




Combined roles for breeding synchrony, habitat and scale as predictors of extrapair paternity



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Despite extensive research on passerine reproduction, it remains difficult to predict which traits of individuals, nesting populations and landscapes drive extrapair paternity (EPP). Two broad categories of drivers, habitat structure and population level factors, have been considered separately or at a single spatial or temporal scale. We used a 6-year nesting data set of scissor-tailed flycatcher, *Tyrannus forficatus*, which have high rates of cuckoldry (73% of nests, 59% of nestlings), to explore how nest density, breeding synchrony, habitat structure and clutch initiation date affect EPP rates. We further considered synchrony at two temporal and habitat structure at two spatial scales. We predicted that visual occlusion from vertical habitat structuring on breeding territories would allow extrapair males to go unnoticed and provide cover for extrapair copulations. Predictions for effects of nest density and fertility synchrony were double-edged: EPP may either increase as extrapair mate availability and ease of comparison with social mates increases or decrease as social mates increase their efforts to assure paternity. Using Bayesian techniques, we found a combination of population level factors and habitat structure, including interactions among the latter, at different scales best accounted for variation in EPP. EPP declined with increasing population synchrony. Variation in EPP was also explained by fine-scale habitat measures, decreasing with increasing nest tree diameter at breast height and woody vegetation cover but increasing with tree density. Notably, EPP increased with a coarse-scale habitat measure, linear extent of fence or powerline, suggesting a role for human alteration of habitat. Fences are used as communal perches by neighbours and floater males, potentially increasing interactions between asynchronous individuals. Our study demonstrates that breeding synchrony influences the probability of EPP and that habitat structure on individual territories is a strong predictor of paternity that acts independently of breeding density or synchrony at our scale of measurement.

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Monogamy was once thought to be the most common bird mating system (Lack, 1968), but genetic polygamy is the norm among sampled species: <25% of socially monogamous passerines are genetically monogamous (Griffith et al., 2002; Westneat & Stewart, 2003). Genetic polygamy in socially monogamous species usually occurs as extrapair paternity (EPP), in which a female

has her eggs fertilized by a male that is not her social mate. Benefits of EPP are unclear: there may be no genetic benefits, with many hypotheses in favour ill-supported (Akçay & Roughgarden, 2007), so a role of direct benefits (see Griffith et al., 2002) may be more likely. Putative benefits aside, paternity can be divided into two categories, within-pair paternity (WPP) and EPP. Paternity patterns in passerines have been explored extensively, but we know little about which features of individuals, nesting populations and landscapes drive frequency of EPP, in part because so many different predictors could account for variation (Brouwer & Griffith, 2019; Crouch & Mason-Gamer, 2018; Lifjeld et al., 2019).

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Variation in cuckoldry across a season may be linked to arrival and pairing dates on the breeding grounds under two conditions (Spottiswoode & Møller, 2004). (1) 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. (2) 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 are newly paired (Weatherhead & Yezerinac, 1998). As nests fail and birds with breeding experience either retain a mate or pair with a new one, EPP should decline (Arct et al., 2022). Even so, EPP may not correlate with nest timing and clutch initiation dates if nest failure rates are high and the number of nesting individuals does not decline through the season (Krokene & Lifjeld, 2000).

The spatial distribution of nests in a population may also affect the incidence of EPP. The density hypothesis posits that increased nest density, and thus proximity of individuals, will increase encounter rate (Birkhead, 1978; Taff et al., 2013), thereby reducing the cost of searching for extrapair partners (Charmantier & Perret, 2004). As a result, EPP should be less frequent as nearest-neighbour distance increases and nesting density decreases both within and across populations (Mayer & Pasinelli, 2013; Stewart et al., 2010). A corollary is that bolder and more exploratory males are more likely to engage in EPP (Edwards et al., 2018).

Life history traits, too, affect incidence of EPP, especially those traits associated with rates of individual interactions (Brouwer et al., 2017; Westneat et al., 1990). For example, the incidence of EPP may depend on nest initiation date, nearest-neighbour distance, breeding density and breeding synchrony of fertility (often called 'breeding synchrony'; Brouwer & Griffith, 2019; Griffith et al., 2002). Breeding synchrony – the extent of overlap between the fertile period of breeding females – combines both nest timing and spatial distribution (Stutchbury & Morton, 1995; Weatherhead, 1997). It can be measured between females at local and population levels. The synchrony hypothesis posits that increasing synchrony will result in higher rates of EPP under two conditions (Arlt et al., 2004; Stutchbury & Morton, 1995). (1) If females control extrapair copulations (EPC) and select the highest-quality mate of those available, then increasing synchrony leads to higher EPP rates because it facilitates comparisons among a greater number of potential extrapair males (Kempnaers et al., 1992). (2) When synchrony is high, EPP may increase because males will have a greater opportunity to seek EPCs as more females become fertile simultaneously (Stutchbury & 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 level (Stewart et al., 2010; Wang & Lu, 2014) and the local level (Chuang et al., 1999; Stewart et al., 2010; Wang & Lu, 2014). The asynchrony hypothesis (Neudorf, 2004), by contrast, suggests that increased synchrony lowers EPP if increased neighbour proximity spurs mate guarding by a female's social mate – i.e. the mate-guarding hypothesis (Westneat et al., 1990) and guarding constraint hypothesis (Arlt et al., 2004). This relationship is expected when males face a trade-off between time invested in paternity assurance activities, such as repeated copulations and mate guarding, and time spent pursuing EPCs (Birkhead & Biggins, 1987; Thusius et al., 2001). This hypothesis was formalized for synchrony, but its reasoning holds for spatial distribution of nests: if mate guarding increases with increased neighbour proximity, which typically is treated as independent of synchrony, then EPP should decrease as inter-nest distance decreases and density increases.

Spatial distribution of nests and its interaction with timing of fertility may affect EPP strongly, but these effects may not be independent of the habitat in which they occur (Sherman & Morton,

1988). Indeed, a factor little explored as a potential driver of EPP within populations is habitat structure, which may affect rates of cuckoldry within a territory via effects on both mate guarding, because of visual occlusion (Blomqvist et al., 2006; Sherman & Morton, 1988), and movements of both territory holders and extrapair individuals (Mays & Ritchison, 2004; Ramos et al., 2014; Sherman & Morton, 1988). If habitat complexity and vertical structure increase occlusion, then territorial males will be unable to guard mates as efficiently as on territories with sparser vegetation (Blomqvist et al., 2006). Moreover, tall, dense vegetation may provide cover for extraterritorial forays for both sexes and provide secluded sites for EPCs (Mays & Ritchison, 2004; Tryjanowski et al., 2007). Spatial distribution and synchrony vary by habitat type, which reflects availability of nest sites or differential nest settlement in territories of different quality (Barber et al., 1996; Thusius et al., 2001), yet studies that have 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 & Mays, 2005). Such fine-scale measures of habitat structure may better reflect nesting opportunities and provide insight into how habitat structure affects cuckoldry (Sherman & Morton, 1988).

We investigated simultaneously how breeding population characteristics, such as timing, spacing, density and synchrony of nests, and habitat characteristics on nesting territories influence rates of EPP. We further considered both classes of predictors at multiple temporal or spatial scales. Our focal species was a subsocial passerine, the scissor-tailed flycatcher, *Tyrannus forficatus*, which is socially monogamous but has high rates of EPP (73% of nests and 59% of nestlings; Roeder et al., 2016). Males perform aerial displays visible from a distance that are thought to both attract mates and reinforce territory boundaries (Regosin, 2020; Roeder et al., 2019). Both members of a pair aggressively defend their territory from conspecifics and predators (Regosin, 2020), and mate guarding has been suggested as a constraint on EPP (Roeder et al., 2019). 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 dispersed. Nests suffer high depredation rates (32% average success rate; Landoll, 2011), which results in variable breeding density and egg-laying synchrony, making the species ideal to investigate the relationship between cuckoldry, nest spatial distribution, breeding synchrony and habitat structure.

We predicted that cuckoldry would be less common in focal nests with nearer neighbours. If males invest more time mate guarding as the number of neighbours increases, then focal nests should have a lower EPP when neighbour density is higher. Likewise, EPP should occur rarely when synchrony is high, both at the local and population scale. We predicted that greater visual obstruction would lead to higher EPP and that greater foraging area in a territory would lead to lower EPP. We predicted that visual obstruction would interact with the density of neighbours such that territories with greater vertical structuring and higher neighbour density would have a greater probability of EPP. We evaluated hypotheses for two estimates of the female fertile period drawn from the literature and that reflect 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 (Hammers et al., 2009; Krokene & Lifjeld, 2000; Weatherhead, 1997). We challenged these hypotheses at two spatial extents 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, U.S.A. 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, rocky 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 balance tracking nest stage/fate with minimizing the impact of human presence at the nest (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 and playback calls as lures. Adults were fitted with an aluminium United States Fish and Wildlife Service (USFWS) band and a unique combination of three coloured 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 notch (also called attenuation) length of the ninth primary (Pyle, 1997). We collected the minimum blood sample volume necessary for analysis (50 μ l from adults and 25 μ l 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 4 °C. 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 later resighted 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, U.S.A.: catalogue number 69504) and genetically confirmed the sex of all individuals following Fridolfsson and Ellegren (1999). We amplified eight polymorphic microsatellite loci for parentage analysis (see Roeder et al., 2016 for details) using polymerase chain reaction (PCR) using Type-It Microsatellite PCR Kits (Qiagen; catalogue number 206243). We used nonlabelled reverse microsatellite loci primers and forward primers labelled with a universal M13(-21) tail to which we could attach different fluorescent dyes during multiplexing (Schuelke, 2000). PCR fragments were amplified in 25 μ l reactions following conditions given in Roeder et al. (2016). We separated amplified fragments by capillary electrophoresis using an ABI 3130 XL DNA Sequencer (Applied Biosystems, Inc., Foster City, CA, U.S.A.) and analysed using Peak Scanner 2 (Applied Biosystems). All eight loci were in Hardy–Weinberg equilibrium, and null allele probability was 0.

We assigned 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 $n = 100\,000$, 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 female mismatched her offspring at any locus. After mother/offspring pairs were evaluated, all candidate father/offspring pairs were assigned a paternity likelihood if the difference between the candidate father's 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 of extrapair origin. All such pairs had at least one allele mismatch. CERVUS provided paternity assignments at both an 80% and 95% confidence interval (CI). Because we captured ~60% of the males in the population, we used the conservative 95% CI to assign males as extrapair sires to avoid assigning the wrong male as genetic sire. At this level, no extrapair sire mismatched his putative offspring at any locus.

Nest Timing, Spacing and Synchrony

We used clutch initiation date (= day of first egg of a clutch) to describe nesting seasonality. We standardized these by setting the clutch initiation date of the first nest in each year as day 1, from which we counted continuously to assign dates to all other nests. We used two different estimates of female fertile period to calculate nearest-neighbour 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 3 days before egg laying and ended on the date the first egg was laid. Scissor-tailed flycatchers typically lay five-egg clutches, with a single egg laid daily (Regosin, 2020). To account for the possibility of short-term sperm storage from fertilizations prior to peak fertility and for fertilizations during egg laying (Hammers et al., 2009; Krokene & Lifjeld, 2000; Weatherhead, 1997), we expanded the fertile window to encompass a 10-day period ending on the day the penultimate egg was laid.

We measured nearest-neighbour and average-neighbour distances as our estimate of spatial distribution of nests (Mayer & Pasinelli, 2013). We calculated nearest-neighbour 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 neighbour (Mayer & Pasinelli, 2013), where synchrony was defined as any nesting female that was concurrently fertile with the focal female. We estimated the average distance to available extrapair 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 roughly three times the average nearest-neighbour distance from previous accounts (Regosin & Pruett-Jones, 1995) and, when extreme distances were removed, was near the average distance to the nest of identified extrapair sires (following Mayer & Pasinelli, 2013). Thus, it represents the distance at which most interactions with potential extrapair mates were likely to occur.

To estimate nest density, we counted the number of active nests when a focal female was in her fertile period, as well as the number of nests in which females 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 the focal female's fertile period does not overlap that of any other female's fertile period) to 1 (when the focal female's fertile period

overlaps that of all other females) (Kempnaers, 1993). We calculated SI for focal nests both locally (i.e. ≤ 700 m radius circle around each nest; Dunn et al., 1994; Wang & Lu, 2014) and at the population level for all females at each site in each year (Kempnaers, 1993).

Habitat Structure

In addition to measuring the height, diameter at breast height (DBH), and extent of the crown of the nest tree (taken as the median of a north–south measure (in metres) and of an east–west measure (in metres)), we estimated habitat structure at two scales surrounding each focal nest. We centred on the nest to obtain a snapshot of how its surroundings, which by extension apply to both the social male and female, may affect paternity. We did not, then, attempt to quantify how space use differed between males and females. 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 (i.e. a 400 m² circle) plot centred 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 most 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 vertical structure of vegetation influenced EPP. 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 (1 ha area) centred on the nest tree, corresponding to the core territory in which breeding pairs foraged and which they defended from conspecifics and predators (Fitch, 1950; Landoll, 2011). 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 along warm road surfaces and use fences and powerlines as perches (Regosin, 2020), we measured the total linear length of roads and fences within the 57 m radius plots.

Statistical Analysis

All analyses were carried out in the R software environment (R Foundation for Statistical Computing, Vienna). We evaluated how presence/absence of EPP and the proportion of extrapair young (EPY) in each nest were associated with potential predictors in each of four data sets: (1) 4-day fertile period nest timing, spacing and synchrony variables; (2) 10-day fertile period nest timing, spacing and synchrony variables; (3) 11.3 m habitat structure; (4) 57 m habitat structure. To these data we added clutch initiation date and interactions between it and synchrony. Across the 6 years of the study, ~19% of females and ~23% of males accounted for multiple nests, but we did not control for these repeats because (a) the vast majority of repeats were new pairings of males and females rather than re-pairings of the same social pair and (b) pairs seldom re-nested in the same tree or even within the same small-scale area, either within or across years. Hence, even when individuals or pairings were repeated in the data set, they did not occur in the same environmental or social setting (i.e. in terms of nesting date, synchrony, population spacing, habitat use, etc.).

A specific goal was to estimate predictive ability in each data set and across all data sets. We used Bayesian model averaging of linear models using the package 'BMA' (Raftery et al., 2021), and in our case, using a model analogous to frequentist logistic regression

with EPP presence/absence as the response. Unlike model selection techniques founded on information criteria, the Bayesian approach does not ignore uncertainty in the model selection process but instead estimates variable importance from the posterior probability distribution of candidate models (Hinne et al., 2020). Results for the proportion of EPY as a response variable were broadly similar and correlated highly with those using EPP as a response variable – e.g. importance: $r = 0.75$; posterior probability of inclusion: $r = 0.84$; directionality of relationship: same in 28/32 cases, with sign changes solely for weaker predictors – so we herein report results only for EPP.

We used Bayes factors, the posterior odds of support for one hypothesis over another (Kass & Raftery, 1995), to estimate evidence in support of a fit model ('alternative hypothesis') over a null hypothesis of no association. Estimates were obtained via the 'generalTest' function in the package 'BayesFactor' (Morey & Rouder, 2018). Support in favour of the alternative or the null was evaluated using generally accepted 'evidence categories' (Kass & Raftery, 1995): Bayes factors of 1–3.2 indicate no support for the alternative, 3.2–10 'substantial' support, 10–100 'strong' support and >100 'decisive' support. To be certain repeat females had no effect, we ran key combinations of predictors with female as a random factor, but results did not change, so we report results solely for the fixed-effects models. We used thin plate spline regression using the package 'fields' (Nychka et al., 2021) to visualize interaction terms.

Lastly, we assessed mean differences of some predictors for the two states of EPP (present or absent) by means of custom-built Bayesian model with Γ distributions for the data and flat priors. Models were built in JAGS and run via the package 'rjags' (Plummer, 2019). We plot results as the median of the posterior distribution \pm the 95% highest-density credible interval (obtained via the package 'HDInterval'; Meredith & Kruschke, 2020).

Ethical Note

The methods used in this study were approved by the University of Oklahoma Institutional Animal Care and Use board (institutional tracking numbers R08-024, R12-010 and R15-006) under the United States Department of the Interior Federal Bird Banding permit 23215. All necessary permissions were provided by the Oklahoma Department of Wildlife Conservation, Wichita Mountains Wildlife Refuge and Fort Sill Artillery Base. We took care to handle birds for as short a time as possible, generally less than 10 min per bird. We took the minimum blood sample volume necessary for DNA isolation and ensured blood loss had stopped before release by applying gentle pressure with a cotton ball. We observed no injuries beyond several lost feathers upon capture and all birds flew and acted normally upon release. Birds were observed for a short time after release and all breeding birds were resighted at later dates after banding.

RESULTS

We assessed parentage at 140 nests and for 550 nestlings across all years of the study (see Table 1 in Roeder et al., 2019 for a breakdown of yearly sample sizes and EPP rates). Scissor-tailed flycatcher EPP was high across all years of the study and ranged from 43% to 87% of nests across years ($\bar{x} = 73\%$), with 29–72% ($\bar{x} = 59\%$) of nestlings resulting from EPP. On the surface, this variability seems high, but relatively small sample sizes each year assures that uncertainty is high, too: a binomial estimate with flat priors of annual EPP revealed that 95% credible intervals overlapped each year, even for the highest (2009: 0.57–0.99) and lowest (2011: 0.23–0.63) estimates. This result implies apparent

annual variation is the result of sampling error, so we did not control for year. 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 (comparable to 31% of nests in the congeneric *Tyrannus tyrannus*; Dolan et al., 2007). We measured spatiotemporal and habitat parameters for 127 nests for which we had EPP data during 2009–2014, including 66 nests from Fort Sill and 61 nests from the refuge. Mean \pm SE. \bar{x} nearest concurrently active neighbouring nest distances ranged from 347.1 ± 241.6 m on Ft. Sill to a more widely spaced and variable mean of 478.3 ± 110.4 m on the refuge. Across both sites, 87% of nearest-neighbour distances ranged from 10 m to 600 m, with only five nests <10 m and 11 nests >600 m distant.

Cuckolded Males versus Their Cuckolders

We identified both the social and extrapair sire at 61 nests and assigned 26 of those extrapair males to their social nests. For these 26 males, we identified the stage of nesting of the extrapair sire's mate when he cuckolded the other male. In only nine cases were mates of extrapair sires fertile during the cuckolded female's 10-day estimate. In all other cases where extrapair sire nesting status was known, extrapair males had social mates that were nonfertile (i.e. prenesting, $N = 4$; nest building, $N = 2$; incubating, $N = 3$; brooding, $N = 4$; feeding fledglings, $N = 3$; post-nest failure, $N = 1$). In some cases, we were able to classify extrapair sires as floaters in the population ($N = 11$) because they had no nest in the area and were males returning for their first breeding season (Roeder et al., 2019) (Fig. 1 – inset). Half of all cuckolders (13 of 26) nested <700 m from the cuckolded males' nests (Fig. 1). When we removed three extreme outliers (>9500 m), the mean (\pm SE) distance between nests with extrapair young and nests of their extrapair sires was 1017.1 ± 207.5 m. We could not compare nearest-neighbour distance, density, synchrony or habitat structure of extrapair males to the males they cuckolded because so few of their social mates were concurrently fertile.

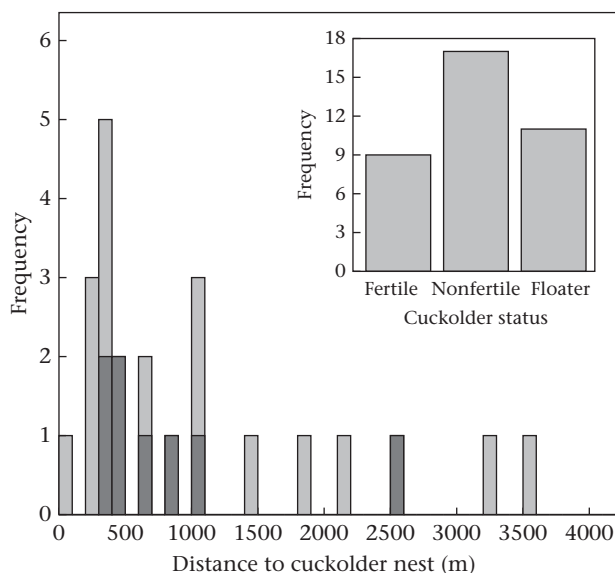


Figure 1. Histogram of the distance (m) between the nests of cuckolded males and their cuckolders. Light grey bars represent the distribution of all social male–cuckolder distances. Dark grey bars represent cuckolders whose mates were in their fertile period when cuckoldry occurred. Inset: total number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

Nest Timing, Spacing and Synchrony

For both the 4-day and 10-day fertile period model sets, the best predictor of EPP was the population level SI (Fig. 2), although 10-day population level SI had a greater posterior probability of inclusion in global models than did the 4-day estimate (Fig. 3). Population SI was negatively related to the incidence of EPP such that EPP occurred more frequently when fewer females across the population were simultaneously fertile (Fig. 4a). Population SI declined across the breeding season, such that EPP was more common as fewer birds nested simultaneously (Fig. 4b). None of our other metrics of nesting spatial distribution or timing of fertility had high posterior probabilities of inclusion in best-fit models (Fig. 3).

Population SI for the 10-day estimate of fertility and clutch initiation date were negatively correlated (10-day estimate: $r = -0.71$; Fig. 4b). Population synchrony increased quickly as nesting began and remained high for the first third of the season. Synchrony then declined until reaching very low levels at the end of the season. While EPP was not linearly related to clutch initiation date (likely due to the initial low level of synchrony at the very start of the season), when EPP was overlaid on clutch initiation date, a greater percentage of nests initiated in the last half of the season had EPP than did those initiated in the first half when synchrony was at its peak ($\chi^2_1 = 5.35$, $P = 0.02$; Fig. 4b).

Neither clutch initiation date (CID) nor interactions with it appeared among the top 35 models (the top model with CID as a main effect had a Bayes factor = 29.3; the model with a CID*synchrony interaction term had a Bayes factor = 53.2).

Habitat Structure

Incidence of EPP at the 11.3 m radius plot scale was best predicted by the size of the nest tree, the proportion of a plot covered by woody vegetation and the number of trees in the plot (Figs 2, 3). Nests with EPY were more likely to be found in smaller trees (low DBH; Fig. 5a) and on sites with less woody cover (Fig. 5b) but more trees (Fig. 5c) than nests without EPY. At the 57 m radius scale, the total length of fence and utility wire was the strongest predictor of EPP (Figs 2, 3). Territories containing the nests of cuckolded males had longer fence and powerline lengths than did territories where males were not cuckolded (Fig. 5d). However, when global models were considered, fence and utility wire length had a lower probability of inclusion (Fig. 3).

Combined Models

Territory-scale habitat variables were independent of any measure of nest spacing, density or synchrony ($r < 0.20$ for all pairwise comparisons). Additive models containing population SI during the 10-day fertile period, nest tree DBH, the proportion of woody cover and number of trees within an 11.3 m radius, the length of fence and utility wire within a 57 m radius and the interaction between nest tree DBH and fence/utility wire length had 'decisive' evidence (Bayes factor >100; sensu Kass & Raftery, 1995) to explain EPP against a null hypothesis of no effect (Fig. 2). Various other combinations of predictors likewise produced 'decisive' evidence; however, the five predictors listed above were nearly always included in those models.

The only interaction terms to appear in models with 'decisive' evidence were nest tree DBH*fence/utility wire length (Fig. 6a) and proportion woody vegetation cover*number of trees within an 11.3 m radius (Fig. 6b). The first of those interactions was strong and appeared in all but one of the 'best' models. The probability of EPP was lowest in large trees, particularly where there was little fencing

Bayes factor	4-day						10-day				11.3 m				57 m				X			
	Local SI	Population SI	Number of neighbours	Nearest-neighbour distance	Number of synchronous neighbours	Nearest synchronous neighbour distance	Population SI	Nest tree DBH	Nest tree crown extent	Bare ground cover	Woody vegetation cover	Number of trees	Bare ground cover	Shrub cover	Tree cover	Short vegetation cover	Tall vegetation cover	Fence/powerline length	Road length	Woody vegetation cover x number of trees	Nest tree DBH x fence/powerline length	
264.5																						
212.0																						
143.1																						
142.9																						
136.2																						
129.1																						
128.6																						
125.3																						
121.9																						
118.0																						
115.0																						
114.4																						
111.4																						
108.2																						
104.9																						
93.9																						
93.8																						
93.7																						
93.4																						
82.5																						

Figure 2. Strength of evidence in support of the top 20 models of predictors of incidence of extrapair paternity in the scissor-tailed flycatcher. Each of these models represents at least strong support (Bayes factor >10 indicate 'strong' support and >100 indicate 'decisive' support, sensu Kass & Raftery, 1995) against a null hypothesis of no effect of the predictor(s). Models are arranged in order of highest to lowest support, akin to a model comparison table ordered by Akaike's information criterion (AIC) or an alternative information criterion. Variables present in each model are indicated with grey squares. Brackets at the top of the figure indicate the data set from which each variable originated: 4-day data set includes spatiotemporal variables measured from the 4-day estimation of fertile period; 10-day data set includes spatiotemporal variables measured from the 10-day estimation of fertile period; 11.3 m includes habitat variables measured at the 11.3 m scale; 57 m includes habitat variables measured at the 57 m scale. × indicates interaction terms; SI: synchrony index; DBH: diameter at breast height.

or powerline nearby. As tree DBH declined, the probability increased and peaked when there was also more fencing and powerline. The second interaction term was weaker and only appeared in two models. When woody vegetation cover was high and the number of trees were simultaneously low (i.e. most woody cover was composed of shrubs), the probability of EPP was low. When most vegetation was made up of trees, however, EPP was much more likely. This was true regardless of how much of a plot was covered by woody vegetation. Thus, tree cover was always associated with an increase in the likelihood of EPP while shrub cover was only associated with a lower likelihood of EPP when there were few trees.

DISCUSSION

Our study demonstrates that synchrony of fertility during breeding, nest tree size and habitat features influence extrapair paternity in scissor-tailed flycatchers, both independently and in conjunction with each other. Our results thus support the guarding constraint hypothesis (Birkhead & Biggins, 1987), which suggests that cuckoldry decreases with increasing breeding synchrony. In addition, our study is one of the first to examine the effect of nest site and territory habitat structure on cuckoldry in passerines since it was suggested as a potential driver of EPP over 30 years ago (Sherman & Morton, 1988). We found that increasing vertical

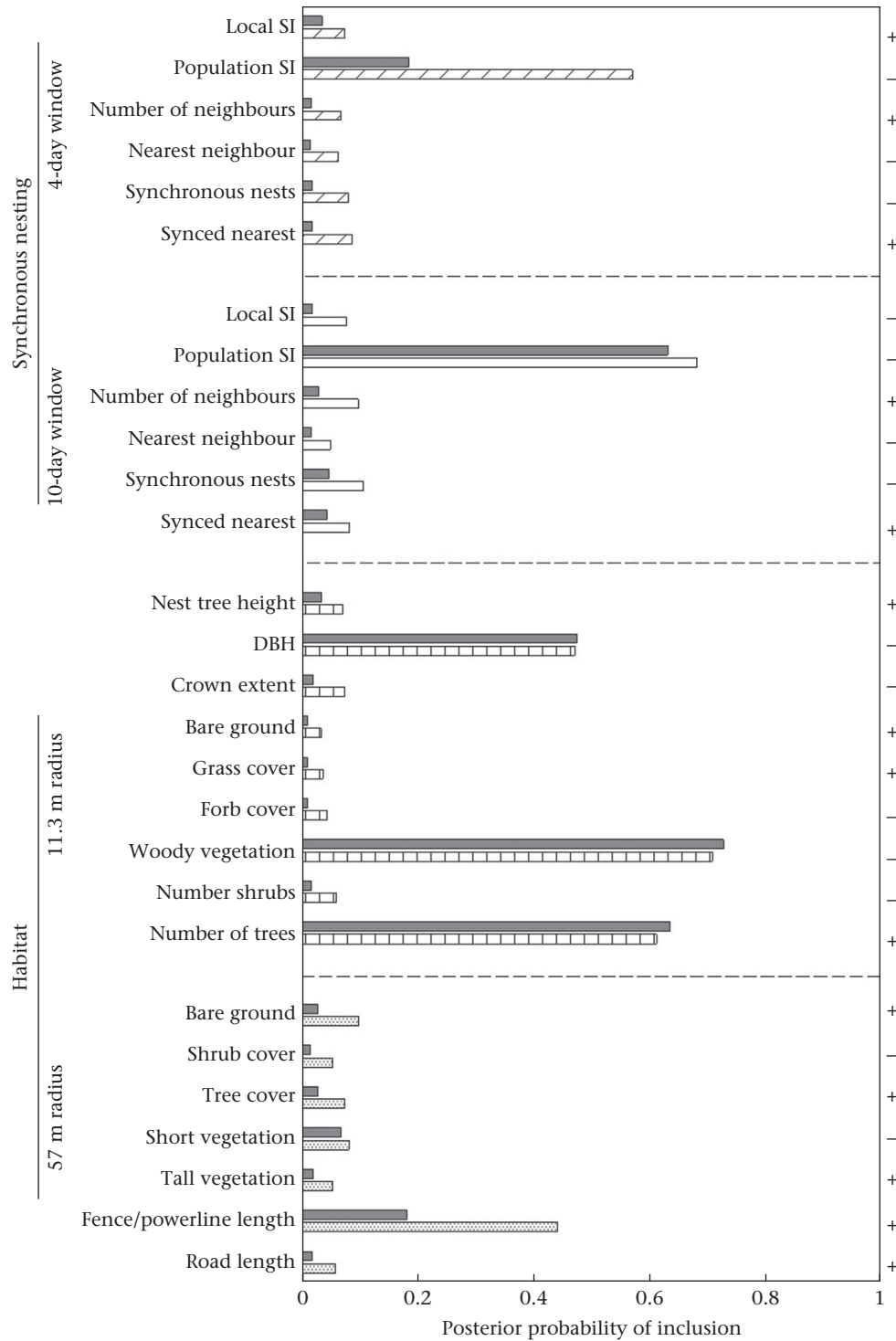


Figure 3. Estimates of predictor importance for models of extrapair paternity in the scissor-tailed flycatcher derived from posterior probabilities from Bayesian model averaging of linear models with a binomial response. Posterior probabilities of inclusion for models constructed for each data set (4-day spatiotemporal, 10-day spatiotemporal, 11.3 m radius plot habitat and 57 m radius plot habitat variables) are shown with open bars, with a unique pattern for each data set. Posterior probabilities for inclusion for global models containing variables drawn from all data sets are shown with grey bars. + or - on the right side of the figure indicate a positive or negative effect of a particular variable. Definitions of variables are as follows: local SI = local synchrony index; population SI = population synchrony index; number of neighbours = number of neighbours within 700 m; nearest neighbour = nearest-neighbour distance; synchronous neighbours = number of synchronous neighbours; synced nearest = nearest synchronous neighbour distance; nest tree height = height of focal nest tree; DBH (diameter at breast height) = nest tree DBH; crown extent = median of north-south and east-west measures of crown diameter; bare ground = proportion of plot covered by bare ground; grass cover = proportion of plot covered by grass; forb cover = percentage of plot covered by forbs; woody vegetation = proportion of plot covered by woody vegetation; short vegetation = proportion of plot covered by grass or forbs <0.5 m tall; tall vegetation = proportion of plot covered by grass or forbs >0.5 m tall; number shrubs = number of shrubs in a plot; number trees = number of trees in a plot; fence/powerline length = total length of fence and powerline in a plot; road length = total length of road (i.e. paved or gravel) in a plot.

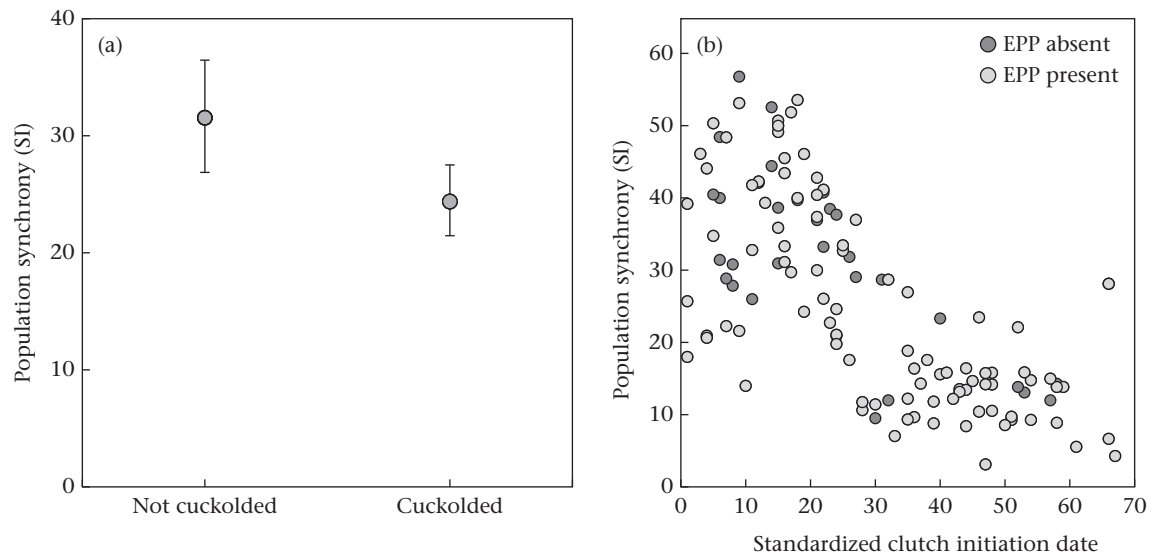


Figure 4. Difference in population synchrony based on a 10-day estimate of female scissor-tailed flycatchers' fertile period (median of the posterior distribution \pm the highest-density credible interval) for (a) nests with and without cuckoldry and (b) across standardized clutch initiation dates during the breeding seasons of 2009–2014 in Comanche County, Oklahoma, U.S.A. SI: synchrony index; EPP: extrapair paternity.

habitat structure (i.e. visual occlusion) led to a higher probability of cuckoldry. Most important, though, was definitive evidence in support of combined models that included predictors measured at different temporal and spatial scales. Any model that included only predictors from a given temporal scale (4-day versus 10-day fertile period) or spatial scale (11.3 m versus 57 m radius around the nest) did not fare as well as one that included predictors from a mix of scales.

Nest Timing, Spacing and Synchrony

We found support for the guarding constraint hypotheses in the context of population breeding synchrony (Westneat & Gray, 1998). When synchrony was high and many females were concurrently fertile, the probability of EPP was lower, presumably because most males were guarding their fertile mates instead of investing time into pursuing EPCs (Neudorf, 2004; Westneat et al., 1990). Additionally, if most males were engaged in mate guarding as opposed to extraterritorial 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 extraterritorial forays of their own (Houtman, 1992). Scissor-tailed flycatchers may do the same, although territorial females aggressively defend their territories from intruding females (Regosin, 2020), potentially lowering the effectiveness of such forays, although just as with males territorial defense can only go so far, and high synchrony may facilitate a female's quick foray into a neighbouring territory in search of EPCs. Alternatively, if pairs that breed earlier in the season, when nesting attempts are more synchronous, are of higher quality than those breeding later, as some studies have shown (Spottiswoode & Møller, 2004), then females may have been less likely to attempt to cuckold their social mates (Thusius et al., 2001).

We found little support for an effect of local breeding synchrony. Because scissor-tailed flycatcher breeding territories are relatively large and individuals tend to easily cover large distances while foraging and collecting nest materials, local estimates of synchrony and neighbour density may have been too narrow of a measure to reflect the true availability of fertile females or extrapair mates. Some authors have suggested that local synchrony is instead too coarse a measure of fertile period overlap and instead recommend

that the synchrony between a focal female and the female of her extrapair mate, or individual level synchrony, is the proper metric (Wang & Lu, 2014). Our results support this position, as the majority of cuckolding males (75%) were either floaters with no known nest in the area or had mates that were not fertile at the time of extrapair activity. Only 25% of extrapair males had mates that were concurrently fertile. Similarly, European pied flycatcher, *Ficedula hypoleuca*, males gain EPCs only after their mate has 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 studies of other species (Mayer & Pasinelli, 2013; Thusius et al., 2001).

We found no support for the density hypothesis – the probability of EPP was unrelated to the density of or distance to neighbouring pairs. Other studies similarly failed to find such a relationship (Barber et al., 1996; Chuang et al., 1999; Dunn et al., 1994; Moore et al., 1999; Sundberg & Dixon, 1996; Tarof et al., 1998), although a density/EPP relationship may be complicated by the actual origin of extrapair sires. Extrapair sires often originate from within a two-territory distance from focal nests (Chuang et al., 1999; Dunn et al., 1994; Gibbs et al., 1990; Mayer & Pasinelli, 2013; Stutchbury et al., 1994; Westneat, 1993), but in some species they originate, albeit at a lower frequency, from farther away (Canal et al., 2012; Charmantier & Perret, 2004; Mayer & Pasinelli, 2013). Most identified extrapair sires in our study were from within a two-territory distance from one another, yet they were relatively evenly spread across that distance, and increasing the number of neighbours did not increase the chances of cuckoldry. Additionally, 30% of extrapair sires did not have nests in the area at all, further reducing the chances of finding an effect of either nearest-neighbour distance or density. Finally, mate guarding at high nesting densities may compensate for what would otherwise be an increase in the presence or proportion of EPP in nests (Kokko & Rankin, 2006; Komdeur, 2001).

An interaction term for synchrony and clutch initiation date did not appear among the top models, but that term nevertheless yielded 'strong' model support (i.e. a Bayes factor between 10 and 100; Kass & Raftery, 1995). Logically, synchrony varies with CID, in that any measure of it deteriorates across the nesting season,

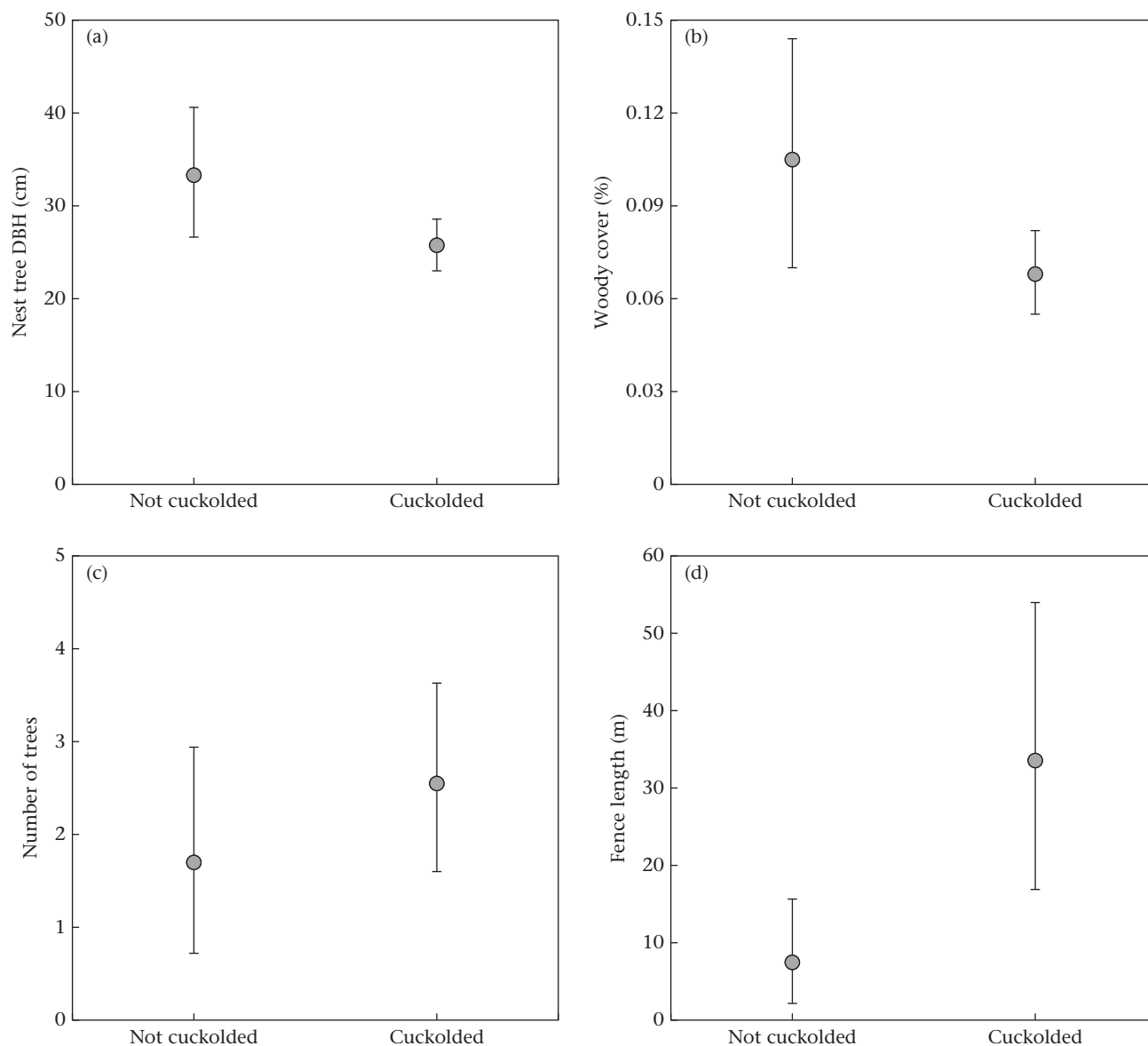


Figure 5. Best habitat predictors of the probability of extrapair paternity (EPP) in nests of scissor-tailed flycatchers at three scales: (a) nest tree diameter at breast height (DBH) for nests with or without cuckoldry; (b) proportion of the 11.3 m radius plot surrounding nest trees covered with woody vegetation for nests with or without cuckoldry; (c) number of trees in the 11.3 m radius plot surrounding nest trees for nests with and without cuckoldry; (d) total length of fences and utility wires/powerlines within the home territory (57 m radius plot) of males that were and were not cuckolded. Results are the median of the posterior distribution \pm the highest-density credible interval.

especially affecting short-term metrics, such as our 4-day estimate of fertility. Future research could focus on characterizing the nature of the interaction as well as identifying the point in a season when synchrony metrics lose their signal.

Habitat Structure

As predicted by [Sherman and Morton's \(1988\)](#) habitat structure hypothesis (see also [Mays & Ritchison, 2004](#)), but in contrast to a study by [Biagolini et al. \(2017\)](#), we found that several structural habitat characteristics predicted the probability of cuckoldry. When the number of trees on a territory increased and woody vegetation cover decreased, the probability of EPP increased. In savannah systems such as ours, we suggest that high shrub cover in combination with visual occlusion from trees allowed extrapair males less contested access to females on such territories by providing cover to approach females and solicit EPCs ([Mays & Ritchison, 2004](#)).

Alternately, these features may have made it difficult for social males to accompany their mates, who were then freer to foray on or off their own territories ([Westneat & Sherman, 1997](#)). It is likely that some combination of these is actually the case since males of other *Tyrannus* species vocalize to attract extrapair females ([Dolan et al., 2007](#)), and dense vegetation may allow cover for EPCs in either scenario ([Tryjanowski et al., 2007](#)), although few studies have examined the location of EPCs because they are difficult to observe in most species. When woody vegetation is made up mostly of short shrubs, lack of both visual occlusion and elevated perches likely allows males to survey their territories more effectively. Higher levels of shrub cover in this population of scissor-tailed flycatchers is also an important predictor of greater nest success ([Landoll, 2011](#)), probably because shrubs provide perches above grass and forbs from which both males and females can be vigilant for airborne predators ([Foreman, 1978](#)). This is reinforced by our finding that when both woody vegetation cover and tree

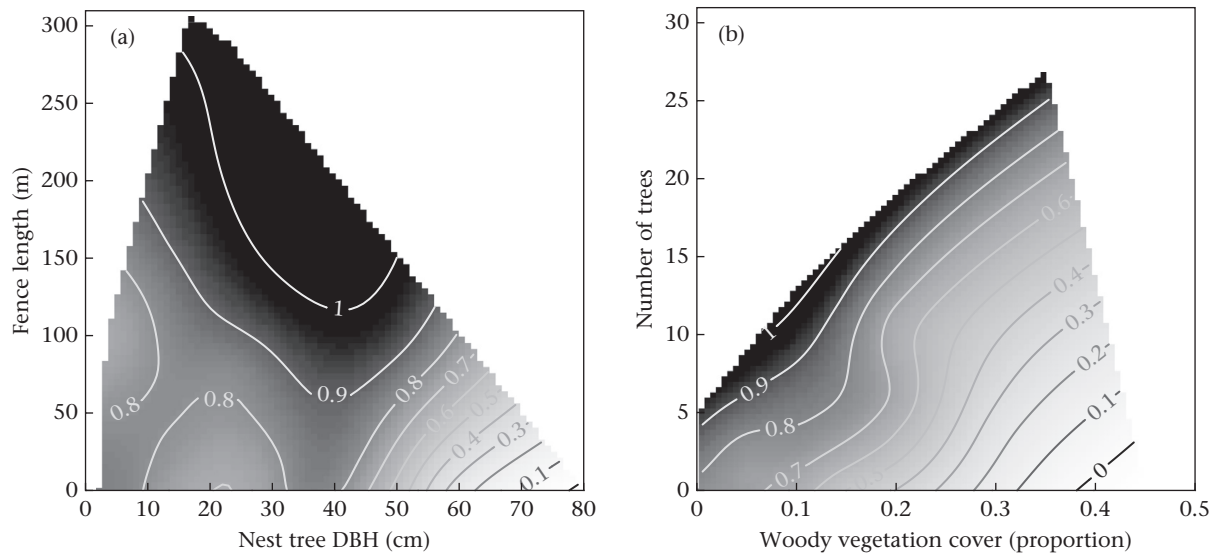


Figure 6. Response surfaces of predicted extrapair paternity (EPP) probabilities for two important interaction terms that occurred in the top 20 models with 'definitive' support: (a) nest tree diameter at breast height (DBH)*fence length at the 57 m radius scale; (b) proportion woody vegetation cover*number of trees in the 11.3 m radius plot surrounding the nest tree.

number were low, EPP occurrence was also high, indicating the importance of perches for surveillance. Note, however, that we lacked data on space use of males versus females. It may be that sexes differ in how habitat is occupied (e.g. Mays & Ritchison, 2004), which has consequences for EPP. In a previous study we found that females with higher body condition cuckolded mates more frequently (Roeder et al., 2019), which adds an intrasexual dimension because such birds likewise may use habitat differently. Future research ought to explore both inter- and intrasexual variation in space use and how any differences affect paternity.

We did not find a link between the proportion of short grass or forbs on a territory and EPP. Both land cover types are associated with higher food abundance and a lower time investment in 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) is probably responsible for the association between habitat and EPP.

Interestingly, we found that the probability of cuckoldry increased with an important anthropogenic habitat feature – fencing and powerlines – at our largest scale of habitat measurement. 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 cut across or border many territories, as foraging perches may put birds in greater contact than when perches are discrete plants located within the borders of discrete territories. Because not all of these foragers will breed synchronously, there may be a greater opportunity for EPCs in such a situation (Dunn et al., 1994; Hammers et al., 2009; Reyer et al., 1997). Fences may also attract floater males that are more difficult for territorial males to repel because of the transitory and unpredictable nature of their visits (Ewen et al., 1999; Tarof et al., 1998). Although the effect of transitory visits on EPP are not well known (Westneat et al., 1990), there is evidence that floater males do in fact sire a nontrivial number of EPY in scissor-tailed flycatchers (Roeder et al., 2019). Fence length also had an important interaction with nest tree size: fence length was associated with a greater probability of cuckoldry except when nest trees were large. Nest trees with greater DBH in our study site generally had more branches with denser leaf clusters on each branch, potentially obscuring nest sites from view of extrapair males surveying for mating opportunities. This may indicate an

interesting feature of visual occlusion – it is beneficial to territorial males when it obscures the destination of his fertile female who is nest building or egg laying. Regardless of mechanism, use of anthropogenic features and consequences thereof suggests an avenue for future experimental research in which artificial perches are erected in an array or at varying distances in territories or near potential nest sites. Such a design would facilitate estimates of distance thresholds as well as magnitude of effect size for metrics such as EPP or EPY.

Combined Models

We expected that breeding density and nearest-neighbour 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 & Morton, 1988). Even so, we found no interactive effects of habitat structure and nearest-neighbour distance, density or synchrony when we combined the best predictors of cuckoldry from each data set in additive and interaction models. Instead, we suggest that if population breeding asynchrony reflects the pressure from extrapair males populationwide, then visual occlusion from more trees allows those males better opportunities to obtain EPCs. This was represented in the variables that ranked highest from the combined data set, where the additive effects of population synchrony, nest tree DBH, woody vegetation cover and the number of trees were the most important predictors of the probability of cuckoldry.

Conclusions

Our results emphasize the importance of breeding synchrony and habitat structure in predicting cuckoldry. We found that nests initiated during periods of high populationwide breeding synchrony were less likely to contain EPY. We suggest this was primarily due to mate guarding; at times of high synchrony, more males were simultaneously invested in mate guarding rather than seeking EPCs. Linear artificial structures such as fences and powerlines may alter foraging behaviour and concentrate many individuals into a small area, therefore increasing interactions between potential extrapair partners that might lead to EPCs (Smith et al., 2016). Our study also provides support for the

hypothesis that visual complexity from increased vertical habitat structure (i.e. trees) may provide opportunities for EPCs, regardless of the spatial distribution, density or synchrony of breeding pairs – 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. 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. Combined, our results suggest that males face a trade-off between mate guarding and extrapair activity, particularly when there is an abundance of males whose mates are not in their fertile period, when there are many floater males with no mates to guard and when nesting in habitat with vertical structuring or human modifications that alter normal patterns of behaviour.

Author Contributions

Diane V. Roeder: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, writing – original draft, editing. **Michael S. Husak:** conceptualization, funding acquisition investigation, methodology, writing – review and editing. **Michael T. Murphy:** conceptualization, funding acquisition, methodology, writing – review and editing. **Michael A. Patten:** conceptualization, formal analysis, methodology, writing – review and editing.

Data Availability

Data have been provided in a supplementary Excel file.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2022.09.016>.

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