Ornithology, 2026, **00**, 1–15
https://doi.org/10.1093/ornithology/ukag013
Advance access publication 15 March 2026
Special Feature

Ornithology
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Extra-pair fertilizations are more strongly associated with female traits than male traits or fecundity in *Hirundo rustica erythrogaster* (North American Barn Swallow)

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ABSTRACT

Many socially monogamous bird species engage in multiple mating through extra-pair (EP) fertilizations, yet the role of female plumage in EP outcomes is under studied. Sexual selection involving EP fertilization is hypothesized to influence female trait evolution if heritable plumage variation informs EP mating decisions and EP mating decisions affect fitness. Here, we test for 2 key prerequisite patterns of sexual selection through EP fertilizations by asking: (1) is female reproductive success associated with EP fertilizations, and (2) are EP fertilizations associated with female plumage traits? Studying these 2 patterns is essential for better understanding how the costs and benefits of EP fertilizations should translate to sexual selection on female plumage. We provide a conceptual diagram to highlight how plumage traits of both members of a social pair can influence fertilizations within and outside their pair bond from the perspective of each sex. In our sample of 47 *Hirundo rustica erythrogaster* (North American Barn Swallow) social pairs, females who engaged in EP mating tended to fledge more offspring, and females with longer tails were more likely to mate with EP sires. Furthermore, female traits were more strongly associated with EP fertilizations than male traits for predicting both female and male EP outcomes. Finally, we found that female traits were not correlated with fecundity (total eggs laid) and found no association between fecundity and EP fertilizations. Thus, sexual selection on EP fertilizations may be more important than selection on fecundity for understanding female plumage variation in our study population. Taken together, we provide evidence for multiple conditions necessary for sexual selection on female plumage traits in *H. r. erythrogaster* that are likely also relevant for understanding female trait evolution in other socially monogamous birds.

Keywords: barn swallow, extra-pair mating, fecundity, female plumage, *Hirundo rustica erythrogaster*, reproductive success, sex-differences, sexual selection

How to Cite

Kenny-Duddela, H. V., D. R. Schield, Z. M. Laubach, I. I. Levin, K. P. Keller, and R. J. Safran (2026). Extra-pair fertilizations are more strongly associated with female traits than male traits or fecundity in *Hirundo rustica erythrogaster* (North American Barn Swallow). *Ornithology* 143:ukag013.

LAY SUMMARY

- Understanding how traits evolve in female birds is essential for explaining the diversity of bird species.
- Fertilizations with birds other than a social mate in a shared nest (“extra-pair” fertilizations) are common in songbirds, yet we know little about how this process relates to the evolution of female plumage traits.
- We found that female *Hirundo rustica* (Barn Swallow) with longer tails were more likely to mate with multiple extra-pair males, and females with more extra-pair offspring also raised more total offspring over the course of a single breeding season.
- These findings mean that selection for extra-pair mating could help us understand how and why female plumage traits change over time.
- By giving female birds equal attention as male birds, we can gain a better understanding of how the phenotypic traits of birds change in populations and species overall.

Las fertilizaciones extrapareja se asocian más fuertemente con rasgos femeninos que con rasgos masculinos o la fecundidad en *Hirundo rustica erythrogaster*

RESUMEN

Muchas especies de aves socialmente monógamas participan en apareamientos múltiples mediante fertilizaciones extrapareja (EP); sin embargo, el papel del plumaje femenino en los resultados EP ha sido poco estudiado. Se plantea que la selección sexual que involucra fertilizaciones EP

Submission Date: June 13, 2025; Editorial Acceptance Date: February 10, 2026

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puede influir en la evolución de los rasgos femeninos si la variación heredable del plumaje influye en las decisiones de apareamiento EP y si dichas decisiones afectan la aptitud biológica. Aquí evaluamos dos patrones clave que constituyen prerrequisitos de la selección sexual a través de fertilizaciones EP preguntando: (1) ¿está el éxito reproductivo femenino asociado con las fertilizaciones EP?, y (2) ¿están las fertilizaciones EP asociadas con rasgos del plumaje femenino? El estudio de estos dos patrones es esencial para comprender mejor cómo los costos y beneficios de las fertilizaciones EP deberían traducirse en selección sexual sobre el plumaje femenino. Presentamos un diagrama conceptual para resaltar cómo los rasgos del plumaje de ambos miembros de una pareja social pueden influir en las fertilizaciones dentro y fuera del vínculo de pareja desde la perspectiva de cada sexo. En nuestra muestra de 47 parejas sociales de *Hirundo rustica erythrogaster*, las hembras que participaron en apareamientos EP tendieron a sacar adelante más crías, y las hembras con colas más largas tuvieron mayor probabilidad de aparearse con machos EP. Además, los rasgos femeninos estuvieron más fuertemente asociados con las fertilizaciones EP que los rasgos masculinos para predecir tanto los resultados EP femeninos como masculinos. Finalmente, encontramos que los rasgos femeninos no estuvieron correlacionados con la fecundidad (total de huevos puestos) y no hallamos asociación entre fecundidad y fertilizaciones EP. Por lo tanto, la selección sexual sobre las fertilizaciones EP puede ser más importante que la selección sobre la fecundidad para comprender la variación del plumaje femenino en nuestra población de estudio. En conjunto, aportamos evidencia de múltiples condiciones necesarias para la selección sexual sobre los rasgos del plumaje femenino en *H. r. erythrogaster*, que probablemente también sean relevantes para comprender la evolución de rasgos femeninos en otras aves socialmente monógamas.

Palabras clave: apareamiento extrapareja, diferencias entre sexos, éxito reproductivo, fecundidad, *Hirundo rustica erythrogaster*, plumaje femenino, selección sexual

INTRODUCTION

Our understanding of plumage signal evolution has historically focused on sexual selection to explain the exaggeration of male traits, either through female choice or male–male competition (Payne 1984, Kirkpatrick et al. 1990, Andersson and Iwasa 1996, Gontard-Danek 1999, Mendelson and Safran 2021, Ah-King 2022). As a result, the processes that influence female plumage signals and other female traits have received relatively less attention (Gowaty 1996, Odom and Benedict 2018, Lipshutz 2018, Riebel et al. 2019, Smiley et al. 2022). Recent review papers show that sexual selection on female ornaments and behaviors is consistently present across species and populations (reviewed by Hare and Simmons 2019, Doutrelant et al. 2020). Additionally, studies of female signals are most often considered in the context of securing an attractive social mate with a high-quality breeding territory (Amundsen 2000, Tobias et al. 2012). These findings have been important for linking female traits to measures such as fecundity or fledging success and for understanding how female phenotypes influence social pair formation (Morosse et al. 2025). Yet, we understand very little about how female traits influence fertilizations outside the social pair bond. This will help improve our understanding of how differences in extra-pair (EP) fertilizations translate to selection on female plumage for the many species of socially monogamous birds.

The constrained female hypothesis suggests that traits associated with a female's ability to control fertilizations—such as her physical size, energy reserves, access to resources, or reliance on male parental care—should be associated with rates of EP paternity (Gowaty 1996). Variation in these aspects of female quality may also be correlated with plumage phenotype, especially if individuals with certain phenotypes are socially dominant and do not need to expend extra energy on social challenges (Vitousek et al. 2013, López-Idiáquez et al. 2016), or if they are more experienced breeders and less reliant on male parental care. Rates of EP paternity can be either high or low for both "constrained" and "unconstrained" females. Constrained females may be unable to avoid EP copulations, or they may be prevented from pursuing EP copulations by mate guarding from their social partner. Unconstrained females may seek out EP copulations with preferred males, or may be better able to repel unwanted EP copulations. Therefore, the direction of the relationship between phenotype and rates of EP fertilizations can be variable. While EP mating increases individual male reproductive success in most cases (Webster et al. 1995, Griffith et al. 2002, Whittingham and Dunn 2005, Brouwer and Griffith 2019), evidence is mixed as to whether mating with multiple partners influences female fitness positively (Gray 1997, Gerlach et al. 2012a; and reviews in Hare and Simmons 2019, Doutrelant et al. 2020), negatively (Sardell et al. 2012), or not at all (reviewed in Akçay and Roughgarden 2007, Tang-Martínez 2016).

These mixed patterns related to female reproductive success are mirrored when considering female phenotypes and EP fertilizations. Previous examples include cases where high-quality female traits correlate with higher rates of EP fertilizations (Torres and Velando 2005, Costanzo et al. 2017, Plaza et al. 2019a, Benítez Saldívar et al. 2022), and other cases where high-quality traits correlate with lower rates of EP fertilization (Moreno et al. 2015, Ferretti et al. 2018, Plaza et al. 2019b, Lyon and Chaine 2022). Unfortunately, studies rarely address both the association between EP fertilizations and fitness in females, and the association between plumage and EP fertilizations together for a single species. By measuring just one of these associations at a time, studies are missing information about why such patterns matter in an evolutionary context (in the case of not linking to fitness proxies) or how such patterns happen (in the case of not linking to signal traits). Conducting research that measures both of these associations together is necessary for advancing our understanding of when and how variation in female plumage traits should be informative about EP fertilizations.

In addition to measuring female reproductive success, 2 important comparisons can be leveraged to better link EP mating and female plumage variation. First, measuring and directly comparing associations between plumage and EP outcomes for both females and males of the same species is a powerful, yet rarely utilized, way to reveal sex-specific drivers of plumage trait variation (Grunst and Grunst 2014). This helps illuminate differences and similarities in processes that shape female and male plumage evolution, and is important for explaining plumage variation within populations over evolutionary timescales (Dale et al. 2015, Doutrelant et al. 2020, Nolazco et al. 2023). Second, we can compare trait associations with EP outcomes to trait associations with other important measures of female fitness, such as fecundity. Fecundity is often a target of selection by male choice, because males can directly increase their reproductive success by pairing with a female who produces many offspring, and female plumage traits may be reliable signals of fecundity (Monaghan et al. 1996, Jones et al. 2001, Potti et al. 2013). While a measure like fledging success depends on contributions from both the female and male parents, fecundity is

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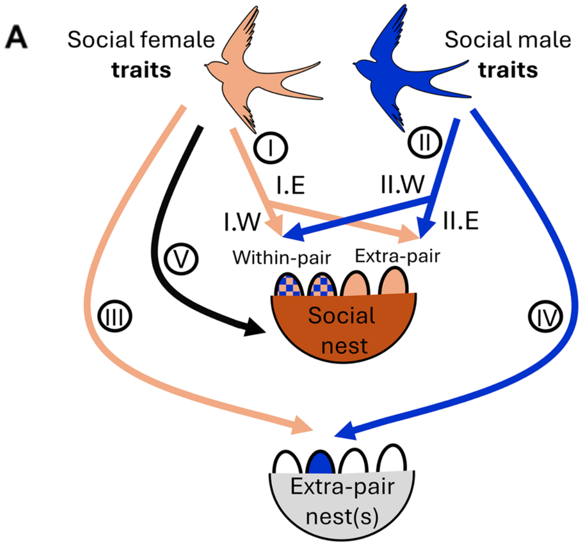
a female-specific contribution to reproductive success that may have a more direct association with female plumage. If female plumage communicates variation in fecundity, these females may be preferred by males and thus have more EP fertilizations (Gerlach et al. 2012b, Henshaw et al. 2018). On the other hand, female plumage may signal qualities other than fecundity which are predictive of her ability to gain or avoid EP fertilizations. Thus, multiple selective forces, both male mate choice on fecundity and female access to (or avoidance of) EP fertilizations, may contribute to variation in one or multiple female plumage traits. By directly comparing plumage associations with EP fertilizations and fecundity, we can gain a better understanding of the relative importance of each component of fitness for shaping female plumage variation.

To highlight gaps in knowledge addressed in this study, we introduce a graphical representation of how female and male traits may be associated with fertilizations within and outside the social nest in Figure 1. Studies often account for social male plumage traits when predicting the proportion of within-pair (arrow II.W) and EP (arrow II.E) fertilizations in the social nest, or a male's fertilization success with EP females (arrow IV) (Yezerinac and Weatherhead 1997, Karubian 2002, Jacobs et al. 2015, Whittingham and Dunn 2016). However, the importance of female plumage signals for reproductive interactions has been underexplored, including how female plumage signals influence social male within-pair fertilizations (arrow I.W), how female plumage functions as a signal to potential EP males (arrow I.E), and how female plumage determines her social mate's EP paternity with other females (arrow III). If plumage phenotypes influence social interactions, and social interactions influence EP fertilizations, then we would expect an association between plumage phenotype and EP mating for both sexes. We represent arrows I and II as double-headed because the combined outcome of 2 separate pathways, (W) increasing or decreasing within-pair fertilizations, and (E) increasing or decreasing EP fertilizations, is what determines the proportion of fertilization types in the social nest. In the majority of EP fertilization studies, including the current one, these pathways are impossible to disentangle because the 2 outcomes are perfectly correlated. However, it is important to acknowledge that there are 2 distinct pathways impacting both measures. We emphasize EP fertilizations in the social nest as our outcome variable of interest and highlight the female's role in controlling this outcome by coloring the EP eggs to match the color of the female icon. For simplicity going forward, we use the terms "arrow I" and "arrow II" to mean the female or male trait impacts on EP fertilizations (arrows I.E and II.E) in the social nest.

Hirundo rustica (Barn Swallow) are a useful system in which to investigate associations between phenotype and EP fertilizations because the species is socially monogamous with moderate rates of EP paternity, and females and males exhibit the same types of plumage traits with substantial variation between individuals (e.g., from 12 sites in NY mean tail streamer length ± SD among 42 males was 89.75 ± 7.14 mm, and among 67 females was 76.83 ± 3.87 mm, Safran and McGraw 2004; see figure 2 in Safran and McGraw 2004 and figures 1 and 3 in Hubbard et al. 2015 for variation in color metrics for populations in NY and



B

Model	Outcome	Predictors	Arrow	N
A	Female EP ferts in the social nest (tan eggs)	Female traits	I	47
		Social male traits	II	
B	Male EP ferts in outside nests (blue eggs)	Social female traits	III	48
		Male traits	IV	
C	Female fecundity	Female traits	V	47

FIGURE 1. Diagram of how female and male traits can influence fertilizations and the models used to represent these relationships. Panel (**A**) shows the conceptual diagram by which traits of the social female and social male can influence paternity in the shared nest and in outside nests. Arrows represent the influence of social female or social male traits on different reproductive outcomes. Roman numerals indicate different pathways: (I) Influence of social female traits on (I.W) within-pair fertilizations and (I.E) extra-pair fertilizations in the social nest; (II) influence of social male traits on (II.W) within-pair fertilizations and (I.E) extra-pair fertilizations in the social nest; (III) influence of social female traits on fertilization success of the social male with extra-pair females; (IV) influence of social male traits on his fertilization success with extra-pair females; and (V) influence of social female traits on her fecundity (number of eggs laid). Note that in the current analysis, trait influences on within-pair offspring cannot be separated from trait influence on extra-pair offspring in the social nest (parts (W) and (E) for arrows I and II), although it is useful to acknowledge that these are distinct pathways. The shade of the eggs in the nests indicate whether fertilization decisions were made by the social female (lighter shade), by the social male (darker shade), by both (checkered), or by birds not pictured in the diagram (white). Panel (**B**) summarizes the models used to test for the associations of different traits with female and male extra-pair outcomes. EP = extra-pair, ferts = fertilizations. We fit a total of 5 models, because we used 2 separate measures of extra-pair outcomes for models A and B: the count of extra-pair offspring for females and males (negative binomial for both sexes, with an offset term for the total number of offspring for the female model), and the total number of genetic mates for females and males (Gaussian for females and Poisson for males). All models include female traits of tail streamer length, breast color, and throat color, as well as male traits of tail streamer length, breast color, and throat color. Clutch initiation date for the social female's first clutch is also included in all models as a covariate. Swallow icon by Agne Alesiute from TheNounProject.com.

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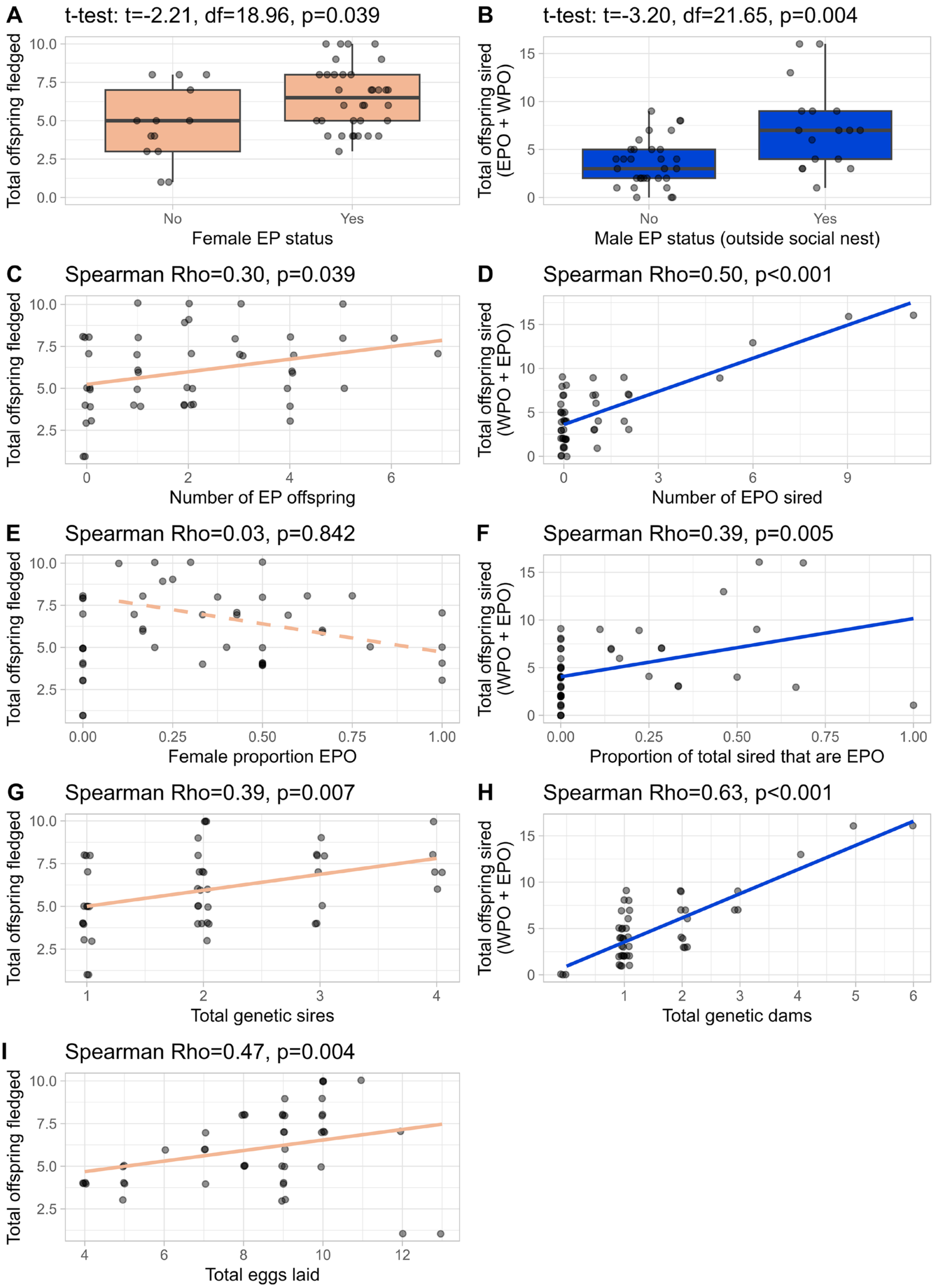

FIGURE 2. Relationships of EP mating and fecundity with annual reproductive success for females and males. Females are shown in the left column ($n = 47$). Males are shown in the right column ($n = 48$). Female reproductive success is measured as total offspring fledged and is plotted against (**A**) female extra-pair status, (**C**) number of extra-pair offspring, (**E**) the proportion of a female's total offspring that are extra-pair, (**G**) a female's total number of genetic sires, and (**I**) the total number of eggs laid by each female. Male reproductive success is measured as the total number of offspring sired (the sum of extra-pair and within-pair offspring) and is plotted againts (**B**) male extra-pair status, (**D**) number of extra-pair offspring, (**F**) proportion of total sired offspring that are extra-pair, and (**H**) a male's total number of genetic dams. Solid lines indicate a significant correlation ($P < 0.05$), and dotted lines indicate a non-significant correlation. Raw data are shown in gray transparent points and overlapping observations appear as darker shades. Points are slightly jittered for plots with integer variables on the x-axis. For box plots, the thick horizontal lines show the median value, the boxes show the second and third quartiles, and the whiskers show the first and fourth quartiles. EPO = extra-pair offspring.

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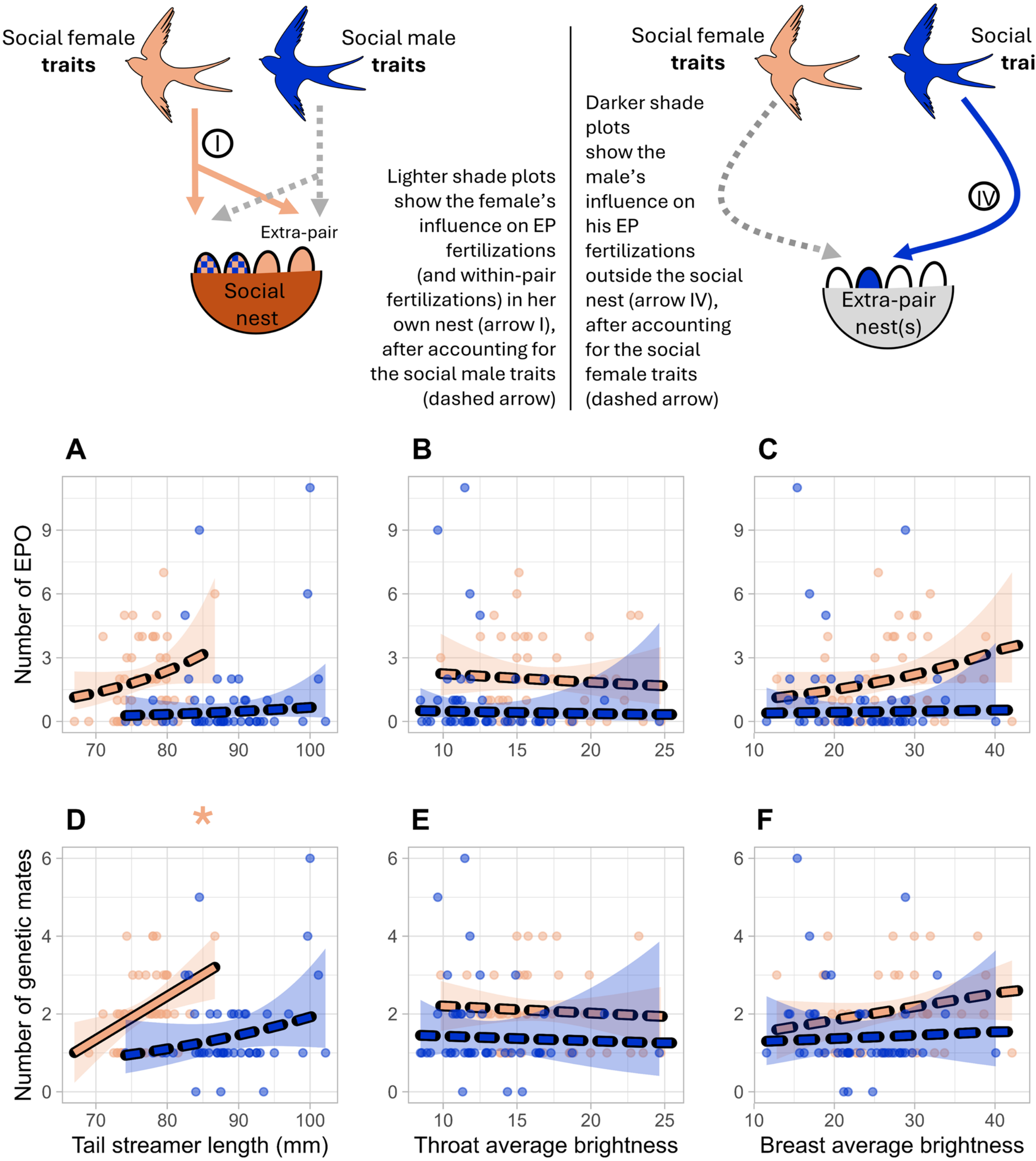

FIGURE 3. Model results for focal female (lighter shade lines and points) and focal male (darker shade lines and points) EP fertilizations. Each row shows results from a different model, and female and male EP fertilizations were modeled separately. Axes labels have sex-specific interpretations. For females, number of EPO (extra-pair offspring), refers to the number of total extra-pair offspring that the female had across all of her clutches (from model A). For males, number of EPO refers to the total number of extra-pair offspring sired by the male (from model B). For both sexes, number of genetic mates is the total number of unique individuals with which the focal bird shared fertilizations, including their social mate. Traits shown on the *x*-axes correspond to female values for the lighter shade plots and male values for the darker shade plots. Points show the raw data, lines show model predictions with all other variables set to the mean values, and ribbons show 95% confidence intervals. Statistically significant effects are shown in solid lines and non-significant effects are shown in dashed lines. Stars above panels also indicate significant results. Panels (**A–C**) show the number of EP offspring as a count variable from negative binomial models. The social nest EPO model (for females) included an offset term for the number of offspring that were analyzed for paternity. Panels (**D–F**) show results for the number of genetic mates from a Gaussian linear model (for females) and a Poisson model (for males). All models include clutch initiation date as a covariate to control for variation in the timing of breeding and bird age class. Swallow icon by Agne Alesiute from TheNounProject.com.

CO). For populations at our study sites in Colorado, on average, 41% of offspring are the result of EP fertilization, and 67% of nests have at least one EP offspring (Hubbard et al. 2015). Although male outer tail streamer length is under sexual selection in European populations of *H. r. rustica* (Møller et al. 1998), ventral plumage color is the target of sexual selection in male *H. r. erythrogaster* (North American Barn Swallow) in North America (Safran 2005, Safran et al. 2016, Hund et al. 2020), and

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TABLE 1. Description of research questions, relation to arrows in Figure 1, and statistical tests used to evaluate each question.

Question	Description	Sex	Location of EP fertilizations	Arrow in Figure 1	Statistical test
1	Are EP fertilizations positively correlated with female and male annual reproductive success?	–	–	–	Correlation tests
2	Are female and male plumage traits associated with their own EP fertilizations?	Female Male	Social nest Outside nests	Arrow I Arrow IV	Model A Model B
3	Are female and male plumage traits associated with EP fertilizations by their social partner?	Female Male	Outside nests Social nest	Arrow III Arrow II	Model B Model A
4	Are female traits associated with fecundity?	–	–	Arrow V	Model C

EP = extra-pair.

is correlated to the timing of breeding and seasonal reproductive success (offspring fledged) for females (Safran and McGraw 2004).

Older individuals tend to sire and fledge more offspring, are darker with longer tail streamers, and begin breeding earlier (Møller and De Lope 1999, Lifjeld et al. 2011, 2022, Bradley et al. 2014). However, the patterns are complex. Phenotypic variation means that younger males may have longer tail streamers than older males, and reproductive variation means males with darker ventral colors or longer tails may not sire more offspring (Lifjeld et al. 2011, 2022). Among females, individuals did not change the number of EP offspring in their nest over time (Bradley et al. 2014). It is possible that individuals may use conspecific plumage traits as indicators of age, although the strength of age/plumage correlations can be variable and should be evaluated in each population of interest. Despite the potential for trait correlations with age, the similarity of female and male plumage phenotypes, together with the fact that they are heritable sexual signals (Hubbard et al. 2015), presents an excellent opportunity to compare the influence of ventral color and tail streamer length on EP fertilizations for females versus males. Here, we investigate the questions listed in Table 1 to test the hypothesis that EP fertilizations can exert sexual selection on female plumage in wild *H. r. erythrogaster*.

METHODS

Field Methods

We monitored *H. r. erythrogaster* breeding at 10 sites (barns) in Boulder County, Colorado, United States, during the summer of 2022. Breeding sites ranged in group size from 1 to 33 social pairs actively breeding during first clutches. We checked nest contents every 2–3 days from May to September to record clutch initiation, clutch completion, incubation, hatching, and fledging for all breeding attempts. We captured adult swallows using mist nets and by hand, marked them with USGS bands and plastic color bands, measured outer tail streamer length, and collected ventral feather samples and a small blood sample from the brachial vein. We identified social pairs using binoculars through observations at the nest and color band combinations. When nestlings were ~12 days old, we banded them with USGS bands and collected blood and feather samples. We also banded adult male swallows from 16 additional sites that were within 2.2 km of our core study sites in order to sample potential EP sires. We based our search for additional sites on the fertile period movement ranges of female *H. r. erythrogaster* in this same population that were measured in 2021 (Kenny-Duddela et al. 2025). Across our 10 core sites, we banded 95% of adults (minimum of 92% per site) and sampled paternity from 87% of clutches that survived to nestling day 12 (81 out of 93).

Feather Color Measurements

For each adult swallow, we collected a small patch of feathers from 4 different ventral regions: throat, breast, belly, and vent. Feathers were stored in paper envelopes at room temperature for later processing. We measured plumage color by taping 5–10 feathers from each ventral patch 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 for each patch using an Ocean Optics UV-VIS spectrometer and pulsed xenon light (P-X2, Ocean Optics) as in Hubbard et al. (2015). We ensured independent replicate measures by lifting and replacing the probe between measurements, and previous work showed that brightness has high repeatability using this method ($r = 0.88$–0.93; Hubbard et al. 2015). Feather patches with a lower brightness value are visually darker in color and have more melanin (McGraw et al. 2005). We used brightness because it is the least prone to measurement error and noise from the instrument, and is correlated with other color metrics like hue and saturation within each ventral region (Safran and McGraw 2004, Hubbard et al. 2015). Brightness is also a good indicator of condition because it can be influenced by the microstructure of the feather in addition to pigment concentration (D'Alba et al. 2014).

Paternity Assignment

We sequenced the genomes of parents and offspring to reconstruct a fertilization network based on estimated pairwise relatedness among individuals, following our previous procedure described in Kenny-Duddela et al. (2025). Briefly, we extracted genomic DNA from blood samples and whole genomes were sequenced by NovoGene (Sacramento, CA, United States) targeting 2x coverage. We aligned filtered sequence data to the *H. rustica* reference genome (Secomandi et al. 2023), and identified 92,438 unlinked single nucleotide polymorphisms to estimate pairwise relatedness among all sampled individuals using lcMLkin (https://github.com/COMBINE-lab/maximum-likelihood-relatedness-estimation) based on recalculated genotype likelihoods. We used the minimum relatedness value from known mother-offspring relationships as a threshold value to assign genetic sires. The identity of genetic sires was then used to categorize within-pair and EP offspring. In cases where the genetic sire was not sampled, we classified

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TABLE 2. Summary statistics for outcome and predictor variables.

	Models from female perspective		Models from male perspective	
	n	(mean ± SD)	*n*	(mean ± SD)
Extra-pair fertilizations				
Binary EP status (proportion yes)	47	0.72	48	0.35
Proportion EP offspring	47	0.35 ± 0.31	48	0.14 ± 0.24
Number of EP offspring	47	2.04 ± 1.86	48	1.02 ± 2.26
Number of genetic mates (sires or dams)	47	2.06 ± 0.96	48	1.52 ± 1.15
Reproductive measures				
Number of offspring fledged (day 12)	47	5.87 ± 2.28	–	–
Fecundity (total eggs laid)	47	8.26 ± 2.25	–	–
Number of offspring sired (EPO + WPO)	–	–	48	4.90 ± 3.71
Female phenotypes				
Tail streamer length (mm)	47	76.62 ± 3.63	48	76.60 ± 3.59
Throat average brightness (% reflectance)	47	16.77 ± 3.45	48	16.86 ± 3.43
Breast average brightness (% reflectance)	46	26.98 ± 6.17	47	26.96 ± 6.11
Male phenotypes				
Tail streamer length (mm)	46	88.32 ± 6.42	47	88.44 ± 6.39
Throat average brightness (% reflectance)	46	12.70 ± 2.82	47	12.96 ± 3.29
Breast average brightness (% reflectance)	46	23.06 ± 6.01	47	23.22 ± 5.82
Timing of breeding				
Lay date of first clutch	47	28 May ± 11.2	48	28 May ± 11.2

For the female perspective models, data were filtered using females as the focal individuals. For the male perspective models, data were filtered using males as the focal individuals. These 2 datasets both include information about female and male social pairs, but differ slightly in number and identity of the birds that are included. Note that the phenotype summaries are very similar across columns but not exactly the same. EPO = extra-pair offspring, WPO = within-pair offspring. Lay date of first clutch for males was calculated based on egg-laying by his social partner.

offspring as EP since we could confidently rule out the social male as the genetic sire. For a detailed description of the bioinformatics workflow, software versions, and additional details about the paternity analysis, see the Supplementary Material and methods in Kenny-Duddela et al. (2025).

Statistical Methods

Exclusion criteria

Because we were interested in EP fertilizations relative to the social pair over the whole breeding season, we excluded any adults who changed social partners during the season (3 cases). We also excluded individuals whose first recorded clutch initiation date was later than July 15th as these birds likely had unrecorded first nesting attempts prior to nesting at our study sites. Any excluded males were not analyzed as focal individuals but were still included as potential EP sires. We only included focal individuals where both members of the pair were banded, where the social nest(s) were monitored for the full duration of the breeding season, and where at least one offspring could be sampled for paternity from the social nest. This means we did not include pairs that had zero offspring survive to day 12 due to unhatched eggs or nest depredation (11 cases). The final sample sizes were 47 focal females and 48 focal males. See methods section in Supplementary Material for additional details about constructing data tables for females and males.

Metrics for EP fertilizations and fecundity

We used multiple metrics for the EP outcomes to explore which measures were correlated with female and male annual reproductive success. For females, we used: (1) binary EP status, where 0 means the female did not have any EP offspring and 1 means at least one EP offspring was detected; (2) the number of EP offspring as a count variable; (3) the proportion of a female's total offspring that were EP; and (4) the total number of unique genetic sires detected including the social male (genetic sires). We used an equivalent set of metrics for males, which reflect his success at siring offspring outside of the social nest: (1) binary EP status, where 0 means the male did not sire any EP offspring outside of his social nest and 1 means he sired at least one EP offspring with a female other than his social partner; (2) the number of EP offspring sired as a count variable; (3) the proportion of a male's total sired offspring that were EP; and (4) the number of females with which the male shared genetic offspring (genetic dams).

We measured fecundity as the total number of eggs laid by each female across all of its clutches for the entire breeding season. Predation on eggs may inflate this fecundity measure for females whose nests are depredated. However, the nest depredation rate for focal females was low and only 4 females had clutches that failed due to predation or fallen nests. Each of these females had only one nesting attempt that was impacted. Therefore, we consider total eggs laid to be a reliable measure of fecundity.

Relationships between EP fertilizations and annual reproductive success (Question 1)

First, we established the relevance of EP fertilizations for individual fitness. We determined the relationship between EP fertilizations and annual reproductive success (total number of offspring fledged for females, and total offspring sired for males) using Student's *t*-tests for the binary categorization of EP status, and Spearman rank correlations for the continuous EP outcomes, with significance at the $\alpha = 0.05$ level. We also used Spearman rank correlations to determine the relationship between fecundity and total offspring fledged for females.

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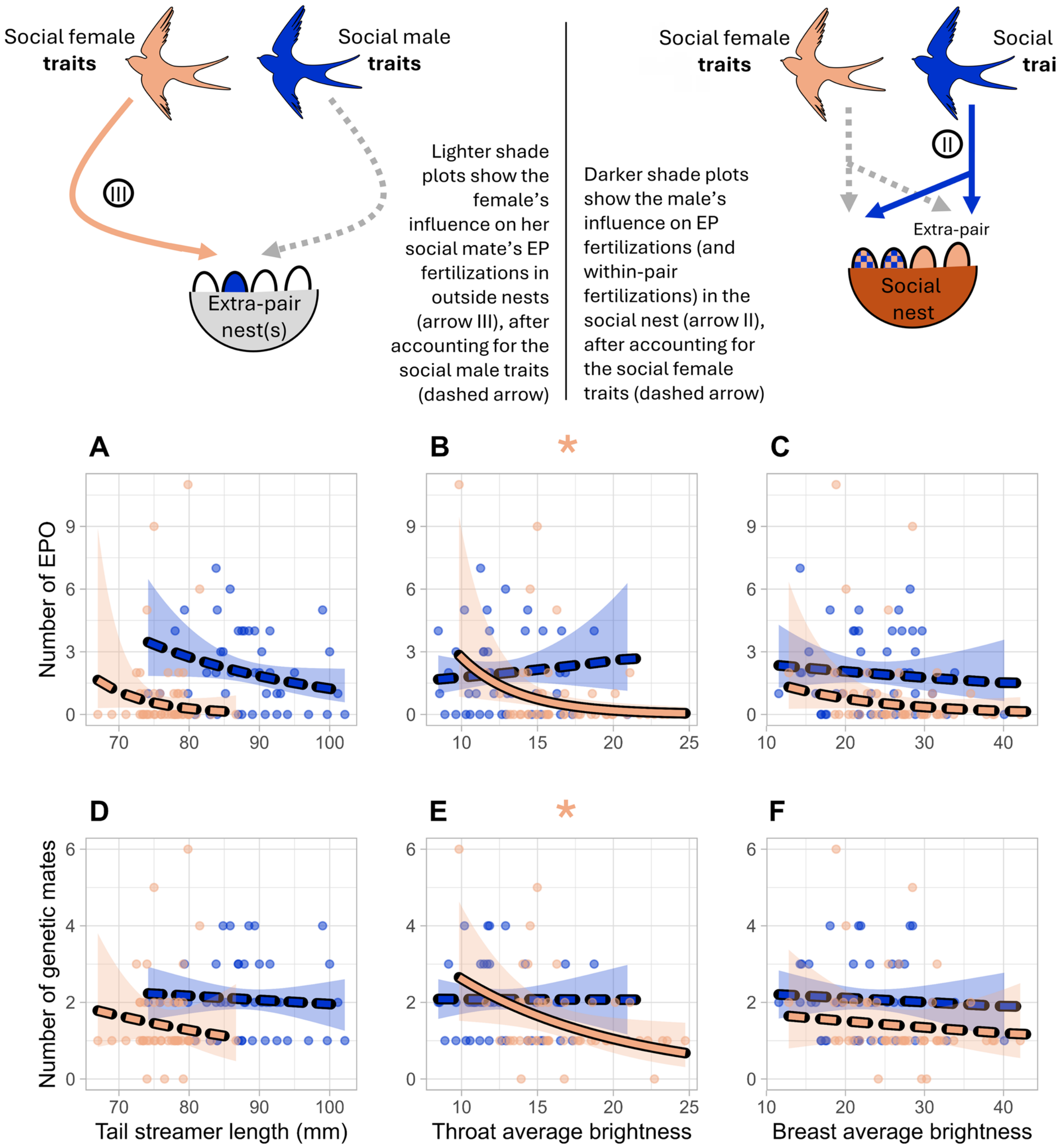

FIGURE 4. Model results for the influence of focal bird traits on EP fertilizations of their social partner for females (lighter shade lines and points) and males (darker shade lines and points). Response variables for females are EP fertilizations by her social male. Response variables for males are EP fertilizations in his social nest. Each row shows results from a different model, and female and male outcomes were modeled separately. Axes labels have sex-specific interpretations. For females, number of EPO (extra-pair offspring) refers to the total number of offspring that were sired in outside nests by her social male (from model B). For males, number of EPO refers to the total number of EPO in the social nest across all clutches (from model A). For females, number of genetic mates is the total number of unique females with which her social male shared fertilizations, including the social female. For males, number of genetic mates is the total number of unique males with which his social female shared fertilizations, including the social male. Traits shown on the x-axes correspond to female values for the lighter shade plots and male values for the darker shade plots. Points show the raw data, lines show model predictions with all other variables set to the mean values, and ribbons show 95% confidence intervals. Statistically significant effects are shown in solid lines and non-significant effects are shown in dashed lines. Stars above the panels also indicate significant results. Panels (**A–C**) show the number of EPO as a count variable from negative binomial models. The social nest EPO model (darker shade plots) included an offset term for the number of offspring that were analyzed for paternity. Panels (**D–F**) show the number of genetic mates (sires or dams) from a linear model for number of sires, and a Poisson model for number of dams. All models include clutch initiation date as a covariate to control for variation in timing of breeding and bird age class. Swallow icon by Agne Alesiute from TheNounProject.com.

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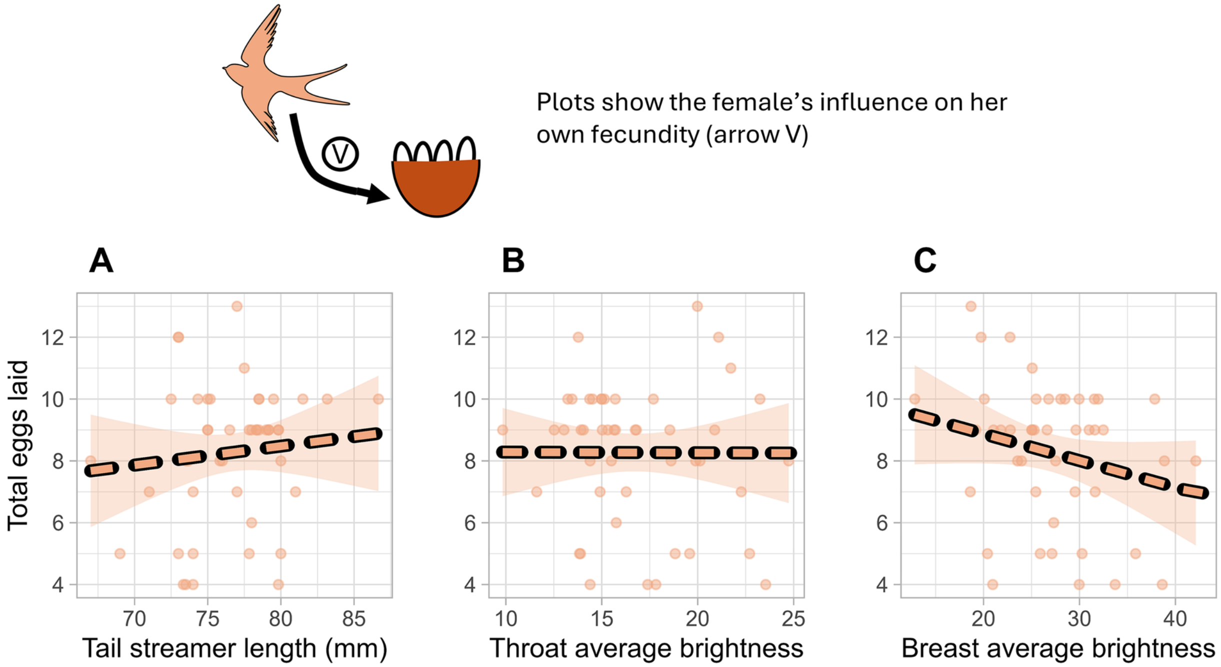

FIGURE 5. Model results for the effect of female traits on fecundity: (**A**) tail streamer length, (**B**) throat color, (**C**) breast color. Fecundity was measured as the total number of eggs laid, and was fit using a linear model. Points show the raw data, lines show model predictions with all other variables set to the mean values, and ribbons show 95% confidence intervals. Clutch initiation date was included as a covariate. Swallow icon by Agne Alesiute from TheNounProject.com.

Finally, we assessed the associations between fecundity and EP fertilizations using Student's t-tests for binary EP status and Spearman rank correlations for the continuous EP outcomes.

Separating timing and age from traits

As in many other migratory birds, there is strong selection for breeding early in *H. r. erythrogaster* (Perrins 1970, Verhulst and Nilsson 2008, Saino et al. 2012). The previously documented correlation between plumage color and reproductive success in female *H. r. erythrogaster* may be driven by timing of breeding (Safran and McGraw 2004). Here, we wanted to assess the potential effect of plumage traits while statistically accounting for timing of egg-laying. Thus, we included first clutch initiation date as a covariate in all models. This approach more clearly provides information about how birds may be using plumage signals to inform reproductive decisions once already on the breeding grounds. It allows us to assess whether plumage traits of potential partners are informative in and of themselves, separate from the simple presence of an individual at the breeding site by a certain time. Furthermore, including clutch initiation date in the models helps account for variation in age class. We were not able to directly control for age because exact ages were unknown for one-third of sampled birds, and these birds primarily occurred at the largest breeding site. However, for plumage traits of the known-age birds (64 known-age birds out of 96 total sampled), only female tail length significantly differed by age class (t-test of second year [SY] vs. after second year [ASY]: $t = -2.21$, $\mathrm{df} = 29.9$, $n = 32$, $P\text{-value} = 0.035$; see methods section in Supplementary Material for other trait t-tests). Additionally, for the known-age birds in our sample and in other studies (Møller and De Lope 1999, Lifjeld et al. 2011), age class was significantly correlated with first clutch initiation date for both females (t-test: $t = 3.67$, $\mathrm{df} = 28.4$, $n = 32$, $P < 0.001$; ASY females started breeding an average of 13 days earlier than SY females) and males (t-test: $t = 4.10$, $\mathrm{df} = 23.5$, $n = 32$, $P < 0.001$; ASY males started breeding an average of 15 days before SY males). Including clutch initiation date in our statistical models thus helps control for both seasonal and age-related variation.

Details of models for female and male EP fertilizations and female fecundity (Questions 2–4)

See Figure 1 for general model structures and Table 1 for how the models were used to answer each research question. We modeled the 2 continuous EP outcomes that were positively associated with annual reproductive success for both females and males. In this study, those EP outcomes were count of EP offspring and number of genetic mates. While these 2 outcome variables are strongly correlated with each other (for females, Spearman $\rho = 0.74$, $P < 0.001$; for males Spearman $\rho = 0.92$, $P < 0.001$), we model both because the count of EP offspring is relevant for understanding the allocation of within-pair vs. EP fertilizations, and the number of genetic mates is relevant for understanding sexual selection in the context of Bateman gradients (Bateman 1948, Tang-Martínez 2016, Lehtonen 2022). Because we were interested in comparing the association strengths of bird traits with different EP outcomes, rather than optimizing the fit of each model, we kept the model structures the same for all EP outcome variables. For each model, we included focal bird tail streamer length, throat average brightness, and breast average brightness, plus the social mate tail streamer length, throat average brightness and breast average brightness (see the results section in Supplementary Material for details about selecting predictor variables). For the female and male number of EP offspring, we fit negative binomial models because these count variables were over dispersed, and we included a log offset term for the total number of offspring

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that were analyzed for paternity for the female models because females are constrained by clutch size while males are not. For the number of genetic sires, we fit linear models, and for the number of genetic dams, we fit Poisson models because this distribution was more skewed than number of sires. All explanatory variables were *z*-scored for model fitting, and model effects reported throughout the results correspond to an increase in each EP measure for each 1 SD increase in the indicated trait. For the model predicting female fecundity, we fit a linear model and included the focal female tail streamer length, throat brightness, and breast brightness along with clutch initiation date as predictors. We conducted additional data exploration and determined that it was not necessary to include sampling site or breeding group size in our final models (Supplementary Material). All analyses were conducted in the statistical software R and R Studio, version 4.4.1 (R Core Team 2024). Figures were created in R and edited for clarity in Microsoft PowerPoint.

RESULTS

Summary of Plumage Trait Distributions and EP Fertilizations

After filtering to exclude individuals who switched social mates during the breeding season (*n* = 3 adults), we had full breeding and paternity data from 47 females and 48 males. The sample sizes, means, and standard deviations of the outcome and predictor variables are reported in Table 2. Of 320 offspring that were sampled for paternity, 67% were within-pair 21% were EP where the sire was a known male identified in our sample of possible sires, and 12% were EP where none of the sampled males were identified as the sire and thus the sire identity was unknown.

Correlation between Annual Reproductive Success and EP Fertilizations (Question 1)

We found that EP status, number of EP offspring, and total genetic mates were positively correlated with annual reproductive success for both sexes, whereas the proportion of EP offspring was only positively related to reproductive success for males (Figure 2). Female fecundity was also positively correlated with annual reproductive success (Spearman ρ = 0.47, *P* = 0.004), but was not correlated with any of the measures of EP mating (Supplementary Material Table 4). These results confirm that both female fecundity, and EP fertilizations for both males and females, contribute to their overall fitness. Thus, the behaviors associated with EP fertilizations are highly relevant for seasonal reproductive success in males and females.

Associations of Female and Male Plumage Traits with Their Own EP Fertilizations (Question 2)

For a female's number of EP offspring, none of the female traits were significant predictors (Figure 3A–C, Supplementary Material Table 5). For a female's total number of sires, females with longer tails (β = 0.4, 95% CI: 0.13, 0.68 per 1 SD increase in tail length) tended to have a higher number of total sires (Figure 3D, Supplementary Material Table 5). None of a male's own plumage traits were significant predictors of either metric of EP fertilizations in outside nests (Figure 3, Supplementary Material Table 6).

Associations of Female and Male Plumage Traits with EP Fertilizations by Their Social Partner (Question 3)

Female throat color was associated with EP fertilizations by her social partner. For the models of male EP fertilizations, males that were paired to females with darker (lower brightness value) throats had higher metrics of EP fertilizations across both models (number of EP offspring rate ratio = 0.41, 95% CI: 0.2, 0.75; number of dams rate ratio = 0.73, 95% CI: 0.55, 0.96; Figure 4 center column, Supplementary Material Table 6). None of the male traits were associated with EP fertilizations by his social partner in the social nest (Figure 4, Supplementary Material Table 5).

Association of Female Plumage Traits with Fecundity (Question 4)

None of the focal female traits were significant predictors of her fecundity (Figure 5, Supplementary Material Table 7).

DISCUSSION

Sexual Selection Can Act on Female Plumage Traits through EP Fertilizations

We provide evidence that sexual selection can operate on female plumage through EP mating, in addition to more widely acknowledged sexual processes such as social pairing and selection for fecundity (Amundsen et al. 1997, Siefferman and Hill 2005). Here, we established 2 of the key prerequisites for this type of selection to be possible: (1) measures of EP fertilizations are associated with female annual fledging success, and (2) female plumage is associated with EP fertilizations. Importantly, it appears that associations between female traits and EP fertilizations were not driven by differences in timing of breeding (which was statistically controlled for in all models) or fecundity. We did not find any significant associations between female traits and fecundity in our populations, nor were EP fertilization metrics correlated with fecundity. Thus, variation in female *H. r. erythrogaster* traits could be shaped directly by EP mating behavior. Overall, equivalent plumage traits of females and males did not equally predict equivalent EP outcomes for each sex. Female plumage traits significantly predicted EP outcomes both of the female herself and of her social male, while male traits were not significant predictors of his own EP outcomes nor those of his social female.

Female Traits Significantly Predict Her EP Fertilizations in the Social Nest

We found that a female's traits were associated with her number of genetic mates, even after accounting for traits of her social partner. This suggests that patterns of female EP outcomes were not driven only by differences in male quality. Females with longer tails tended to mate with a higher number of genetic sires. This pattern was also present for the number of EP offspring for females, although the effect was not significant. While there is no evidence that longer tail streamers correlate with higher reproductive success in female North American *H. rustica* (Safran and McGraw 2004), tail streamer length is positively correlated with wing length (Wilkins et al. 2015 and in the current study: Pearson's correlation = 0.462, *t* = 3.50, df = 45, *P*-value = 0.001). Females with longer tail streamers may have a larger overall body size and therefore

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have more physical control over their own paternity outcomes. Larger females may be better at avoiding mate guarding from their social partner, or more capable of pursuing and attracting fertilizations from EP males. Similar patterns in which larger females have greater EP fertilizations have been found in other species (Costanzo et al. 2017, Plaza et al. 2019a, Roeder et al. 2019, Benítez Saldívar et al. 2022). We cannot disentangle the effects of age vs. tail length in the current study, but tail length may be a cue used by males to assess female age. For the subset of known-age females in our sample, ASY birds had longer tails than SY birds. In a study that examined *H. r. erythrogaster* across 3–4 age classes, female tail length tended to increase with age class across both years sampled, and wing length increased with age class in one of the 2 years (Lifjeld et al. 2022). If longer-tailed females are older, their additional breeding experience may allow them to have more control over EP copulations and pursue fertilizations with a greater number of sires.

Additionally, males may prefer females with longer tail streamers (perhaps because they are older) and thus pursue EP copulations with these females more often than shorter-tailed females. While *H. r. erythrogaster* do show mutual mate choice and assortativity by plumage color (Safran and McGraw 2004, Morosse et al. 2025), there is not currently evidence to support assortativity by wing length or tail length, especially for EP partners (Morosse et al. 2025). It has been shown in male songbirds that traits associated with social pairing and within-pair fertilizations may differ from those preferred for EP mating (Yezerinac and Weatherhead 1997, Delhey et al. 2003, Taff et al. 2012, Grunst and Grunst 2014), and more research is needed to understand whether the association we found between multiple mating and female tail length could be driven by male preferences. Levin et al. (2018) used radio proximity tags to track social interactions before and after experimental manipulation of male plumage color. A similar study with experimental manipulation of female tail length could illuminate the causal links between female traits and EP fertilizations.

Female Traits Influence EP Fertilizations of the Social Male

In the current study, we found that the throat color of females helps explain variation in EP fertilizations by the social male. This finding is noteworthy because it is a rarely considered trait signaling pathway (Figure 1, arrow III), yet it explains significant variation in male fertilization success. We did not have *a priori* predictions about this association, and can only speculate about the potential mechanistic drivers. It is possible that females with dark throats tend to pair with high-quality males who are attractive as both social and EP partners. However, we did not find a signal of male traits as being predictive of his own EP success, so it is unclear which aspects of these males signal higher quality. It is also possible that EP females gain some additional information about a male from assessing the social pair composition as a whole. For example, in *Malurus amabilis* (Lovely Fairy-Wren), individual female and male color did not explain EP fertilizations, but there was a significant interaction effect where less colorful males had higher EP fertilizations when paired with more colorful females (Leitão et al. 2021).

An alternative explanation for how female traits may influence EP fertilizations of the social male is through changes in the male's behavior or time budgets. A recent study in *Parus major* (Great Tit) found that when males were socially paired with older females, they were more likely to sire offspring with EP females (Roth et al. 2019). Their findings suggest that older females copulate more frequently with their social males and thus induce a "spillover" of copulation behavior so that those males also show increased fertilizations with EP females. If dark-throated females in our study also copulate more with their social partners, the higher EP outcomes of these males could be explained by copulation behavior spillover. Future research could explore the possibility of copulation behavior spillover in addition to other potential explanations such as differences in male time budgets when paired to females with pale or dark throats.

Trait Associations with EP Fertilizations Differ for Females and Males

Unlike for females, the traits of focal males did not predict his EP fertilization success. This result matches with a previous study of *H. r. erythrogaster* in which neither male tail length nor color significantly explained the probability of siring EP offspring and the number of EP offspring sired (Eikenaar et al. 2011). The contrasting associations between traits and EP outcomes for females and males in our study highlights the different reproductive behaviors at play across the sexes. We may find traits in females that are informative of 2 distinct behaviors, her ability to both gain and repel EP copulations. Thus, it may be more likely for associations to exist between female plumage and EP outcomes across a range of social and environmental conditions where at least one of these behaviors can be expressed. In males we only expect traits to be informative about a single behavior, his ability to gain EP copulations. Associations between male traits and EP outcomes could be more sensitive to spatial and temporal variation in factors like breeding synchrony or relative attractiveness compared to neighboring males. We could therefore fail to find associations in a particular population or year for males, despite the fact that certain phenotypes may be favored under some breeding conditions. Because the majority of EP studies focus on male traits and assume a single behavioral mechanism, little work has been done so far to distinguish between the plural behavioral mechanisms which operate for females.

Interestingly, focal male traits did not predict variation in EP fertilizations by his social female for the metrics that we analyzed. While previous studies found that darker male plumage was associated with a lower proportion of EP offspring in the social nest (Safran and McGraw 2004, Safran et al. 2016), we did not find similar patterns when we modeled a female's count of EP offspring and number of genetic sires. This result may be partly due to interannual variation, and the fact that female choice may be variable across time, in both adaptive and non-adaptive ways (Chaine and Lyon 2008, DuVal et al. 2023). Furthermore, the generalizability of our findings is limited because we were only able to extensively sample paternity for a single breeding season. In another well-studied songbird species, *Cyanistes caeruleus* (Blue Tit), reviews and meta-analyses show that associations between plumage and individual quality or mate preferences are variable across studies—possibly due to spatiotemporal variation in environmental conditions or small sample sizes—and average effect sizes are near zero (Parker 2013, Doutrelant et al. 2020).

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Experimental manipulations of both female and male plumage traits, in addition to paternity analyses across multiple years and environmental conditions are needed to understand the consistency of the findings reported here.

Conclusions

Additional research is needed to understand how EP mating may contribute to selection on female plumage traits by using data across multiple breeding seasons and generations, and fitting models that partition the influence of within-pair and EP offspring on total reproductive success (Henshaw et al. 2018). Our detailed sampling from a single breeding season revealed intriguing associations between EP outcomes and plumage which in some cases differ from previous results, suggesting that selection may act differently on phenotype across years. As associations found here between female traits and EP outcomes, and between EP outcomes and female fitness, are not present in all species and populations (for associations between multiple mating and female fitness see Table 2 in both Arnqvist and Kirkpatrick 2005 and Doutrelant et al. 2020), an important direction for further research will be to collect this information across a broader sample of species and investigate why the relationships exist in some populations but not others. Such studies will provide a stronger foundation upon which to develop theories about how the costs and benefits of EP mating should translate to female plumage evolution.

Our results highlight the importance of considering female trait variation, in addition to variation among male traits, to understand variation in EP paternity and the evolution of plumage. By exploring the correlations between female plumage traits and measures of EP mating, we have shown that EP reproductive processes likely are relevant for understanding variation in female phenotype in *H. r. erythrogaster*, but may operate differently in females than males. More work is needed to disentangle the plural mechanisms of female solicitation and avoidance of EP copulations, and how these behaviors are associated with female plumage traits and reproductive success across different species and populations. While sexual selection may not act as strongly on females in general (Hare and Simmons 2019), this does not mean it should be ignored or untested. Exploring the influence of EP mating from the perspective of both sexes is critical to our understanding of how female traits evolve.

Supplementary material

Supplementary material is available at *Ornithology* online.

Acknowledgments

We are grateful to the 2022 field assistants who collected data for this study: Avani Fachon, Natalie Cloutier-Chaine, Aleea Pardue, Isabelle Meredith, and Sara Garica. Avani Fachon and Toni Schuerg assisted with lab work. 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. 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 appreciate input from the Associate Editor and 2 anonymous reviewers which greatly improved the manuscript.

Ethics statement

All animal handling, marking, and sample collection for this study were 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.

Funding statement

Funding support for this article was provided by the Ecology and Evolutionary Biology Department at the University of Colorado Boulder, University of Colorado Boulder Graduate School, Wilson Ornithological Society, Society of Systematic Biologists, National Science Foundation (IOS 1856266 to RJS, DGE 1650115 to HKD, DBI-1906188 to DRS, IOS-DEB-1856266 to DRS, IOS 1856229 to KPK, IOS 1856254 to IIL).

Conflict of interest statement

The authors have no conflicts of interest.

Author contributions

H.K.D. and R.J.S. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). H.K.D. and R.J.S. performed the experiments (collected data, conducted the research). H.K.D., R.J.S., Z.L., D.R.S., I.I.L., and K.P.K. wrote the paper (or substantially edited the paper). R.J.S., H.K.D., and D.R.S. developed or designed methods. H.K.D., D.R.S., and K.P.K. analyzed the data. R.J.S., I.I.L., and K.P.K. contributed substantial materials, resources, or funding.

Data availability

Analyses reported in this article can be reproduced using the data and code provided by Kenny-Duddela et al. (2026). Raw genomics data are available on the NCBI Sequence Read Archive accession PRJNA323498.

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