Behavioral Ecology and Sociobiology (2025) 79:31
https://doi.org/10.1007/s00265-025-03570-y

ORIGINAL ARTICLE

Female space use correlates with extra-pair mating in barn swallow replacement clutches

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Received: 6 December 2024 / Revised: 20 January 2025 / Accepted: 22 January 2025 / Published online: 15 February 2025

Abstract

Extra-pair mating is common in avian species and can modulate the strength of sexual selection. Mate searching behavior of female birds may be an important predictor of mating opportunities and extra-pair mating, yet important knowledge is lacking as we have little data on fine-scale movement of females during the peak fertilization period. Accordingly, much is still unknown about whether and how female phenotypes contribute to extra-pair mating. Here, we examined how female space use and female plumage color are associated with extra-pair mating outcomes in wild barn swallows (*Hirundo rustica erythrogaster*). We tracked 10 females breeding in Colorado, USA with GPS backpack tags for two hours each morning during their fertile period following an experimental nest failure. We then used low-coverage whole-genome sequencing to determine offspring paternity and to quantify extra-pair mating in the removed clutch and the replacement clutch. Plumage and movement did not correlate with changes in paternity between successive clutches, but movement did correlate with paternity in the replacement clutch. Females that spent more time away from the nest had a higher proportion and number of extra-pair offspring in the clutch laid immediately after the tracking period. These results suggest that differences in female space use contribute to differences in extra-pair fertilizations. In contrast to the historic emphasis on male traits, our study highlights female movement behavior as an important variable associated with mating outcomes in natural populations.

Significance statement

Mate choice is a critical step in reproduction, but variation in how extensively individuals in the wild search for and sample potential mates is not well understood. We measured movement behavior of female barn swallows during their fertile period to assess variation in mate sampling and linked this to variation in mating outcomes. We expected that females that flew farther would encounter more potential mates and produce offspring with multiple males. By tracking females' movement after removing their first clutch of eggs, we were able to correlate female movements with paternity in the collected and replacement clutches. We found that females that spent more time away from the nest, but didn't necessarily cover a larger distance, were more likely to have offspring with mixed paternity in their replacement clutch.

Keywords Extra-pair mating · Movement ecology · Mate searching · Sexual selection · Barn swallows · Female bird

Introduction

Extra-pair (EP) mating is common in many avian systems, yet our ability to predict the EP mating behavior of individual birds remains limited (Brouwer and Griffith 2019), partly due to a lack of information about variation in mate sampling. We thus have an incomplete view of the influence of EP mating on evolutionary processes within populations. Measuring variation in mate sampling and EP mating across individuals is necessary for understanding the geographic scale of mate selection behavior and its outcomes for

Communicated by K. McGraw.

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population genetic structure. Because female choice is an important component controlling EP fertilizations in many bird species (Lifjeld and Robertson 1992; Kempenaers and Dhondt 1993), exploring factors that help explain variation in EP mating among individual females is pivotal to understanding this very common reproductive strategy.

EP mating by females has mostly been investigated relative to the traits of their social mates, as well as the abundance and quality of possible EP males. The indirect genetic benefits hypothesis (aka "good genes") is often used as an adaptive explanation for EP mating by females (Kempenaers and Dhondt 1993), but variation in proximate drivers such as access to potential mates or phenotype variation among individual females could also influence their propensity to engage in EP mating. These proximate variables may shape female mating behavior irrespective of variation in available males. For example, in blue tits (*Cyanistes caeruleus*), individuals that interact with a greater number of opposite sex partners are more likely to have extra-pair offspring (with similar effect sizes for females and males, although the effect was only statistically significant in males) (Beck et al. 2021). Similarly, in red jungle fowl (*Gallus gallus*), females that interact with a greater number of males are more polyandrous (McDonald et al. 2019).

In addition to variation in social interactions, female phenotype and morphology may influence EP mating by impacting a female's ability to solicit or repel EP mating attempts, as described in the "Constrained Female" hypothesis (Gowaty 1996a). Recent studies in barn swallows (*Hirundo rustica*) show that female flight feather size (Costanzo et al. 2017) and age (Michálková et al. 2019) are positively correlated with EP mating, even after accounting for traits of the social male. Females with higher body condition in scissor-tailed flycatchers (*Tyrannus forficatus*) had higher rates of EP paternity (Roeder et al. 2019), and experimental manipulations of wing shape (Plaza et al. 2019a) and body condition (Plaza et al. 2019b) in female pied flycatchers (*Ficedula hypoleuca*) caused increases in EP paternity. These patterns could be driven either by reduced flight ability of females that decreases their ability to avoid EP copulations, or by increased energy (from higher body condition) that improves the ability of females to avoid mate guarding and seek out preferred EP males. Thus, female traits, especially those that may be indicators of individual condition or social interactions, deserve greater attention in studies of EP mating.

We highlight female movement behavior and plumage phenotype as two key variables that may be associated with EP mating in birds. In the absence of data on direct mate encounters, individual movement during the fertile period is a useful proxy for mate sampling (Luepold et al. 2024). Movements away from territories during the fertilization period are associated with EP copulations (Norris and Stutchbury 2001), and individuals do not always share fertilizations with EP mates that are in close proximity (Mennill et al. 2004; Canal et al. 2012). Distance and time spent away from the nest may therefore have important associations with individual EP mating. Evidence from birds (Double and Cockburn 2000; Stapleton and Robertson 2006; Dunn and Whittingham 2007) and other taxa (e.g., crickets, lizards, and shrews) (Hissmann 1990; Stockley et al. 1994; Kamath and Losos 2018) show that individuals that move farther do indeed encounter a greater number of potential mates, and in some cases this is positively correlated with multiple mating (Stockley et al. 1994; Double and Cockburn 2000; Kamath and Losos 2018). Importantly, movement behavior determines the sex ratio and trait distributions experienced by each individual, which could differ from the population-level and ultimately control the overall strength of sexual selection (Kasumovic et al. 2008; McDonald and Pizzari 2018; Daupagne et al. 2023). Therefore, the spatial scale of individual mate sampling and access should be directly measured in order to improve our understanding of EP mating and its role in sexual selection (Schlicht et al. 2015; Maldonado-Chaparro et al. 2018).

Female phenotype may also correlate with EP mating. Plumage phenotypes are a common target of sexual selection in birds, and many species exhibit ornamented plumage in females and/or males (Amundsen 2000). In some cases more ornamented females have more EP offspring (Torres and Velando 2005; Costanzo et al. 2017) – mirroring patterns seen in males (Wells et al. 2016) (but see also (Grunst and Grunst 2014; Jacobs et al. 2015; Berzins and Dawson 2020), and female ornamentation may be a signal of quality as suggested by assortative mating (MacDougall and Montgomerie 2003; Zwaan et al. 2019). In general, female plumage is likely an important signal in social interactions. Female tree swallows (*Tachycineta bicolor*) with brighter breast plumage appear to be more social than dull females (Taff et al. 2019), and manipulation of plumage color in female barn swallows caused shifts in testosterone and markers of oxidative stress which were likely mediated by changes in social interactions (Vitousek et al. 2013). Female plumage color may also be an indicator of the female's own physical condition and ability to invest energy into mate choice (Byers et al. 2005; Vitousek 2009; Nolazco et al. 2022). Because ornamented plumage is often associated with diet quality, parasite load, or age (Roulin et al. 2001; Siefferman and Hill 2005; Hegyi et al. 2008; Griggio et al. 2010; Vergara et al. 2011; Bradley et al. 2014), more ornamented females may be healthier or more experienced and be able to invest more energy into mating decisions. Thus, female plumage is likely relevant for EP mating, but we know little about how it relates to space use during the fertilization period, a time during which movement is most likely associated with the search for extra-pair males.

Barn swallows are a well-studied, socially monogamous songbird and experimental manipulations in males have shown that plumage traits are targets of sexual selection. Interestingly, outer tail length and ventral plumage color vary across different global regions and subspecies, female phenotype is similar to male phenotype within subspecies, and differences are maintained at least partly by sexual selection (Møller and Gregersen 1994; Scordato and Safran 2014; Safran et al. 2016a; Romano et al. 2017). While tail length is the main sexual signal in the European subspecies, *Hirundo rustica rustica* (Møller et al. 1998), darker ventral plumage color is under sexual selection in North American (*Hirundo rustica erythrogaster*) and some Asian subspecies (Safran and McGraw 2004; Hasegawa et al. 2010; Vortman et al. 2011). Experimentally darkened males in Colorado and New York sired a higher proportion of the offspring in their social nest (Safran 2005; Safran et al. 2016b), and darkened males in Colorado increased interactivity with their social mate (Levin et al. 2018). These experiments show that female barn swallows are sensitive to changes in male phenotypes during the breeding season, and dynamically update their mating decisions based on these changes. Therefore, females may also be sensitive to encounters with potential mates when making dynamic decisions about paternity allocation both within and outside of the pair bond throughout the breeding season.

There is some evidence that EP mating is correlated with female plumage color and morphology in barn swallows. In Europe, females with larger wings and tails had a higher proportion of EP offspring, and significant variation in EP mating was explained by pair ID but not female age class (Costanzo et al. 2017). These authors also reported that females with lower UV reflectance of ventral plumage were more likely to engage in EP mating, but this finding is inconsistent with previous studies which found little to no reflectance of pigmented ventral feathers in the UV range for multiple subspecies (*H. r. rustica*, *H. r. erythrogaster*, *and H. r. transitiva*) (McGraw et al. 2004, 2005; Vortman et al. 2011; Saino et al. 2013; Hubbard et al. 2017). For the North American subspecies, female ventral plumage within individuals tends to get darker with age, although the full range of plumage color is present within each age class (Bradley et al. 2014). As such, plumage color per se is not a reliable indicator of age. In a study that did not account for female age, darker females started breeding earlier and had higher reproductive success than pale females (Safran and McGraw 2004). We build upon existing studies of barn swallows by investigating ventral plumage color in the visible spectrum as a predictor of EP mating in female North American barn swallows.

Here, we explore the idea that female plumage color and female movement may both influence EP mating outcomes in barn swallows breeding in Colorado, USA. Females vary in EP mating with individual clutches containing from 0 to 100% extra-pair offspring (Hubbard et al. 2015). Breeding pairs are semi-colonial and clustered across the landscape, yet variation in colony size is not correlated with rates of EP offspring (Safran 2007). We expect to see large variation in female movement behavior during the fertile period and predict that this variation relates to EP mating. We hypothesize that female movement away from the nest increases female encounters with potential EP mates and reduces opportunity for mate guarding by the social male. Our prediction is that longer distances and more time away from the nest will be associated with a higher proportion and number of EP offspring and a greater number of EP sires. Dark females should have higher EP mating overall, since they may be more attractive, healthier, or better at avoiding mate guarding than pale females. Similarly, female movement and plumage may correlate with the change in paternity allocation between successive clutches. On average, females tend to allocate less paternity to their social mate after a nest failure (Safran 2005; Safran et al. 2016b). In this situation, we expect dark females or those that move farther or more often to have the greatest increase in EP paternity between first and second nesting attempts. We leverage experimental nest failures to directly study female movement during the fertile period in association with paternity patterns in the replacement clutch, and the change in paternity between initial and replacement clutches. To accomplish this, we simulated a commonly occurring nest failure event and then tracked females using GPS tags to analyze fine-scale movements during the peak fertility period associated with clutch replacement. The strength of this study is our ability to directly link female movements during the fertile period to individual plumage phenotype and mating outcomes, which we use to explore the importance of understudied female traits.

Materials and methods

To analyse the relationship between individual space use and mating in female barn swallows, we tracked movement using GPS backpack tags on 11 females in June 2021 for two hours each morning. We then related measures of each female's movement to her proportion of EP offspring, number of EP offspring, and number of EP sires. We allowed birds to settle at breeding sites (barns) in Boulder County, Colorado and lay their first clutch of eggs. We then collected the eggs 11–13 days into incubation and captured females off the nest using mist nets and by hand. We attached a 1 g

(5–8% of bird body mass) GPS tag (Lotek 'Pinpoint 10', Lotek Wireless, Inc., Newmarket, ON, Canada) to each female, banded birds with metal and color bands, and collected ventral body feathers and a small blood sample from the brachial vein. Tags recorded GPS coordinates every 10 min from 7-9am each day until the batteries died (range of 7–11 tracking days). We chose to record movement data in the morning because this is when the birds are typically most active, and other tagging studies of barn swallows have used a similar time window (Levin et al. 2016, 2018; Madden et al. 2022). The tags are constrained by battery life, and we elected to maximize replication across multiple days, rather than recording data for a longer period each day. After tagged females laid their replacement clutch, we recaptured them and removed their tag. We also captured males throughout the breeding season to sample blood from all social mates and as many potential EP mates as possible. We conducted observations at active nests to determine the identity of social pairs. It was not possible to record data blind because our study involved focal animals in the field. We monitored breeding success for the remainder of the breeding season and collected nestling blood samples for paternity analysis at 12 days old (full field methods are in Supplementary Information Section S1).

Processing spatial data

We calculated five metrics from the GPS data which could represent different biological processes related to mating decisions as follows:

1) Maximum distance traveled from the nesting barn, representing the farthest recorded extent of the female's movement. Mating may be related simply to single encounters of potential mates, with no importance of repeated visits to a location (Gibson and Langen 1996).
2) Area of the estimated 90% density region for GPS points ("90% KDE area"), representing the "home range" area for a female. Mating may be related to total space use, but with less importance given to one-off visits to distant locations.
3) Area of the estimated 50% density region for GPS points ("50% KDE area"), representing a female's "core use area". Mating may be related to mates encountered within the core use area, which are likely visited more than once during the fertile period (Trail and Adams 1989).
4) Proportion of GPS points past 50 m of the nesting barn, representing the proportion of time a female spends away from her nest and the immediate area around the barn. Mating may be related to time spent sampling other males in her home barn, or time spent with her social mate near the nest (Chiver et al. 2008; Maldonado-Chaparro et al. 2018).
5) Proportion of GPS points past 100 m of the nesting barn, representing the proportion of time a female spends at more distant locations. Mating may be related to time spent at more distant locations (> 100 m) if mate guarding by the social male occurs at closer locations to the barn (Møller 1985, 1987).

We used R version 4.4.1 (R Core Team 2024) and R Studio (R Studio Team 2024) to perform all analyses and generate plots, and used the package adehabitatHR to calculate the KDE metrics (Calenge 2006) (Supplementary Information Section S2).

Measuring plumage color

We measured plumage color by taping 5–10 belly feathers to a white notecard such that the feathers overlapped as they do on the body of the bird. We recorded average brightness (relative percent reflectance averaged across the 300–700 nm wavelength spectrum) in triplicate using an Ocean Optics UV-VIS spectrometer and pulsed xenon light (P-X2, Ocean Optics) as in Hubbard et al. (2015). The probe was held perpendicular to the feather patch such that a 2.5 mm diameter was illuminated. The probe was lifted and replaced on the sample after each replicate to ensure independent measurements. Reflectance was calibrated against a white standard (Labsphere, Inc., North Sutton, NH, USA) and a dark standard (reflectance in the absence of light). Feather patches with a lower brightness value have more melanin and are visually darker in color (McGraw et al. 2005). We used brightness because it is the least prone to measurement error and noise from the instrument. We sampled feathers from the belly because this is the largest ventral area and tends to be the most variable in color across individuals.

Paternity analysis

We sequenced the genomes of parents and offspring to reconstruct a fertilization network based on estimated pairwise relatedness among individuals. We extracted genomic DNA from blood samples and shipped samples to NovoGene (Sacramento, CA) for library preparation and whole genome Illumina sequencing, targeting 2x coverage. We trimmed and filtered sequencing data, aligned to the barn swallow reference (Secomandi et al. 2023), and called single nucleotide polymorphisms (SNPs). After filtering, we calculated genotype likelihoods for 92,438 unlinked SNPs that were used for relatedness calculations. We used lcMLkin (Lipatov et al. 2015) to estimate pairwise relatedness among all sampled individuals. This method uses maximum likelihood to estimate relatedness coefficients from genotype likelihoods rather than genotype calls, which is optimal for low-coverage data. In all cases, the mother assigned to each nest through behavioral observations matched the genetic maternity assignments. Therefore, we did not have to account for intraspecific brood parasitism and were confident that we could accurately identify genetic sires using known mother-offspring relationships as a benchmark. Here, we used the minimum relatedness value from known mother-offspring relationships as a threshold value to assign sires. The distribution of relatedness values for mother-offspring and sire-offspring relationships did not significantly differ (Welch two sample t-test, t=-0.332, $p=0.740$; Supplementary Fig. S1). The identity of genetic sires was then used to categorize within-pair and EP offspring, and to count the number of unique EP sires for each female. For a detailed description of the bioinformatics workflow and software versions, and additional details about the paternity analysis, see Supplementary Information Section S3.

Statistical analyses

We assessed EP mating in the replacement clutch, and the change in EP mating between the collected and replacement clutches, using three response variables: (1) the proportion of EP offspring, (2) the number of EP offspring, and (3) the number of EP sires. This allowed us to assess variation in the allocation of paternity to the social mate, as well as variation in multiple mating. We calculated the change in EP mating between clutches as the difference between the replacement and collected clutch. Thus, a positive difference indicates an increase in EP mating between time points.

Before fitting models for EP mating by females, we checked for possible confounding variables that could cause spurious correlations between EP mating and female movement, or between EP mating and female plumage color. We first considered social male plumage color (belly average brightness, measured as in females) and breeding group size (number of active breeding pairs in a barn during first clutches), since these could both influence patterns of mating and movement. We assessed these possible confounding relationships using Spearman rank correlations and checked for statistical significance at the $\alpha = 0.05$ level. We used Spearman (rank) correlations because these were appropriate for our small sample size and generally non-Gaussian variable distributions. We also measured the correlation between female age class (SY, second year; ASY, after second year) and plumage color in our sample using a Wilcoxon rank sum exact test.

To avoid fitting models for all combinations of movement and mating variables, we first evaluated the association between each movement component and the three EP mating measures in the replacement clutch. Although several of the movement components were highly correlated with each other (Supplementary Fig. S2), they may have distinct biological importance for mating behavior and thus we examined all movement components separately. We used the corrected Akaike Information Criterion, AICc, (Hurvich and Tsai 1989; Akaike 1998) to choose the best movement component for predicting proportion of EP offspring, number of EP offspring, and number of EP mates in the replacement clutch. We then carried the same movement components into the models for change in EP mating.

We fitted a separate model for each EP mating outcome. First, we give details for the replacement clutch models. For proportion of EP offspring, we fitted logistic regression models and accounted for variation in clutch size by weighting observations by clutch size. For one of the tagged females (Cooks 27), the replacement clutch failed before the offspring could be sampled for DNA, so this individual was excluded, leaving 10 individuals for all analyses. For the number of EP offspring, we fitted Poisson regression models, which did not include a covariate for the clutch size in order to model the absolute number of EP offspring rather than the number given a constant clutch size. For the number of EP sires, we fitted Poisson regression models with clutch size as a fixed effect to account for any influence of number of offspring sampled on the number of EP sires detected. To avoid over fitting models with our limited sample size, we did not include group size or social male plumage color as predictors in the models of EP mating.

To model the change in EP mating between clutches, we fitted linear regression models for all three paternity measures. We used the same movement and plumage variables as in the replacement clutch models as explanatory variables. To simplify the interpretation of results for the change in proportion of EP offspring, we did not include a covariate for clutch size. Generally, clutch sizes are expected to decrease as the breeding season progresses. For change in the number of EP sires, we did not include a covariate for number of offspring sampled since the combined number of offspring between the collected and replacement clutches was not correlated with the change in number of sires (Spearman $\rho=0.02$, $p=0.956$).

Statistical significance of the slope terms was assessed using likelihood ratio tests at the $\alpha = 0.05$ level for all models. We additionally calculated 95% confidence intervals for regression parameters of interest. We visualized the model predictions by back transforming to the original scale. Although our data includes instances of repeated measures within site (multiple females tracked from the same site), we did not statistically account for the effect of site due to our limited sample size. A single female was sampled at two out of six sites, so any estimate of a site effect for these sites would be severely underpowered. All Figs were created using R version 4.4.1 and edited for clarity in Adobe Illustrator or Microsoft PowerPoint.

Results

Female movement was not significantly correlated with group size or social male plumage color in our sample (Supplementary Table S3). Female plumage color tended to be negatively correlated with movement, meaning darker females (those with lower brightness values) moved farther and spent more time away from the nest, although none of the correlations were statistically significant. The correlation coefficients between movement and plumage color also tended to be larger for female color than social male color (Supplementary Table S3). Female plumage color did not differ significantly by age class (second year and after second year; Wilcoxon rank sum exact test $p = 0.83$; Supplementary Fig. S3). Breeding group size and social male plumage color did not significantly correlate with any paternity measures, although patterns tended to be stronger in the collected clutch (Supplementary Table S4). The mean number of GPS points collected for each female was 87.8 (range 61–128, Supplementary Table S5), and movement behavior varied over the course of the tracking period (Fig. 1; Supplementary Table S5; Supplementary Fig. S4). Females were not observed to visit neighbouring breeding sites during the tracking period, and there was very little overlap of home ranges for females from different barns (Fig. 2, Supplementary Figs S5, S6).

In the replacement clutch, the mean (±SD) proportion of EP offspring was 0.48 (±0.39), the mean number of EP offspring was 1.8 (±1.47), and the mean number of EP mates was 0.9 (range 0–2). For the change in EP mating, the mean difference (±SD) in proportion EP offspring was 0.18 (±0.69), the mean difference in number of EP offspring was 0.4 (±2.9), and the mean difference in number of EP sires was 0.5 (±0.97). Figure 3 shows the fertilization types in each clutch for each female. Female EP mating in the replacement clutch was not significantly correlated with EP mating in the collected clutch (Supplementary Table S6). The average proportion of within-pair offspring (±SD) in the collected and replacement clutches were 0.64 (±0.46) and 0.52 (±0.39), respectively. Additional details about collected and replacement clutch paternity are in Supplementary Table S7.

The movement component with lowest AICc for the three mating variables in the replacement clutch was the proportion of points greater than 50 m from the home barn (Supplementary Tables S8-S10). Therefore, we used this measure as the movement variable for all final models of EP mating. The mean proportion of GPS points (±SD) past 50 m was 0.90 (±0.1). This high proportion of points away from the nesting barn reflects the fact that our tracking period is at a time of day when the barn swallows tend to be actively foraging and flying, rather than resting near the barn (HKD and RJS personal observations). Overall, we found support for our hypothesis that female space use is associated with EP mating for replacement clutches in two out of the three mating variables (Table 1; Fig. 4). Females with a greater proportion of points away from the barn were significantly more likely to have a higher proportion of EP offspring, and marginally more likely to have a greater absolute number of EP offspring, than females that spent more time near the barn (Fig. 4). Each additional 10% points of GPS points away from the barn corresponds to 185% higher odds of an additional EP offspring (estimated odds ratio 2.85, 95% CI: 1.31, 7.90); the more often a female stays away from her home territory, the more EP offspring she produces. While the effect of movement on the number of EP sires followed the same pattern as the other two mating variables, it was not statistically significant. For the change in EP mating between successive clutches, females with a greater proportion of points away from the barn tended to increase EP mating to a greater extent in the replacement clutch compared to the collected clutch, but none of the parameter estimates were statistically significant (Table 2). Accounting for female plumage color in the models did not meaningfully change the effect or significance of the movement variable; plumage color was not a significant predictor of EP paternity for any of the models (Tables 1 and 2).

Discussion

We showed evidence that female movement behavior is important for understanding mating outcomes in barn swallows. Our study is based on fine-scale measures of female movement during a critical period of reproduction: fertilization. Although our sample size is limited to 10 females and movement was recorded for only 2 h each day, our sample is representative in terms of EP mating after an experimentally simulated nest failure (Safran et al. 2016b where the average proportions of within-pair offspring in the collected and replacement clutches were respectively 0.77 (±0.39) and 0.53 (±0.37)), and provides valuable information about the spatial scale of mate sampling by females. Our current study complements the findings of Costanzo et al. (2017) by investigating a different subspecies of barn swallow (North American rather than European), focusing on visible ventral plumage color as a locally relevant sexual signal rather than UV ventral reflectance, and measuring female movement during the fertile period to further understand variation in

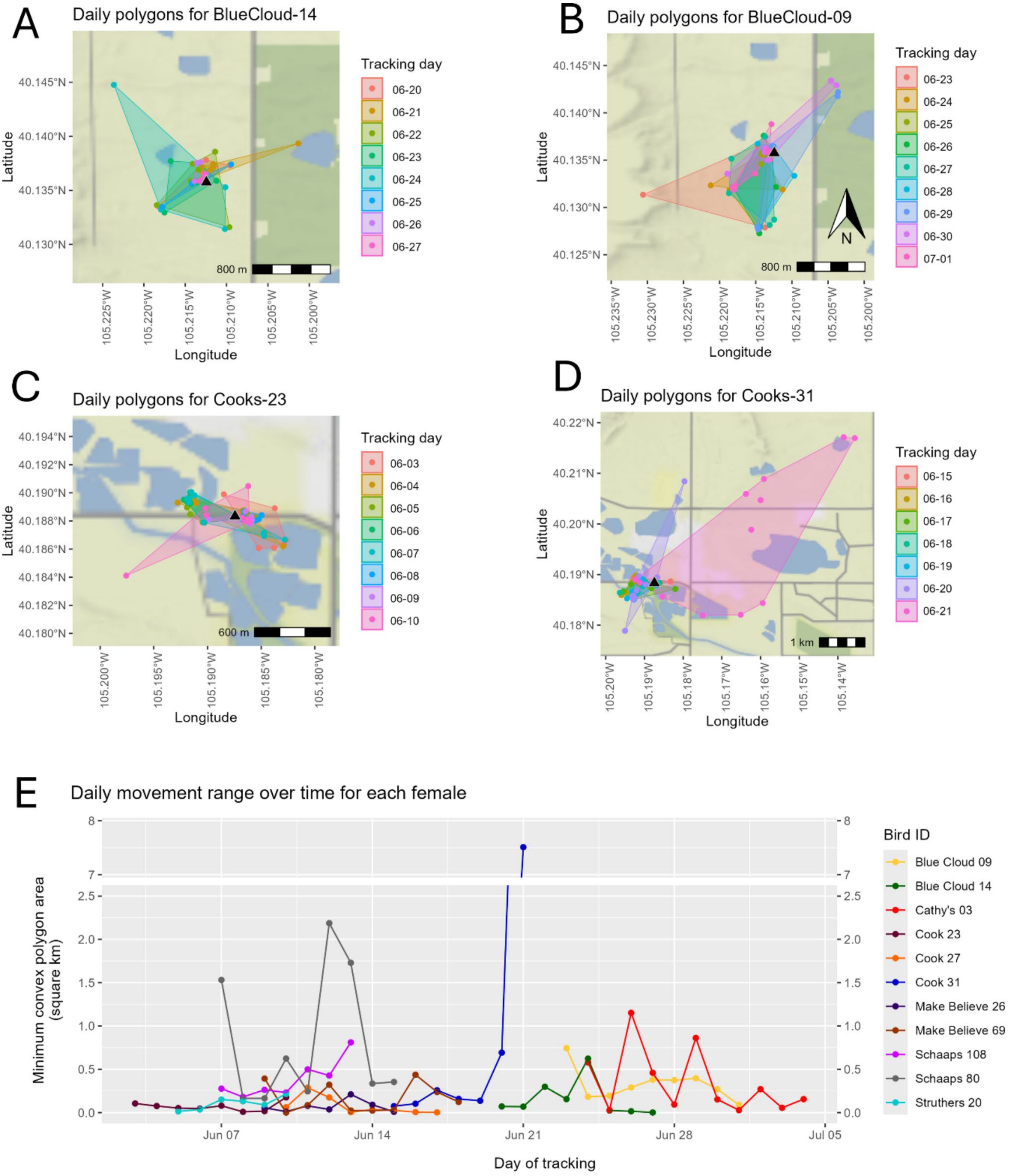

Fig. 1 Daily movement areas for each female. **A-D** show daily minimum convex polygons using 100% of the GPS points each day for four of the ten females. Daily polygons for the other six females are in Supplementary Fig. S4. Tracking days with fewer than 5 points are excluded because polygons cannot be reliably calculated with so few points. Shaded polygons encompass all points recorded in each day and different days are displayed in different colors. Points show the locations of the GPS fixes, and the black triangles show the location of the nesting barn. Note that the scale and dates of tracking vary among panels, and the number next to the scale bar indicates the total length of the bar. Panel **E** shows polygon areas over time for each of the tracked females. Note the y-axis break to show the Cooks-31 large area on 06–21

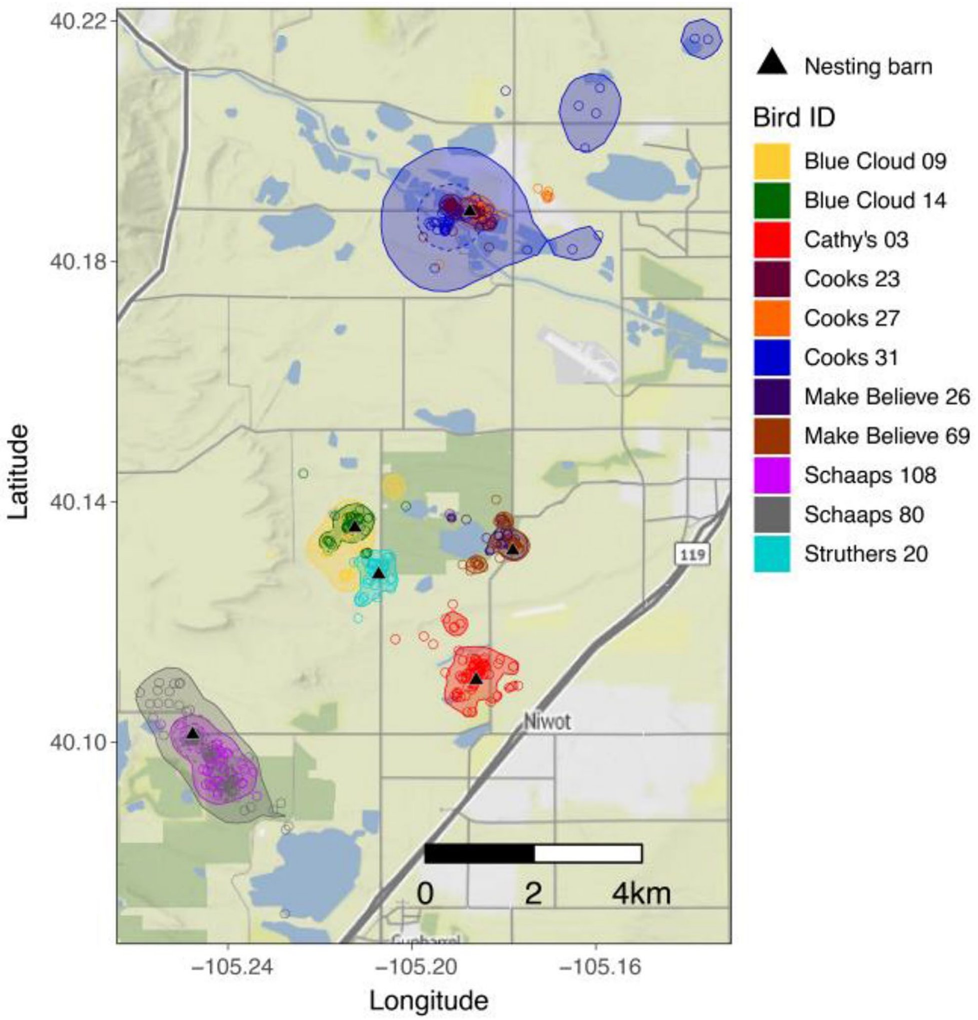

Fig. 2 Movement areas and GPS points for tracked females. Home range (90% KDE, solid borders) and core use areas (50% KDE, dashed borders) for barn swallow females tracked in June 2021 near Boulder, CO. Each female is shown in a different color. Individual GPS points are open circles, and the nesting barns are black triangles. Details of smaller movement ranges are in electronic supplementary material Figs S5, S6. The Cooks 27 female (orange) was excluded from analyses due to missing data

EP mating. The magnitude of movements documented here is similar to those of female barn swallows tracked while caring for nestlings (Madden et al. 2022) which suggests that space use does not change dramatically across stages of breeding. Our results highlight the importance of considering female movement behavior to understand patterns of EP mating in barn swallows. We found that individual females vary substantially in movements during their fertile period, and that the time spent away from the nesting barn is particularly useful for understanding the allocation of extra-pair offspring in the replacement clutch. Female plumage color, on the other hand, was not predictive of EP mating, and we did not find support for the hypothesis that darker females are more likely to have EP paternity than paler females. Plumage color is easier to collect than movement data, and future studies should examine the influence of female plumage color on EP mating, and explore the potential for an interaction between movement behavior and plumage color, in a larger sample. Together, our findings suggest that individual space use is a relevant proxy for social interactions with potential mates, and this pattern remains significant even after accounting for a female's own phenotype.

Female movement correlates with EP mating in the replacement clutch

Our results support the hypothesis that female movement immediately prior to laying influences mating in replacement clutches (both in proportion and number of EP offspring). Spending more time away from the nest may mean that a female spends less time with her social mate, which thus sires fewer offspring in the replacement clutch. Similar relationships between paternity and time spent with the social mate have been found previously in hooded warblers (Chiver et al. 2008) and captive zebra finches (Maldonado-Chaparro et al. 2018). However, other work that directly measured social interactions between barn swallow social pairs found that increased interactivity between social mates did not lead to an increase in the proportion of within-pair

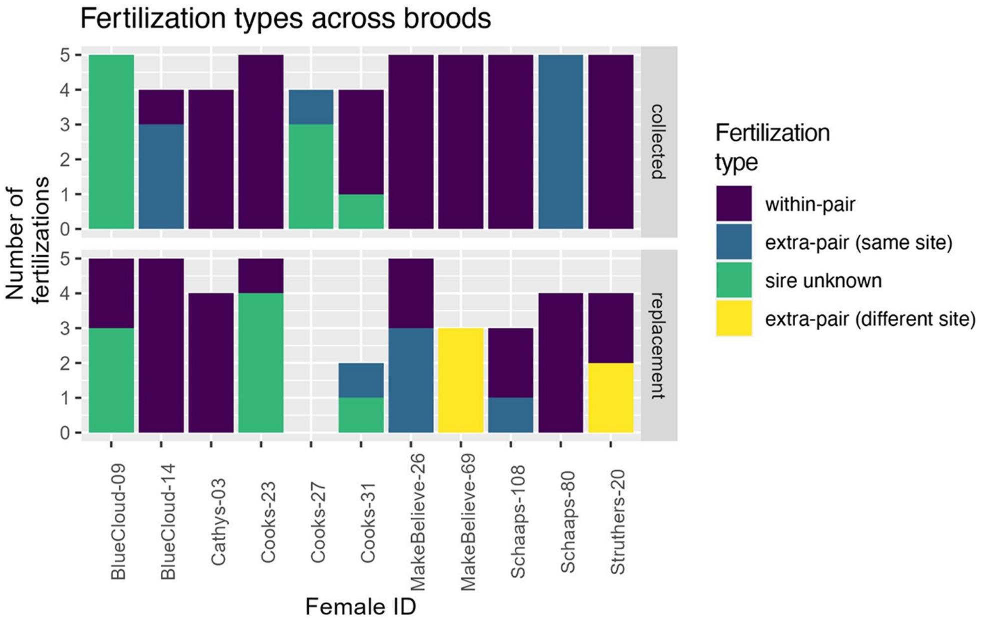

Fig. 3 Fertilization number and type split across broods for 2021 GPS tagged females. The "collected" label refers to the eggs from the first brood that was collected immediately before attaching the GPS tag; "replacement" is the replacement clutch laid immediately after the tracking period. Colors indicate the identity of the genetic sire. For fertilization types, "within-pair" means the sire is the social male, "extra-pair (same site)" means the genetic sire is an EP male of known identity that nested at the same site as the focal female, "extra-pair (different site)" means the genetic sire is an EP male of known identity nesting at a different site than the focal female, and "sire unknown" means the genetic sire was not sampled and his identity is therefore unknown

offspring when the timing of breeding was synchronized (Levin et al. 2018).

One caveat of our results is that we are unable to fully rule out an influence of female age on both movement and EP mating. Our sample consisted of three ASY females and seven SY females. This small and uneven sampling makes it difficult to determine the true age-related patterns. Other studies have found female age as an important predictor of EP paternity (Moreno et al. 2015; Michálková et al. 2019; Raj Pant et al. 2020), although the direction of the pattern is inconsistent across studies. Some females decrease EP paternity with age, others increase, and others have a peak of EP paternity in midlife. The mechanisms underlying this relationship are not known, and females may display age-based movement strategies during the fertile period which act as a proximate mechanism to explain differences in EP paternity across age classes. Explicitly testing the influence of female age on EP paternity and movement patterns is an important area for further research.

Contrary to our predictions, there was no strong evidence that the distance moved away from the barn or the movement area sizes correlated with EP mating in the replacement clutch. The AICc comparisons show that none of the distance or area measures fitted better than the null model (Supplementary Tables S8-S10). This finding could be an indication that distance and area-based movement metrics reflect other types of female movement patterns, such as foraging or exploration, that are not associated with mate searching. Our findings contrast with those from superb fairy-wrens (Double and Cockburn 2000) and tree swallows (Dunn and Whittingham 2007), where the distance moved by females did influence the number and identity of EP sires. This result may reflect mate encounters being jointly influenced by male and female movement patterns. Additionally, our limited tracking window may not have fully captured important movements for EP copulations. Additional work addressing these potential limitations will be valuable for more comprehensively explaining variation in EP mating by female barn swallows.

Female traits do not correlate with dynamic paternity allocation between clutches

Previous experimental studies have shown that female birds dynamically update their reproductive investment based on perceived current male quality (e.g., paternity allocation in barn swallows (Safran 2005; Safran et al. 2016b) and egg size in blue-footed boobies (Velando et al. 2006)). Thus, we predicted that females may also update mating decisions based on movement and assumed spatial encounters with potential males. The direction of the slope estimates matched with this prediction, where females that stayed away from the barn more often tended to increase their EP mating after the experimental nest failure (Table 2). Given

Table 1 Model results for EP mating in the replacement clutches. The models for proportion EP offspring (EPO) are logistic with a weights term for clutch size. The models for number of EPO and number of EP sires are Poisson models. Confidence intervals are upper and lower 95%, and p-values are from Type II ANOVA tests. Coefficients are bolded if the p-value is less than 0.05. All model estimates are on the model scale and have not been back-transformed

Model results for EP mating in the replacement clutch				
Proportion EPO				
	Beta est.	*Lower CI*	*Upper CI*	*p*
(Intercept)	-9.49	-18.73	-2.52	
proportion past 50 m	**10.34**	**2.64**	**20.36**	**0.007**
(Intercept)	-10.17	-21.52	-1.15	
proportion past 50 m	**10.46**	**2.69**	**20.67**	**0.007**
female plumage brightness	0.02	-0.17	0.21	0.820
Number EPO				
	Beta est.	*Lower CI*	*Upper CI*	*p*
(Intercept)	-3.88	-10.33	1.15	
proportion past 50 m	4.88	-0.61	11.66	0.084
(Intercept)	-5.10	-14.36	1.95	
proportion past 50 m	5.33	-0.47	12.86	0.074
female plumage brightness	0.03	-0.10	0.16	0.648
Number EP sires				
	Beta est.	*Lower CI*	*Upper CI*	*p*
(Intercept)	-3.59	-14.43	4.83	
number of chicks in replacement	-0.09	-0.74	0.55	0.771
proportion past 50 m	4.21	-3.60	14.63	0.314
(Intercept)	-4.66	-18.67	6.14	
number of chicks in replacement	-0.10	-0.75	0.54	0.743
proportion past 50 m	4.62	-3.60	15.83	0.293
female plumage brightness	0.03	-0.16	0.22	0.764

that difference variables are especially noisy due to compounded errors, this part of our analysis may suffer from low statistical power with our small data set. It is also possible that changes in paternity after a clutch failure are more influenced by the temporal changes in mate availability than spatial encounters with mates. During first clutches, the earliest breeding females may not have the opportunity to mate with later arriving males. By the time we performed egg collections for this study in early to mid-June, the majority of birds should have arrived and started breeding. Females therefore had access to a different pool of potential mates for their replacement clutches. Temporal synchrony of breeding is a popular ecological factor studied in relation to EP mating, and a recent review paper suggests that higher breeding synchrony does correlate with higher rates of EP mating in barn swallow populations (using high latitude as a proxy for higher breeding synchrony) (Brouwer and Griffith 2019).

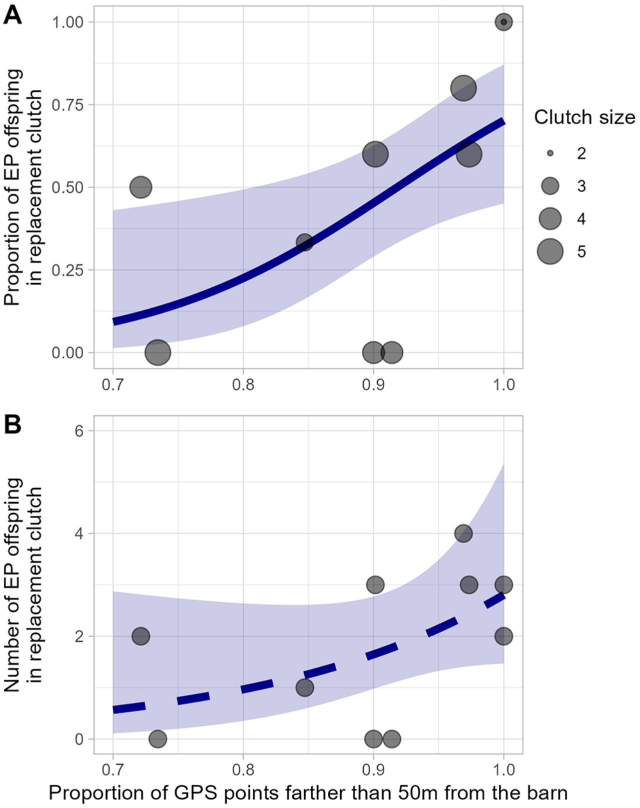

Fig. 4 Model predictions and raw data showing the relationship between the proportion of points past 50 m from the barn and EP mating outcomes in the replacement clutch, after accounting for female plumage color. Shaded areas show 95% confidence intervals, lines show model predictions, and the solid line indicates a significant effect ($p<0.05$) and the dotted line indicates a marginally significant effect ($p<0.1$). (**A**) Proportion of EP offspring in the replacement clutch. Point sizes correspond to the total clutch size. (**B**) Number of EP offspring in the replacement clutch

Future directions

We have found intriguing evidence that female space use during the fertile period correlates with EP mating in a sample of North American barn swallows. We hope these findings motivate further research to determine if this pattern holds across breeding years, across populations, and even across species. While our sample size is limited, this study highlights the potential for variation in female behavior to be more important than previously thought for understanding EP mating. In our preliminary analysis, female traits were more strongly correlated with EP mating than the more conventional predictors of group size and male traits. For the females included in our study, group size did not significantly correlate with female movement or EP mating. While not necessarily intuitive, this pattern does match with previous work where female EP mating did not vary with group size in a much larger sample (Safran 2007). In fact, in our data, females from larger groups tended to be darker

Table 2 Model results for the change in EP mating between the collected and replacement clutches. All models are linear models. Confidence intervals are upper and lower 95%, and p-values are from Type II ANOVA tests

Model results for the change in EP mating between clutches				
Proportion EPO				
	Beta est.	*Lower CI*	*Upper CI*	*p*
(Intercept)	-2.71	-7.13	1.71	
proportion past 50 m	3.23	-1.68	8.14	0.168
(Intercept)	-5.09	-11.02	0.85	
proportion past 50 m	3.79	-1.08	8.66	0.108
female plumage brightness	0.07	-0.05	0.19	0.211
Number EPO				
	Beta est.	*Lower CI*	*Upper CI*	*p*
(Intercept)	-9.26	-28.86	10.33	
proportion past 50 m	10.78	-10.96	32.53	0.286
(Intercept)	-21.87	-46.57	2.84	
proportion past 50 m	13.77	-6.51	34.05	0.152
female plumage brightness	0.37	-0.13	0.88	0.123
Number EP sires				
	Beta est.	*Lower CI*	*Upper CI*	*p*
(Intercept)	-3.04	-9.47	3.38	
proportion past 50 m	3.96	-3.17	11.08	0.236
(Intercept)	-6.79	-15.20	1.61	
proportion past 50 m	4.84	-2.06	11.74	0.141
female plumage brightness	0.11	-0.06	0.28	0.170

and move farther than females from smaller groups, though this may not be the case at the population level (Supplemental Table S3). Female mass tended to be positively correlated with the movement metrics, suggesting that larger females may be in better condition and have more energy to fly around. Collecting additional data on other traits such as fat score that are related to female condition may help to explain proximate drivers of female movement variation during the fertile period.

Social male plumage color also did not correlate significantly with movement, EP mating in the replacement clutch, or change in EP across clutches, but it was more strongly correlated with mating in the collected clutch (Supplementary Table S5). This pattern matches with larger studies of North American barn swallows where male plumage color predicted the proportion of within-pair offspring in his social nest (Eikenaar et al. 2011). An interesting possibility is that female mating decisions are influenced more strongly by social mate plumage color during first clutches, but after a nest failure, other factors such as female movement may play a larger role in mating outcomes. Future experimental work manipulating female plumage color directly and examining the impacts on EP mating would help disentangle the direct effects of female plumage vs. social male plumage color and female body condition.

Conclusions

Many studies of EP mating behavior have exclusively focused on male ornamentation and male access to mates. We have shown that female movement during the fertile period is significantly correlated with EP mating. This emphasizes the importance of accounting for female variation, not just variation in male phenotypes, when predicting mating outcomes. We anticipate that incorporating female movement into studies of EP mating and sexual selection in other systems will further illuminate factors that contribute to the process of trait evolution in natural populations. Indeed, putting equal emphasis on the importance of variation in both females (Gowaty 1996b) and males is crucial for a balanced and clear understanding of evolutionary ecology as a whole.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-025-03570-y.

Acknowledgements We thank Molly McDermott for training on the use of the GPS tags. We also thank Arielle Fogel for suggesting the method used for estimates of relatedness, and to Adi Schuerg for suggesting the method for determining the number of unknown sires. We are also grateful to the 2021 field assistants: Sage Madden, Marina Ayala, Avani Fachon, Grant Gonzales, Liz Mathews, and Zach Laubach. Avani Fachon and Toni Schuerg assisted with lab work. Many thanks to all the members of the Safran Lab for support and useful feedback on this manuscript, and to the landowners who allowed us to work on their properties. We are grateful to the three anonymous reviewers whose comments helped to greatly improve the manuscript.

Author contributions HKD: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, visualization, writing – original draft, writing – review and editing. DRS: data curation, formal analysis, investigation, methodology, software, visualization, writing – review and editing. KPK: formal analysis, methodology, supervision, writing – review and editing. RJS: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing – review and editing.

Funding This research was supported by funding from the Ecology and Evolutionary Biology Department at CU Boulder, and the National Science Foundation (NSF) grant IOS 1856266 to RJS. HKD was supported by NSF Graduate Research Fellowship DGE 1650115. DRS was supported by NSF Postdoctoral Research Fellowship DBI-1906188 and IOS-DEB-1856266. KPK was supported by NSF grant 1856229.

Data availability Raw genomics data are available on the NCBI SRA accession PRJNA323498. Bioinformatics pipelines and associated scripts, plus data and scripts used for statistical models and for generating Figs are available on GitHub (https://github.com/heatherkennyduddela/barn-swallow-gps).

Declarations

Ethics approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. All animal handling, marking, and sample collection for this study was included in IACUC protocol 2685 and approved by the University of Colorado Boulder Institutional Animal Care and Use Committee. Work was also approved under Federal Bird Banding permit 23505, and the State of Colorado Department of Natural Resources and Colorado Parks and Wildlife Mammal and Avian Scientific Collection License 22TRb2005. Study sites were accessed with permission from private landowners.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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