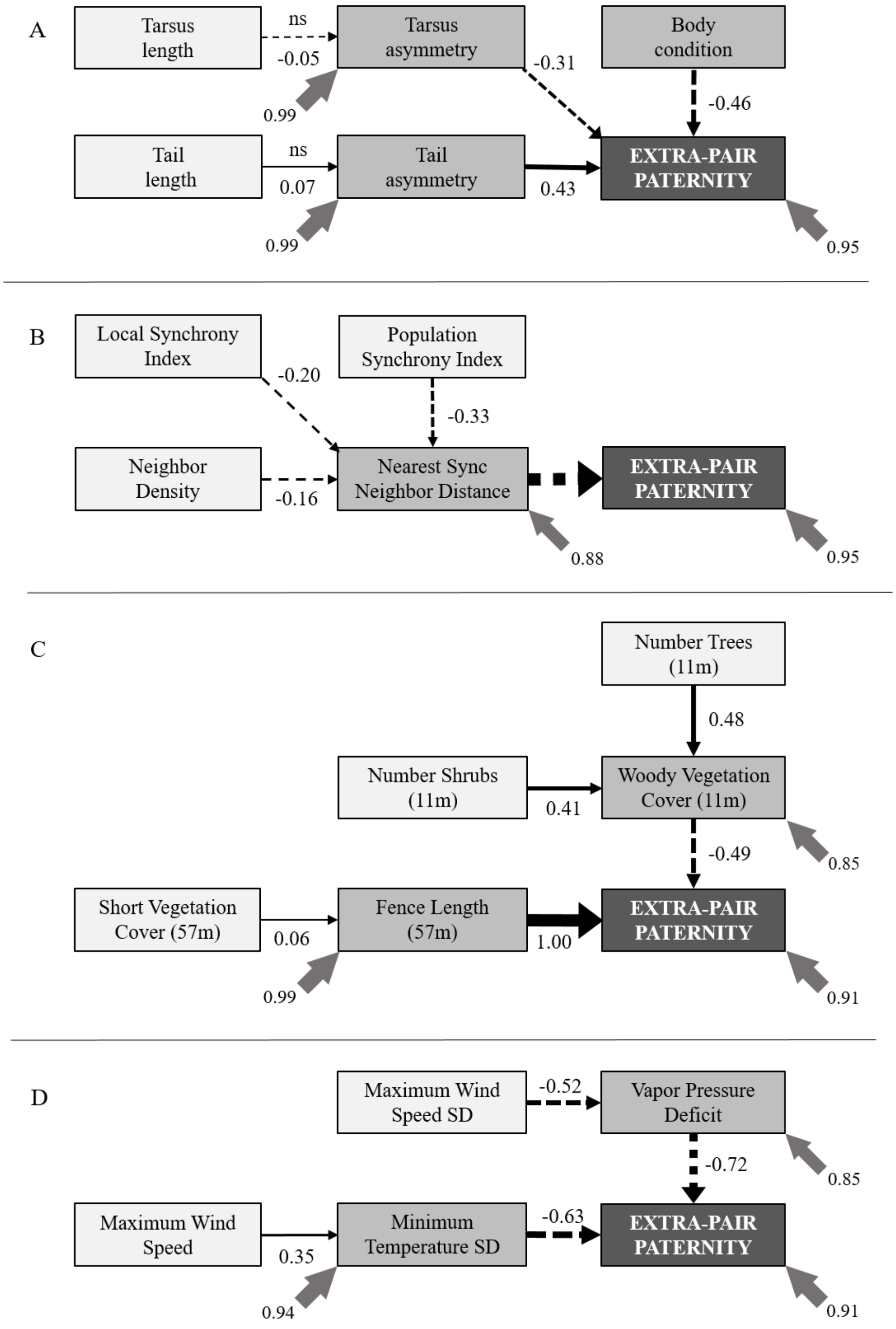
A
Tarsus length
ns
-0.05
Tarsus asymmetry
-0.31
Body condition
-0.46
0.99
Tail length
ns
0.07
Tail asymmetry
0.43
EXTRA-PAIR PATERNITY
0.99
0.95
B
Local Synchrony Index
-0.20
Population Synchrony Index
-0.33
Neighbor Density
-0.16
Nearest Sync Neighbor Distance
EXTRA-PAIR PATERNITY
0.88
0.95
C
Number Trees (11m)
0.48
Number Shrubs (11m)
0.41
Woody Vegetation Cover (11m)
-0.49
0.85
Short Vegetation Cover (57m)
0.06
Fence Length (57m)
1.00
EXTRA-PAIR PATERNITY
0.99
0.91
D
Maximum Wind Speed SD
-0.52
Vapor Pressure Deficit
-0.72
0.85
Maximum Wind Speed
0.35
Minimum Temperature SD
-0.63
EXTRA-PAIR PATERNITY
0.94
0.91

FIGURE 2. Global path model of the influence of indirect (light gray) and direct (medium gray) predictor variables on the probability of EPP (dark gray) in nests of Scissor-tailed Flycatchers in Comanche County, Oklahoma from 2009-2014. Black arrows indicate significant paths and path coefficients are linear or logistic regression coefficients or partial multiple regression coefficients when more than two predictors were present. Solid arrows represent a positive relationship between variables, while dashed lines indicate negative relationships. Arrows are proportional in size to the strength of each coefficient. Gray arrows indicate error calculated as square root * (1 – r^2) from each regression. Total effects for indirect predictors are given in Table 1.