Behavioral Ecology, 2025, Vol. 36, No. 4, araf060
https://doi.org/10.1093/beheco/araf060
Advance access publication 28 May 2025
Original Article

North American barn swallows pair, mate, and interact assortatively

Omar J. Morosse[1], Toshi Tsunekage[1], Heather V. Kenny-Duddela[2], Drew R. Schield[3], Kayleigh P. Keller[4], Rebecca J. Safran[2], Iris I. Levin[1,*]

[1]Department of Biology, Kenyon College, Gambier OH, United States
[2]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder CO, United States
[3]Department of Biology, University of Virginia, Charlottesville VA, United States
[4]Department of Statistics, Colorado State University, Fort Collins CO, United States

[*]Corresponding author: Iris I. Levin, Kenyon College, Department of Biology, 202 N College Rd, Gambier, OH 43022. United States. Email: levin1@kenyon.edu
Handling Editor: Mark Briffa

While female mate choice is well established, mutual choice may play a larger role in mate selection than currently recognized. Assortative mating is a common form of nonrandom mating in animals that can result from mutual choice. However, few studies address assortative patterns beyond the social pair, potentially overlooking assortativity in the mating pair and in the social environment that shapes reproductive decisions. We asked whether North American barn swallows (*Hirundo rustica erythrogaster)* breeding in a large colony form pairs, mate (through both within-pair and extra-pair fertilizations), and interact assortatively by ventral plumage color, wing length, and age. Social interactions were tracked using proximity loggers, which recorded close contact between tagged individuals when birds were mating and laying eggs. Barn swallows paired and mated assortatively by their ventral plumage color; however, the assortative patterns in mating pairs were not as strong as they were in social pairs. Barn swallows also interacted assortatively, associating more often with individuals of both sexes who had similar phenotypes relative to the other birds in the colony. Finally, older males and females with darker ventral plumage achieved the highest reproductive success. Investigation of assortative behavior beyond the level of the social pair provides a more complete understanding of mate choice and suggests a mechanism that may maintain the large variation in ventral plumage color in North American barn swallows.

Keywords: Assortative mating; social pair; extra-pair mating; social network assortativity; plumage color; barn swallow.

Introduction

Female or male mate preferences result in nonrandom mating and cause observed mating patterns to deviate from expected random frequencies of both genotypes and phenotypes within a population (Templeton 2006; Rosenthal 2017). Females can exhibit a uniform preference for the same male phenotype, often because they are thought to provide indirect benefits, ie. "good genes" such as those that confer resistance to pathogens (Fisher 1915; Zahavi 1975; Hamilton and Zuk 1982; Balenger and Zuk 2014; Nolazco et al. 2022). However, male choice based on female phenotype may arise when species exhibit "reversed" sex roles or biparental care (Edward and Chapman 2011). Mutual mate choice is also possible and can result in assortative mating, a pattern where individuals select mates similar to themselves. Assortative mating may be critical for maintaining variation within populations and for behavioral reproductive isolation in divergent populations (Jiang et al. 2013; Vitousek et al. 2013).

Assortative mating is a positive phenotypic correlation among mating individuals in a population, where individuals select one another based on their similarity in morphological, behavioral, or life history traits. Disassortative mating occurs when individuals select each other based on their dissimilarity in a given trait, but this phenomenon is rarely found in animals (Jiang et al. 2013). Assortative mating is well-established in many taxa including fishes (Fernö and Sjölander 1976; Barlow et al. 1977), humans (Versluys et al. 2021), and especially in birds (Jawor et al. 2003; Bitton et al. 2008; Jacobs et al. 2015; Wang et al. 2019). However, the high frequency of assortative mating reported in birds could be at least partly due to publication bias (Wang et al. 2019).

Typically, assortative mating is used to describe when similar individuals form social pairs, but this fails to distinguish social pairs from other pairs that produce offspring (ie. mating pairs), such as in socially monogamous but genetically polygamous species. Throughout this paper, we refer to social pairs as individuals that form a pair bond at the beginning of the breeding season and care for offspring together, while mating pairs are individuals that copulate and produce offspring (these pairs can, but do not necessarily include social pairs). Here we specifically refer to any positive correlation between traits as assortativity, negative correlations as disassortativity, and assortative pairing and mating as distinct reproductive decisions.

It is important to note that assortativity by mutual choice is conceptually distinct from other nonrandom mating patterns such as inbreeding and outbreeding. Assortativity modulates the genotype frequency at a subset of loci associated with the trait in question, while inbreeding and outbreeding do so at all loci. Assortative patterns due to inbreeding are unlikely to occur in species like barn swallows with long-distance natal dispersal.

Received: 9 August 2024; **Revised:** 17 April 2025; **Editorial decision:** 12 May 2025; **Accepted:** 22 May 2025.

However, as with inbreeding and outbreeding, assortativity can shape population genetic structure and is a necessary component of complete speciation because it can generate linkage disequilibrium between preferences and traits at a multi-locus level (Templeton 2006).

Assortativity occurs within a social environment that can be characterized by a social network. This social network fundamentally limits the pool of conspecifics within a population that an individual may affiliate, pair, and mate with (McDonald et al. 2013; Vitousek et al. 2014; Krause 2015). Individuals may modify their social environment by differentially interacting with conspecifics (Noë et al. 2001; Oh and Badyaev 2010); for example, individuals may prefer certain individuals or be limited in their ability to establish and maintain social connections (Shizuka and Farine 2016; Beck et al. 2023). An individual's level of social interactivity can be characterized as a behavioral syndrome (Montiglio et al. 2017; Munson et al. 2020) and thus a potentially informative aspect of the phenotype. Animal-borne sensor technology and the application of social network analysis to behavioral studies provides increasingly granular insight into social interactivity as part of the phenotype, and expands inquiry into how social interactions might shape assortative pairing and mating (Pinter-Wollman et al. 2014; Shizuka and Farine 2016; Ripperger et al. 2020).

Assortativity within the social pair is well documented across several taxa, especially birds. Individuals often pair with conspecifics that are of the same age, condition, size, or that share similar behavioral characteristics or signal traits that indicate individual quality (Jiang et al. 2013). A recent meta-analysis reports that the most frequently found and strongest assortative pattern is assortativity by age, followed by physiology (eg. oxidative damage), behavior (eg. arrival date), and plumage characteristics (Wang et al. 2019). However, socially monogamous but genetically polygamous birds might mate assortatively regardless of any assortative patterns among social pairs. Since many passerines mate outside the social pair bond (Griffith et al. 2002; Brouwer and Griffith 2019), assortativity within mating pairs might disproportionately occur in species where mate search costs are low and extra-pair copulations generate a substantial proportion of offspring (Moller 1992; Brouwer and Griffith 2019; Leitão et al. 2021), such as in socially breeding birds. However, few studies have explored assortativity in birds beyond social pair formation, so whether assortative patterns are consistent for social and mating pairs remains unclear yet has important consequences for understanding sexual selection and phenotypic variation within a population. In the few studies that have examined assortativity in social pairs and extra-pair mates, none have found assortativity between extra-pair mates despite social pair assortativity (Jacobs et al. 2015; Leitão et al. 2021).

Here, we analyze assortative patterns both within and beyond the social pair, including any patterns within mating pairs that generate offspring, and in social interactions that shape the context where pairing and mating occur. Extending the inquiry of assortativity to social interactions and mating provides additional insight into the process of mate selection and the consequences of those decisions in terms of sexual selection and the maintenance of phenotypic variation within a population.

We studied assortative social interaction, pairing, and mating in a population of the North American barn swallow (*Hirundo rustica erythrogaster*), gregarious songbirds that breed in dense colonies in the barns that they typically inhabit (Safran and Levin 2019). Since barn swallows possess a moderately heritable and continuous signal trait in their ventral plumage color (Safran et al. 2005; Saino et al. 2013; Hubbard et al. 2015), they are a useful system to better understand whether and how assortative behaviors maintain phenotypic variation within a population given the evidence for directional selection on ventral plumage color. Female barn swallows preferentially allocate within-pair paternity to males with darker ventral plumage (Safran et al. 2005, 2016; Eikenaar et al. 2011), so there should be directional selection for darker phenotypes. However, North American barn swallows of both sexes exhibit large amounts of variation in their ventral plumage color (Hubbard et al. 2015; Brown and Brown 2020), which could result from non-genetic sources (eg. the developmental environment). Additionally, the maintenance of variation in ventral plumage could result from assortativity; paler individuals may show an assortative preference or be unable to mate with individuals with preferred darker ventral plumage and are therefore relegated to mate with other pale individuals.

Because assortative preferences in the social environment may shape pairing and mating decisions (Kopp et al. 2018), we predicted that barn swallows would pair, mate, and interact assortatively by a well-established social and sexual signal (ventral plumage color) and any of its potential correlates (eg. age). We also predicted that barn swallows would pair and mate assortatively by level of social interaction, and interact dissassortatively by sex. Finally, to better understand how assortativity may help maintain plumage color in this system despite a preferred phenotype, we tested the relationship between ventral plumage color and reproductive success to confirm the established role of directional selection on this plumage trait (Safran et al. 2005, 2016). Here, we predicted that barn swallows of both sexes with darker ventral plumage color would achieve higher total reproductive success (sum of within-pair and extra-pair offspring) than barn swallows with paler ventral plumage color. All predictions are summarized in Table S1.

Methods

Study system

The North American barn swallow (*Hirundo rustica erythrogaster*) is a migratory songbird that inhabits much of North America during its breeding season and overwinters in South America (Safran and Levin 2019). They breed as solitary pairs or in colonies of 2 to 200 pairs, and typically settle in barns, bridges, doorways, or culverts where they build mud cup nests to raise offspring (Safran and Levin 2019; Brown and Brown 2020). Barn swallows show strong breeding site fidelity, which may constrain the pool of available mates. Males typically have darker ventral plumage, longer tail streamers, and weigh less than females. Ventral plumage color tends to darken and tail streamers tend to lengthen as birds age in both sexes (Levin unpubl. data; Bradley et al. 2014). However, these two traits are not always correlated, in that individuals with the darkest ventral plumage do not necessarily possess the longest tail streamers. Furthermore, first-year breeders possess the full range of ventral plumage color in both sexes (Levin unpubl. data). Female North American barn swallows preferentially allocate within-pair paternity to males with darker ventral plumage color, and females with darker ventral plumage tend to have higher annual reproductive success (Safran and McGraw 2004; Safran et al. 2005, 2016; Eikenaar et al. 2011). Detailed characterization of the social network also reveals that darker males interact the most with females (Levin et al. 2016). In the European subspecies, older males arrive to the breeding ground significantly earlier than younger males, and females of all ages (Møller and DE Lope 1999). However, such protandry was not evident in one large North American colony with precise arrival timing information across two years; older individuals of both sexes instead arrive before younger individuals (Levin unpubl. data).

Field methods

Data were collected in 2022 from one large breeding colony (n = 58 individuals) in Knox County, Ohio (40.4575° N, -82.6372° W). Adult birds (54 of the 58) were captured using mist nets placed over barn entrances and windows, and individuals were marked with an aluminum USGS band on one leg and a unique-to-site color band combination on the other. We measured wing length and determined sex by the presence of a brood patch (female) and/or other sexual dimorphisms: plumage color and tail streamer length (male barn swallows will typically have longer tail streamers and darker ventral feathers than females). We collected approximately 20 µL of blood from the brachial vein with a heparinized capillary tube for paternity analyses, and plucked feathers (at least 20 per patch) from the throat, breast, belly and vent for plumage color (brightness) analyses. Additionally, we checked each nest (28 first broods, 19 second broods) every 2-3 d to record active nests and monitor egg laying, hatching, and fledging. Finally, we collected blood from 12-d old nestlings to assign paternity. Sixty-eight percent of pairs raised two broods of offspring; pairs that raised only one initiated clutches up to five weeks later than birds that double-brooded. All animal handling was done with IACUC approval from Kenyon College.

Age determination and pair identification

To test whether barn swallows mate assortatively by age, we determined individual age under the well-supported assumption that adult barn swallows exhibit high breeding site fidelity (Shields 1984). Therefore, we classified unbanded birds as second year (SY) and banded birds as after second year (ASY). Because the colony was fully banded in prior years, we are confident in our age categorization. Social pairs were identified by their unique color band combinations during nestling feeding, using a hunting blind (Ameristep Outhouse Mossy Oak Camouflage Outhouse Hunting Blind, Clio, MI) set 5-8m from the nest.

Plumage color analysis

We stored ventral feathers from each individual in envelopes until analysis. At least 15 of these feathers from each patch (throat, breast, belly, vent) were stacked and taped onto a white index card to closely resemble their orientation and appearance on the bird (Safran and McGraw 2004). To assess the average brightness (an achromatic measure calculated as the area under the reflectance curve between 300 and 700 nm) of each individual, we used an OceanOptics Flame UV/Vis spectrometer with a PX-2 pulsed xenon light source (Dunedin, FL). These data were generated relative to a white standard (OceanOptics WS-1) and a dark standard (no light) using Oceanview 2.0 (OceanOptics, Dunedin, FL, USA). We measured each patch three times, the mean of which we used to generate brightness values for data analysis with the R package Pavo (Maia et al. 2019). Brightness values of the two largest sampled regions of the barn swallow ventral surface (breast, belly) consistently explain variation in social behavior, aspects of physiology, and fitness (Safran et al. 2005; 2009, 2016; Vitousek et al. 2014; Levin et al. 2016, 2018).

Social network data

To analyze social interactions, we equipped birds with miniaturized proximity loggers (Dulog, Nuremberg, Germany) when the majority of females were preparing nests for laying eggs or in the process of laying (36% of females were fertile during the tag deployment, 27% had recently finished laying, and 36% were not yet fertile, calculated using the synchrony index from Kempenaers (1993). These proximity loggers were developed based on BATS proximity loggers (Duda et al. 2018) and additional technical details of the proximity loggers can be found in the supplemental methods. The loggers collected data for three days, sampling for the presence of nearby (<2m) tags every 4 s from 06:00 to 21:00. All active nests were >2m apart except two, which were on opposite sides of at least one rafter and/or light strip, which impedes the radio signal at these larger (1.5-2m) proximities. Unlike other social network studies of wild birds which only capture interactions at fixed locations such as feeders or nest boxes, the proximity loggers used here record interactions everywhere. From these dyadic tag detections, we used a rule set to assemble the logs into continuous interactions, where the absence of interaction between tags for > 8 s indicated a new interaction. For our social interactivity analyses, we compared birds' overall tendency to be social using a network centrality metric, node strength. Node strength was calculated either as the total number of interactions or the summed duration of interactions, excluding interactions with social mates. Interactions between pair-bonded individuals were excluded from these calculations as these interaction counts would be redundant for both members of a social pair and could artificially drive patterns of assortativity. On average, interactions between social mates account for 20 ± 12% of total social interactions for females and 18 ± 13% for males. We used these measures of social interactivity to ask whether birds paired or mated assortatively with respect to their level of social interaction with other birds outside of the social pair.

To ask whether birds interacted assortatively based on aspects of their phenotype, we calculated network assortativity (Farine 2014). This analysis was not restricted to social or mating pairs; instead, we asked whether birds were more likely to interact socially with individuals who had similar phenotypes. We calculated network assortativity using the R package assortnet, which allows for analysis of weighted networks like ours (Farine 2014). Network assortativity analyses produce assortativity coefficients (Newman 2003) between negative one and positive one, where a positive value corresponds to assortativity by the phenotypic trait in question and a negative value indicates disassortativity. We examined network assortativity on both a complete social network that included all interactions between individuals of the same sex (intrasexual) and individuals of different sexes (intersexual), as well as on a bipartite network containing only social interactions between males and females (hereafter, intersexual interactions).

Paternity analysis

We used a Qiagen DNEasy Blood and Tissue kit (Qiagen, Germantown, MD, USA) to extract DNA from the blood of all nestlings and adults from the colony where we deployed proximity loggers. We quantified DNA purity and concentration using an BioTek Epoch 2 microplate reader and a Take3 microplate (Agilent, Santa Clara, CA, USA). Whole genome sequencing libraries were prepared by Novogene and sequenced at 2x coverage using 150bp paired-end reads on an Illumina NovaSeq 6000. Sequences were trimmed and quality filtered using Trimmomatic v0.39 (Bolger et al. 2014) and mapped to the barn swallow reference genome assembly version bHirRus1 (Secomandi et al. 2023) using BWA mem v0.7.17 (Li and Durbin 2009). We produced a set of target SNPs for downstream recalculation of genotype likelihoods by first calling genomic variants using GATK (McKenna et al. 2010; Van der Auwera et al. 2013), using HaplotypeCaller to call individual variants, specifying the "--ERC GVCF" option, followed by GenotypeGVCFs to call variant sites across the cohort of samples, specifying "-stand_call_conf 15." We removed indels and any SNPs within annotated repetitive regions and on the sex chromosomes from downstream analysis using bcftools v.1.10.2 (Li et al. 2009). Finally, we filtered to retain SNPs with minor allele frequencies > 0.05 that were at least 10kb apart to prune for linkage disequilibrium using (Danecek et al. 2011), yielding 92,438 unlinked SNPs for analysis.

We then estimated pairwise relatedness among individuals using lcMLkin (Lipatov et al. 2015). We used the companion script SNPbam2vcf.py to recalculate raw genotype likelihoods for the set of target SNPs described above, then ran lcMLkin on the genotype likelihoods to estimate pairwise coefficients of relatedness (r), specifying "-g all" to sum over all possible genotypes weighted by genotype likelihoods to account for genotype uncertainty. Pairwise relatedness values were then used to identify genetic dams and sires of 155 offspring with 24 females and 24 males as possible parents. lcMLkin does not use any prior information about known parental identities, and genetic dams were successfully assigned for all but one of the sampled nests (two broods, the female was never caught and sampled). In all cases where genetic dams were assigned, the identities matched with the expected maternal identity from behavioral observations at the nest. Thus, we were confident that the relatedness values could be used to accurately assign genetic sires which cannot be confirmed through behavioral observations alone. We used the minimum observed relatedness value (range: 0.372-0.43) among the confirmed mother-offspring pairs as the cutoff value for assigning genetic sires. Males were assigned as sires to offspring when the male-offspring pair relatedness was at or above 0.372. There were no cases where more than one male met this criteria for each offspring. From these paternity results, we identified mating pairs as any male-female pairing that produced at least one offspring. We find no evidence for inbreeding in this population; the average estimated relatedness among adults was 0.009 (range: 0.002 to 0.042).

Statistical analysis

To assess assortativity in social pairs, we calculated Pearson's correlation coefficients (denoted as $r_{pearson}$) for social pairs of birds to compare wing and tail streamer length, throat, breast, belly and vent brightness, as well as social interactivity. Correlation is the most commonly used approach to investigate assortative mating in behavioral studies of animals (Jiang et al. 2013; Wang et al. 2019). A higher positive correlation (closer to 1) indicates stronger assortativity. We report 95% confidence intervals (CIs) and p-values for each Pearson correlation coefficient. The Pearson's correlation is appropriate here (as opposed to the other correlation coefficients used below) because each individual only had a single social partner over the course of the 2022 breeding season. For mating pairs, we calculated correlation coefficients (denoted as r_{mating}) and p-values using a permutation test that accounted for the repeated observations on the same individuals, because males and females will often mate with more than one individual. There is no straightforward way to generate confidence intervals for our analyses that use permutation tests. The ages of social and mating pairs were compared to expected random pairing (using the observed sex/age combinations) in a Chi-square analysis. To assess whether birds interacted assortatively in the social network, we calculated a network assortativity coefficient (denoted as $r_{network}$) and compared the observed network assortativity to a random distribution of permuted assortativity values for the phenotypic trait in question, reporting a permutation-based *P*-value, and jacknife-based standard error (Newman 2003; Farine 2014). We permuted the node attributes (eg. belly brightness) while maintaining the original edge structure of the network (Farine 2014). We modeled reproductive success for each sex separately. Since older individuals can have darker ventral plumage color, we considered age category (SY, ASY) in models of reproductive success for each sex. Additionally, because the timing of breeding can influence the number of broods raised, we investigated the relationship between the first clutch initiation date and total reproductive success (separately for each sex) and clutch initiation date and male or female ventral plumage color.

Results

Males varied more in their breast plumage brightness (coefficient of variation (CV) = 31.8%) than they did in their belly brightness (CV = 25.2%; Figure S1). Additionally, male breast brightness was substantially darker than female breast brightness (t-test; t = 2.748, df = 44.3, p = 0.009), but male belly brightness was not darker than female belly brightness (t-test; t = 1.687, df = 41.1, *P* = 0.099). Females have similar variation in their breast (CV = 30.4%) and belly brightness (CV = 31.5%; Figure S1).

The social network was highly connected (density = 0.95) and consisted of 52,210 interactions between 32 barn swallows (16 males, 16 females) whose proximity loggers worked for three full days. Males tended to have slightly more interactions than females; on average, males logged 3,390 interactions over the three days compared with an average of 3,136 logged by females. Additionally, older (ASY) individuals logged an average of 3,404 interactions compared to the 3,122 average logged by SY individuals.

Barn swallows paired assortatively by breast and belly color, where birds with similar breast ($r_{pearson}$ = 0.55, *P* = 0.007) and belly brightness ($r_{pearson}$ = 0.44, *P* = 0.035) paired with one another (Fig. 1). We did not detect assortative pairing by throat brightness ($r_{pearson}$ = 0.219, *P* = 0.316), vent brightness ($r_{pearson}$ = 0.304, *P* = 0.158), wing length ($r_{pearson}$ = 0.003, *P* = 0.987), nor by their level of social interactivity (number of interactions: $r_{pearson}$ = 0.362, *P* = 0.365, duration: $r_{pearson}$ = 0.507, *P* = 0.164; Table 1) or age (Chi-square; χ^2 = 2.741, df = 3, *P* = 0.433).

Barn swallows mated assortatively by breast color, where birds with similar breast brightness mated with one another (r_{mating} = 0.42, *P* = 0.019; Fig. 2). We did not detect assortative mating by throat brightness (r_{mating} = 0.139, *P* = 0.423), belly brightness (r_{mating} = 0.188, *P* = 0.241), vent brightness (r_{mating} = 0.302, *P* = 0.138), wing length (r_{mating} = 0.005, *P* = 0.973), social interaction (number of interactions: r_{mating} = 0.122, p = 0.640, duration: r = 0.248, *P* = 0.378; Table 1), or age (Chi-square; χ^2 = 1.74, df = 3, *P* = 0.628). Despite the assortative pattern among mating pairs, we did not detect assortativity among extra-pair mates by throat brightness ($r_{pearson}$ = -0.100, *P* = 0.665), breast brightness ($r_{pearson}$ = 0.352, *P* = 0.117), belly brightness ($r_{pearson}$ = 0.051, *P* = 0.826), vent brightness ($r_{pearson}$ = 0.135, *P* = 0.560), wing length ($r_{pearson}$ = 0.109, p = 0.648), or social interaction (number of

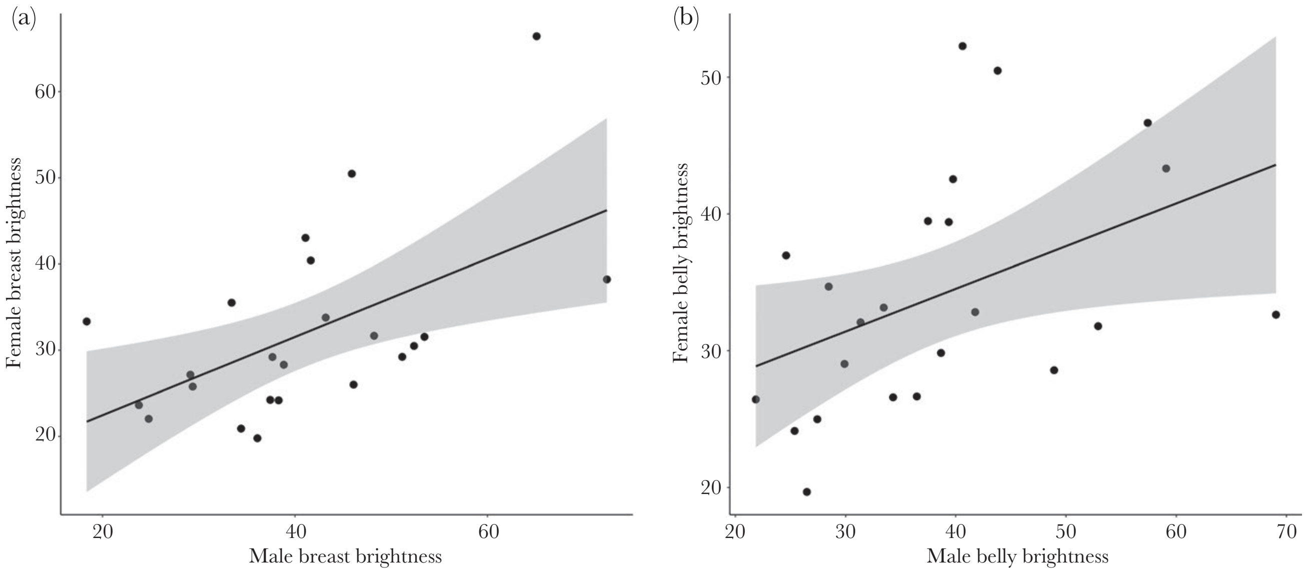

Fig. 1. Barn swallows paired assortatively by ventral plumage color (breast and belly brightness). A. Birds with similar breast ($r = 0.55$, CI: 0.172 – 0.782, $P = 0.007$) and B. belly ($r = 0.44$, CI: 0.036 – 0.722, $P = 0.035$) brightness paired with one another. Darker plumage corresponds to lower brightness values. Pearson's correlation, gray shading shows the 95% confidence interval. n = 23 pairs.

interactions: $r_{\text{pearson}} = -0.591$, $P = 0.217$, duration: $r_{\text{pearson}} = -0.533$, $P = 0.276$; Table 1), indicating that within-pair mating decisions likely drive most of the assortative pattern in the mating pairs.

Barn swallows interacted assortatively by ventral plumage color in the social network that included all intersexual and intrasexual interactions (breast brightness: $r_{\text{network}} = 0.12$, $P = 0.008$, Fig. 3; belly brightness: $r_{\text{network}} = 0.15$, $P = 0.005$; vent brightness: $r_{\text{network}} = 0.07$, $P = 0.035$), as well as age ($r_{\text{network}} = 0.18$, $P = 0.001$), where individuals with similar traits interacted with one another (Table 2). While these coefficients are small, the method of calculating network assortativity on weighted networks like ours is more sensitive and robust compared to assortativity calculated from binary networks (Farine 2014). Birds also interacted disassortatively by sex ($r_{\text{network}} = -0.18$, $P = 0.005$), where individuals interacted most with individuals of the opposite sex (Table 2). We did not detect that barn swallows interacted assortatively by throat brightness ($r_{\text{network}} = 0.042$, $p = 0.077$), or wing length ($r_{\text{network}} = -0.034$, $P = 0.393$; Table 2). When we restricted the network to only intersexual interactions, we found that males and females with similar ventral plumage color (breast brightness: $r_{\text{network}} = 0.188$, $P = 0.014$, belly brightness: $r_{\text{network}} = 0.169$, $P = 0.016$, vent brightness: $r_{\text{network}} = 0.119$, $P = 0.048$) and age ($r_{\text{network}} = 0.229$, $P = 0.001$) interacted assortatively (Table 3). We did not detect that barn swallows in the intersexual network interacted assortatively by throat brightness ($r_{\text{network}} = 0.113$, $P = 0.061$), or wing length ($r_{\text{network}} = 0.007$, $P = 0.686$; Table 3).

When accounting for first-clutch initiation date, females with darker breast plumage produced more offspring than paler females (full model: $R^2 = 0.382$; $\beta_{\text{color}} = -0.080$, CI: -0.144 – -0.016, $P = 0.017$, $\beta_{\text{CI}} = -0.062$, CI: -0.126 – -0.003, $P = 0.060$; Fig. 4a). When accounting for plumage brightness, older males sired more offspring than younger males (full model: $R^2 = 0.293$; $\beta_{\text{Age(SY)}} = -4.404$, CI: -8.671– -0.137, $P = 0.044$, $\beta_{\text{color}} = -0.090$, CI: -0.291 – -0.111, $P = 0.362$; Fig. 4b). The significant effect of age on total male reproductive success was due to differences in the number of extra-pair offspring since only one SY male sired any extra-pair offspring (t-test; $t = 2.960$, $df = 11.071$, $P = 0.013$; Figure S2); we did not detect that SY and ASY males produced different numbers of within-pair offspring (t-test; $t = 0.651$, $df = 19.338$, $P = 0.523$). In cases where females mated outside the pair bond, we did not detect that extra-pair males had darker breast plumage than the females' social mates (paired t-test; breast: $t = 1.624$, $df = 18$, $P = 0.122$). Likewise, when males mated outside the pair bond, we did not detect that extra-pair females had darker breasts than the males' social mates (pair t-test: breast: $t = -0.72854$, $df = 18$, $P = 0.4757$).

Discussion

Few studies investigate assortativity beyond the social pair. When we examined patterns of assortativity within social pairs, mating pairs, and in the context of a social network, we found that barn swallows paired and mated assortatively by their ventral plumage color, a well-established signal trait in this system. Assortativity was stronger in social pairs than in mating pairs. We also found assortativity by ventral plumage color, age, and sex in the social network. Finally, older males and darker females achieved higher reproductive success.

Barn swallows paired assortatively by their ventral plumage color, consistent with our predictions and other studies that examined assortativity within and beyond the social pair (Jacobs et al. 2015; Leitão et al. 2021). Assortative pairing by ventral plumage color suggests that barn swallows may display mutual mate choice, particularly in pairs of darker and potentially higher quality individuals. We know that female barn swallows dynamically allocate paternity to experimentally darkened males (Safran et al. 2005, 2016), and that ventral plumage is moderately heritable (Saino et al. 2013; Hubbard et al. 2015). Consequently, darker males may confer indirect genetic benefits to females by producing attractive offspring (Scordato and Safran 2014). We know much less about male choice relative to female ventral plumage color in this system; males may also be choosy, as demonstrated in other systems that exhibit social monogamy and biparental care (Poirier et al. 2003; Boncoraglio and Saino 2008; Culina et al. 2015). Since females with darker plumage produce more offspring as shown here and in previous studies (Safran and

Table 1. Findings for assortative pairing and mating in barn swallows. Bolded statistics denote where assortativity was found. r = Pearson's correlation coefficient for social pairs, and a permutation-based coefficient for mating pairs, 95% CI = 95% confidence interval, *P* = *P*-value, n = sample size in pairs.

ASSORTATIVE PAIRING

TRAIT	r	95% CI	p	n
Throat brightness	0.219	-0.213-0.579	0.316	25
Breast brightness	**0.546**	**0.172-0.782**	**0.007**	**25**
Belly brightness	**0.442**	**0.036-0.722**	**0.035**	**25**
Vent brightness	0.304	-0.124-0.636	0.158	25
Wing length	0.003	-0.401-0.406	0.987	24
Social interaction: Number of interactions	0.362	-0.347-0.807	0.305	12
Social interaction: Summed duration of interaction	0.507	-0.237-0.876	0.164	12

ASSORTATIVE MATING

TRAIT	r	95% CI	p	n
Throat brightness	0.139	NA	0.423	42
Breast brightness	**0.423**	**NA**	**0.019**	**42**
Belly brightness	0.188	NA	0.241	42
Vent brightness	0.302	NA	0.138	42
Wing length	0.005	NA	0.973	42
Social interaction: Number of interactions	0.122	NA	0.640	7
Social interaction: Summed duration of interaction	0.248	NA	0.378	7

EXTRA-PAIR MATING

TRAIT	r	95% CI	p	n
Throat brightness	-0.100	-0.510-0.346	0.665	21
Breast brightness	0.352	-0.094-0.680	0.117	21
Belly brightness	0.051	-0.389-0.472	0.826	21
Vent brightness	0.135	-0.315-0.535	0.560	21
Wing length	0.109	-0.351-0.526	0.648	21
Social interaction: Number of interactions	-0.591	-0.948-0.424	0.217	7
Social interaction: Summed duration of interaction	-0.533	-0.939-0.490	0.276	7

McGraw 2004), males may gain direct benefits from pairing with a dark female. Consequently, assortativity by ventral plumage color might not be due to strong mutual preference across the entire range of plumage variation. Rather, darker birds pairing by their ventral plumage color might indirectly cause paler birds to pair with one another, and produce a signal of assortative pairing by ventral plumage color in the absence of mutual mate choice in paler individuals. Jacobs et al. (2015) and Leitão et al. (2021) suggest that, as an alternative to mutual choice, social selection in the context of competition for limited nesting cavities and/or territories may explain the assortative social pairing they observed in Western bluebirds (*Sialia mexicana*) and lovely fairy-wrens (*Malurus amibilis*), respectively. More ornamented pairs might have higher success competing for limited territories or nesting sites, and obtain access to the highest quality sites. However, barn swallows are only territorial immediately around their nest and do not appear limited by available nests given that 50% or more of nests (which are often re-used within and across years) are typically unoccupied (Barclay 1988).

Barn swallows mated assortatively by their ventral plumage color, although the pattern was weaker than in social pairs. Since mating pairs include both within-pair and extra-pair partners, this pattern shows that extra-pair mating tends to weaken, rather than strengthen, the assortativity created by within-pair mating. This could be expected given that extra-pair mating is a potentially adaptive mechanism that should allow individuals to respond to variation in the quality of their social mate (Jennions and Petrie 1997; Westneat and Stewart 2003; Neff and Pitcher 2008). If females are paired to less preferred, potentially lower quality males, they may mate with males with darker ventral plumage color, and weaken the assortative pattern. However, similar to Leitão et al. (2021) and Grunst and Grunst (2014), we did not find evidence that extra-pair mates were more ornamented in paired comparisons to social mates. Barn swallows exhibit high rates (30%-45% of offspring) of extra-pair paternity (Saino et al. 1997; Safran et al. 2005) and given their colonial breeding, we might expect low mate search costs and frequent opportunities for comparative mate choice. However, not all individuals of all ventral plumage color phenotypes may be able to gain access to preferred mates. Accordingly, individuals of different phenotypes may employ different mating strategies. Pale individuals might not gain access to preferred mates with dark ventral plumage color and/or pale males may mate guard more than darker males and retain paternity in their own nest and thus never gain extra-pair offspring elsewhere. We did not detect assortativity when we isolated only extra-pair mates, consistent with Jacobs et al. (2015) and Leitão et al. (2021); however, Grunst and Grunst (2014) found that in yellow warblers that paired assortatively by carotenoid plumage color, offspring in the social pair's nest were less likely to have extra-pair sires compared to social pairs that did not assort by this plumage trait. The weaker patterns of assortativity by ventral plumage color we found in mating pairs may be due to either a uniform female preference for darker males or alternative reproductive strategies used by males of different ventral plumage colors, or both. Additionally, males may only prefer darker females in social pairing contexts to ensure high quality maternal care (eg. Bulluck et al. 2017), but discriminate less between female phenotypes during extra-pair copulation.

Arrival timing to the breeding colony may constrain social pair formation and potentially constrain some mating opportunities. Assortative patterns can emerge based on arrival timing if higher quality phenotypes arrive earlier; individuals that arrive to breed early are often in better condition, acquire better territories, and achieve higher reproductive success (Cristol 1995; Aebischer et al. 1996; Kokko 1999; Gienapp and Bregnballe 2012). We have evidence from a Colorado population that barn swallows pair assortatively by their arrival time to the breeding grounds ($r = 0.62$, $P = 0.004$, Levin unpubl. data). Pairing assortatively by arrival timing occurs in several avian systems (Village 1985; Lozano et al. 1996; Bearhop et al. 2005; Ludwig and Becker 2008; Gilsenan et al. 2020), and is likely overlooked due to the challenge of obtaining arrival timing data. We do not have arrival timing data for the individuals in this study, but hypothesize that arrival timing contributes to the strong assortative pairing by ventral plumage color. The fact that darker females achieved higher reproductive success may result from their earlier arrival; variation in female reproductive success typically reflects brood number more than number of offspring per brood. Anecdotally, only seven pairs (of the known-age focal birds breeding in the main barn) in our study failed to double brood and six of them included an

SY female. Male age was an important predictor of male reproductive success. Only one SY male obtained one extra-pair offspring in our study, which suggests that young males are either not selected as extra-pair mates by females or they employ alternative strategies to maximize their within-pair reproductive success. Older males are often more successful at securing extra-pair matings (eg. Ferree and Dickinson 2011; Michálková et al. 2019). Michálková et al. (2019) found that male and female age predicted extra-pair paternity better than male ornamentation (tail streamer length) in European barn swallows. In the North American subspecies however, age and ventral plumage color can sometimes be correlated (Levin unpubl. data; Bradley et al. 2014), which suggests that ventral plumage color might provide information about the age (and thus breeding experience) of a potential mate in these populations.

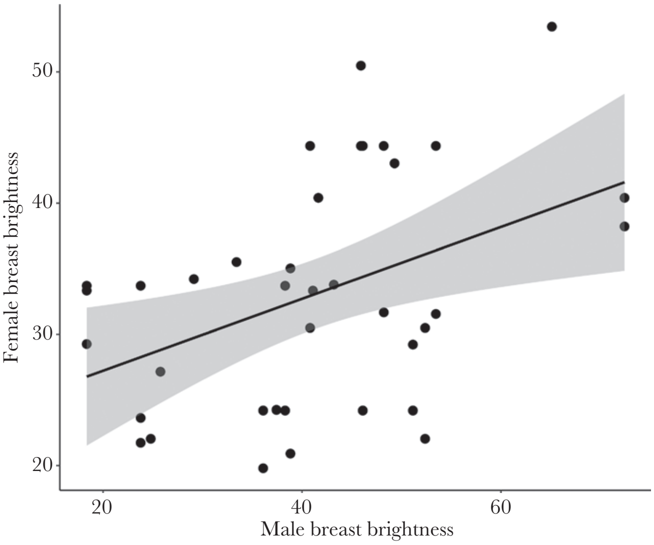

Fig. 2. Barn swallows mated assortatively by ventral plumage color (breast brightness). Birds with similar breast brightness mated with one another (r = 0.42, *P* = 0.019). Darker plumage corresponds to lower brightness values. Pearson's correlation, gray shading shows the 95% confidence interval. n = 42 pairs.

In cases where assortative pairing or mating do not result from habitat selection or arrival timing to the breeding grounds, assortativity can rely on a mechanism by which the animal has information about its own phenotype and can accurately assess the phenotype of a potential social or extra-pair mate. Individuals may develop phenotypic preferences as nestlings by imprinting on their parents' phenotype (Laland 1994; Hauber and Sherman 2001). Similarly, if that phenotype is heritable, this may also be where information is gained about their own phenotype to establish an assortative preference (Morandi et al. 2022). However, in cases of extra-pair paternity, nestlings will imprint on the social mate of their mother rather than on the male that actually sired them, which may weaken the formation of an accurate assortative preference. Alternatively, individuals might gain information about their own phenotype through their interactions with conspecifics, particularly if individuals with similar phenotypes challenge each other socially (Tibbetts 2014). Mutual mate choice via self-referent phenotype matching may only occur when individuals exhibit a preference for a certain phenotype.

We found that barn swallows interacted assortatively by ventral plumage color and age, which provides insight into how social preferences may shape the pool of conspecifics an individual interacts with, and therefore the pool of conspecifics that that individual will ultimately pair and mate with (Noë et al. 2001; Lewis 2008; Oh and Badyaev 2010; Kopp et al. 2018). The coefficients for network assortativity were not especially large; however, the same

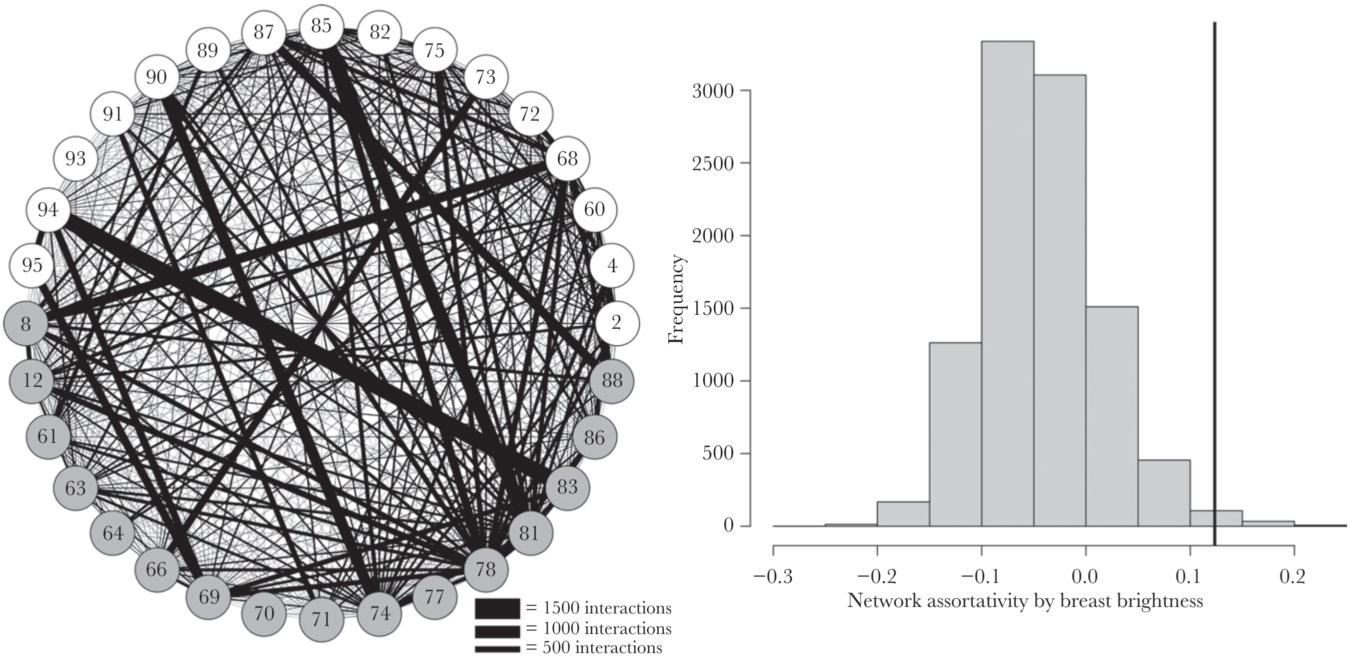

Fig. 3. Barn swallows interacted assortatively by ventral plumage color (breast brightness). Birds with similar breast brightness (sex-specific Z-scores) interacted with one another (r = 0.12, *P* = 0.008). Network shows 52,210 interactions between birds from proximity loggers which collected data for three days for 15 h per day. Gray nodes denote male individuals, and white nodes denote female individuals. An interaction was defined as proximities of 2m or closer based on radio signal strength. The vertical line shows the actual network assortativity by breast brightness. The frequency distribution displays the network assortativity values where node attributes (breast brightness shown) are swapped while maintaining the edge structure of the network. n = 32 individuals.

traits emerged as important for network assortativity as they did for pairing, mating, and reproductive success. The social interactions we recorded may have included both intersexual interactions like copulation, and intrasexual, competitive interactions like aggression or territoriality. Competitive interactions can enforce honest signals of individual quality, whereby individuals may be more likely to challenge conspecifics with similar phenotypes (Tibbetts 2014). These intrasexual (and potentially competitive) interactions may help individuals gain information about their own phenotype from the phenotype of their most frequent social partners. Experimentally darkened females exhibited lower levels of plasma oxidative damage which was likely driven by changes in social interactions post-manipulation (Vitousek et al. 2013). We know from a study that experimentally darkened males' ventral plumage color that females increased their social interactivity with their mate relative to the change in male ventral color (Levin et al. 2018). The network assortativity in the male-female network provides further evidence for mutual preference; however, the pattern may also reinforce the idea that paler individuals cannot access individuals of higher quality, preferred phenotypes.

Table 2. Findings for network assortativity in barn swallows. Bolded statistics denote where assortativity was found. r = assortativity coefficient, *P* = *P*-value, se = standard error, n = sample size in individuals.

ASSORTATIVE SOCIAL INTERACTIONS: COMPLETE NETWORK

TRAIT	r	p	se	n
Throat brightness	0.042	0.077	0.043	24
Breast brightness	**0.124**	**0.008**	**0.064**	**24**
Belly brightness	**0.145**	**0.005**	**0.050**	**24**
Vent brightness	**0.073**	**0.035**	**0.057**	**24**
Wing length	-0.034	0.393	0.060	24
Sex	**-0.178**	**0.005**	**0.055**	**24**
Age	**0.180**	**0.001**	**0.058**	**24**

Table 3. Findings for intersexual network assortativity in barn swallows. Bolded statistics denote where assortativity was found. r = assortativity coefficient, *P* = *P*-value, se = standard error, n = sample size in individuals.

ASSORTATIVE SOCIAL INTERACTIONS: INTERSEXUAL NETWORK

TRAIT	r	p	se	n
Throat brightness	0.113	0.061	0.064	24
Breast brightness	**0.188**	**0.014**	**0.101**	**24**
Belly brightness	**0.169**	**0.016**	**0.068**	**24**
Vent brightness	**0.119**	**0.048**	**0.085**	**24**
Wing length	0.007	0.686	0.088	24
Age	**0.229**	**0.003**	**0.085**	**24**

We predicted that barn swallows would pair and mate assortatively by their level of social interactivity, but found no such pattern in the social network quantified during mating and laying. The amount of social interaction could be considered a behavioral syndrome, and assortative pairing by behavioral syndrome often increases reproductive success in avian systems (Munson et al. 2020). For example, consistently bolder pairs of black-legged kittiwakes (*Rissa tridactyla*) achieve higher reproductive success (Collins et al. 2019). Assortative pairing by behavioral syndrome may improve reproductive success in barn swallows as well; for instance, similar foraging syndromes may reduce sexual conflict associated with differential parental investment and therefore increase intrapair cooperation (eg. Schuett et al. 2011). Alternatively, dissassortativity by behavioral syndrome might be adaptive when individuals within a pair complement one another's parental care syndrome, (ie. provisioner and protector; Scherer et al. 2017; Munson et al. 2020). We did find an insignificant trend where birds paired assortatively by their time spent interacting with other members of the colony (measured as the total time spent within 2m of birds other than the social mate). This was one of the stronger patterns we found (r = 0.51; Table 3), but there were only 12 social pairs where both tags worked well for the duration of the study; this reduced our statistical power and limited our inference.

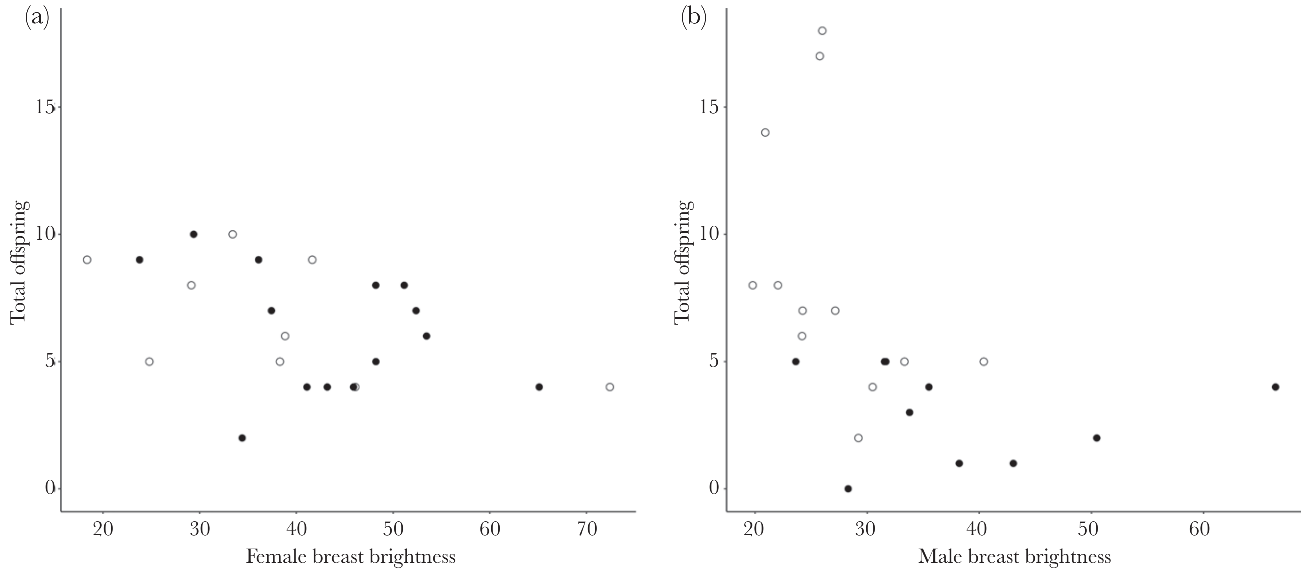

Fig. 4. Patterns in reproductive success. A. Females with darker ventral plumage (lower brightness score) had more offspring, and B. Older males had higher reproductive success; ventral plumage is shown due to its importance in social and mating contexts. Closed circles denote second year (SY) individuals, open circles denote after second year (ASY) individuals. n = 25 individuals of each sex.

In summary, we found evidence for assortativity by sexually selected ventral plumage color in social pairs, mating pairs, and in social interactions among all breeding colony members including those reproductive pairs (Supplemental Table S1). By directly measuring social interactions among individuals during mating, we revealed that assortative patterns may be a result of active behavioral choices by individuals, rather than simply a result of ecological constraints like arrival timing. Individuals might prefer conspecifics similar to themselves; however, this pattern may only reflect mutual preference for darker ventral plumage if paler pairs form due to lack of pairing or mating opportunities with darker individuals. Regardless of the mechanisms involved, these assortative patterns likely contribute to the maintenance of variation in ventral plumage color in barn swallows.

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

Acknowledgments

We thank Lindsay Abramson, Ellie Connor, Yujie (Serena) Liu, Ammar Raslan, Charlie Voirin, and Natalie Wright for their help with data collection and Niklas Duda for his support with the proximity loggers.

Author Contributions

Omar Morosse (Data curation [equal], Formal analysis [lead], Investigation [equal], Methodology [equal], Project administration [equal], Visualization [equal], Writing - original draft [lead], Writing - review & editing [lead]), Toshi Tsunekage (Conceptualization [supporting], Investigation [equal], Methodology [equal], Writing - original draft [supporting], Writing - review & editing [supporting]), Heather Kenny-Duddela (Investigation [supporting], Writing - review & editing [supporting]), Drew Schield (Formal analysis [supporting], Methodology [supporting], Writing - review & editing [supporting]), Kayleigh Keller (Formal analysis [supporting], Funding acquisition [equal], Writing - review & editing [supporting]), R J Safran (Funding acquisition [equal], Writing - original draft [supporting], Writing - review & editing [supporting]), and Iris Levin (Conceptualization [lead], Data curation [equal], Formal analysis [equal], Funding acquisition [lead], Investigation [equal], Methodology [equal], Project administration [lead], Supervision [lead], Visualization [supporting], Writing - original draft [supporting], Writing - review & editing [supporting])

Funding

This work was funded by the Kenyon Summer Science Scholars program, NSF-IOS-1856254 awarded to IIL, NSF-IOS 1856229 to KPK, NSF-IOS 1856266 to RJS, and NSF-DGE-1650115 to HKD.

Conflicts of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data provided by Morosse et al. (2025).

REFERENCES

Aebischer A, Perrin N, Krieg M, Studer J, Meyer DR. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides*. J Avian Biol. 27:143–152. https://doi.org/10.2307/3677143

Balenger SL, Zuk M. 2014. Testing the Hamilton–Zuk Hypothesis: past, present, and future. Integr Comp Biol. 54:601–613. https://doi.org/10.1093/icb/icu059

Barclay RMR. 1988. Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). Auk. 105:53–60. https://doi.org/10.1093/auk/105.1.53

Barlow GW, Rogers W, Cappeto RV. 1977. Incompatibility and assortative mating in the midas cichlid. Behav Ecol Sociobiol. 2:49–59. https://doi.org/10.1007/bf00299288

Bearhop S, *et al*. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science. 310:502–504. https://doi.org/10.1126/science.1115661

Beck KB, Farine DR, Firth JA, Sheldon BC. 2023. Variation in local population size predicts social network structure in wild songbirds. J Anim Ecol. 92:2348–2362. https://doi.org/10.1111/1365-2656.14015

Bitton P-P, Dawson RD, Ochs CL. 2008. Plumage characteristics, reproductive investment and assortative mating in tree swallows *Tachycineta bicolor*. Behav Ecol Sociobiol. 62:1543–1550. https://doi.org/10.1007/s00265-008-0583-7

Bolger AM, Lohse M, Usadel B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics. 30:2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Boncoraglio G, Saino N. 2008. Barn swallow chicks beg more loudly when broodmates are unrelated. J Evol Biol. 21:256–262. https://doi.org/10.1111/j.1420-9101.2007.01441.x

Bradley RJ, Hubbard JK, Jenkins BR, Safran RJ. 2014. Patterns and ecological predictors of age-related performance in female North American barn swallows, *Hirundo rustica erythrogaster*. Behav Ecol Sociobiol. 68:1883–1892. https://doi.org/10.1007/s00265-014-1797-5

Brouwer L, Griffith SC. 2019. Extra-pair paternity in birds. Mol Ecol. 28:4864–4882. https://doi.org/10.1111/mec.15259

Brown MB, Brown CR. 2020. Barn Swallow (*Hirundo rustica*), version 1.0. In: Rodewald PG, editor. Birds of the World. Ithaca, NY, USA. Cornell Lab of Ornithology, https://doi.org/10.2173/bow.barswa.01

Bulluck LP, *et al*. 2017. Feather carotenoid content is correlated with reproductive success and provisioning rate in female Prothonotary Warblers. Auk. 134:229–239. https://doi.org/10.1642/auk-16-151.1

Collins SM, Hatch SA, Elliott KH, Jacobs SR. 2019. Boldness, mate choice and reproductive success in *Rissa tridactyla*. Anim Behav. 154:67–74. https://doi.org/10.1016/j.anbehav.2019.06.007

Cristol DA. 1995. Early arrival, initiation of nesting, and social status: an experimental study of breeding female red-winged blackbirds. Behav Ecol. 6:87–93. https://doi.org/10.1093/beheco/6.1.87

Culina A, Hinde CA, Sheldon BC. 2015. Carry-over effects of the social environment on future divorce probability in a wild bird population. Proc Biol Sci. 282:20150920. https://doi.org/10.1098/rspb.2015.0920

Danecek P, *et al*. 1000 Genomes Project Analysis Group. 2011. The variant call format and VCFtools. Bioinformatics. 27:2156–2158. https://doi.org/10.1093/bioinformatics/btr330

Duda N, *et al*. 2018. BATS: adaptive ultra low power sensor network for animal tracking. Sensors (Basel, Switzerland). 18:3343. https://doi.org/10.3390/s18103343

Edward DA, Chapman T. 2011. The evolution and significance of male mate choice. Trends Ecol Evol. 26:647–654. https://doi.org/10.1016/j.tree.2011.07.012

Eikenaar C, Whitham M, Komdeur J, van der Velde M, Moore IT. 2011. Testosterone, plumage colouration and extra-pair paternity in male North-American Barn Swallows. PLoS One. 6:e23288. https://doi.org/10.1371/journal.pone.0023288

Farine DR. 2014. Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. Anim Behav. 89:141–153. https://doi.org/10.1016/j.anbehav.2014.01.001

Fernö A, Sjölander S. 1976. Influence of previous experience on the mate selection of two colour morphs of the convict cichlid, *Cichlasoma nigrofasciatum* (*Pisces, Cichlidae*). Behav Processes. 1:3–14. https://doi.org/10.1016/0376-6357(76)90003-6

Ferree ED, Dickinson JL. 2011. Natural extrapair paternity matches receptivity patterns in unguarded females: evidence for importance of female choice. Anim Behav. 82:1167–1173. https://doi.org/10.1016/j.anbehav.2011.08.016

Fisher RA. 1915. The evolution of sexual preference. Eugen Rev. 7:184–192.

Gienapp P, Bregnballe T. 2012. Fitness consequences of timing of migration and breeding in cormorants. PLoS One. 7:e46165. https://doi.org/10.1371/journal.pone.0046165

Gilsenan C, Valcu M, Kempenaers B. 2020. Timing of arrival in the breeding area is repeatable and affects reproductive success in a non-migratory population of blue tits. J Anim Ecol. 89:1017–1031. https://doi.org/10.1111/1365-2656.13160

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212. https://doi.org/10.1046/j.1365-294x.2002.01613.x

Grunst AS, Grunst ML. 2014. Multiple sexual pigments, assortative social pairing, and genetic paternity in the yellow warbler (*Setophaga petechia*). Behav Ecol Sociobiol. 68:1451–1463. https://doi.org/10.1007/s00265-014-1752-5

Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites? Science. 218:384–387. https://doi.org/10.1126/science.7123238

Hauber ME, Sherman PW. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. Trends Neurosci. 24:609–616. https://doi.org/10.1016/s0166-2236(00)01916-0

Hubbard JK, Jenkins BR, Safran RJ. 2015. Quantitative genetics of plumage color: lifetime effects of early nest environment on a colorful sexual signal. Ecol Evol. 5:3436–3449. https://doi.org/10.1002/ece3.1602

Jacobs AC, Fair JM, Zuk M. 2015. Coloration, paternity, and assortative mating in Western Bluebirds. Ethology. 121:176–186. https://doi.org/10.1111/eth.12327

Jawor JM, Linville SU, Beall SM, Breitwisch R. 2003. Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). Behav Ecol. 14:515–520. https://doi.org/10.1093/beheco/arg041

Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev Camb Philos Soc. 72:283–327. https://doi.org/10.1017/s0006323196005014

Jiang Y, Bolnick DI, Kirkpatrick M. 2013. Assortative mating in animals. Am Nat. 181:E125–E138. https://doi.org/10.1086/670160

Kempenaers B. 1993. The use of a breeding synchrony index. Ornis Scandinavica. 24:84. https://doi.org/10.2307/3676415

Kokko H. 1999. Competition for early arrival in migratory birds. J Anim Ecol. 68:940–950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Kopp M, *et al*. 2018. Mechanisms of assortative mating in speciation with gene flow: connecting theory and empirical research. Am Nat. 191:1–20. https://doi.org/10.1086/694889

Krause J, editor. 2015. Animal social networks. Oxford University Press.

Laland KN. 1994. On the evolutionary consequences of sexual imprinting. Evolution. 48:477–489. https://doi.org/10.1111/j.1558-5646.1994.tb01325.x

Leitão AV, Hall ML, Mulder RA. 2021. Female and male plumage color is linked to parental quality, pairing, and extrapair mating in a tropical passerine. Behav Ecol. 32:452–463. https://doi.org/10.1093/beheco/araa154

Levin II, *et al*. 2016. Stress response, gut microbial diversity and sexual signals correlate with social interactions. Biol Lett. 12:20160352. https://doi.org/10.1098/rsbl.2016.0352

Levin II, *et al*. 2018. Experimental manipulation of a signal trait reveals complex phenotype-behaviour coordination. Sci Rep. 8:15533. https://doi.org/10.1038/s41598-018-33948-0

Lewis RJ. 2008. Social influences on group membership in *Propithecus verreauxi verreauxi*. Int J Primatol. 29:1249–1270. https://doi.org/10.1007/s10764-008-9304-3

Li H, *et al*. 1000. Genome Project Data Processing Subgroup. 2009. The sequence Alignment/Map format and SAMtools. Bioinformatics. 25:2078–2079. https://doi.org/10.1093/bioinformatics/btp352

Li H, Durbin R. 2009. Fast and accurate short read alignment with Burrows–Wheeler transform. Bioinformatics. 25:1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Lipatov M, Sanjeev K, Patro R, Veeramah KR. 2015. Maximum Likelihood Estimation of Biological Relatedness from Low Coverage Sequencing Data.:023374. doi:10.1101/023374. [accessed 2024 Jul 12]. https://www.biorxiv.org/content/10.1101/023374v1

Lozano GA, Perreault S, Lemon RE. 1996. Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. J Avian Biol. 27:164–170. https://doi.org/10.2307/3677146

Ludwig SC, Becker PH. 2008. Supply and demand: causes and consequences of assortative mating in common terns *Sterna hirundo*. Behav Ecol Sociobiol. 62:1601–1611. https://doi.org/10.1007/s00265-008-0589-1

Maia R, Gruson H, Endler JA, White TE. 2019. pavo 2: new tools for the spectral and spatial analysis of colour in R. Methods Ecol Evol. 10:1097–1107. https://doi.org/10.1111/2041-210x.13174

McDonald GC, James R, Krause J, Pizzari T. 2013. Sexual networks: measuring sexual selection in structured, polyandrous populations. Philos Trans R Soc London Ser B. 368:20120356. https://doi.org/10.1098/rstb.2012.0356

McKenna A, *et al*. 2010. The genome analysis toolkit: a mapreduce framework for analyzing next-generation DNA sequencing data. Genome Res. 20:1297–1303. https://doi.org/10.1101/gr.107524.110

Michálková R, Tomášek O, Adámková M, Kreisinger J, Albrecht T. 2019. Extra-pair paternity patterns in European barn swallows *Hirundo rustica* are best explained by male and female age rather than male ornamentation. Behav Ecol Sociobiol. 73:119. https://doi.org/10.1007/s00265-019-2725-5

Moller AP. 1992. Frequency of female copulations with multiple males and sexual selection. Am Naturalist. 139:1089–1101. https://doi.org/10.1086/285374

Møller AP, DE Lope F. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. J Anim Ecol. 68:163–171. https://doi.org/10.1046/j.1365-2656.1999.00274.x

Montiglio P, McGlothlin JW, Farine DR. 2017. Social structure modulates the evolutionary consequences of social plasticity: a social network perspective on interacting phenotypes. Ecol Evol. 8:1451–1464. https://doi.org/10.1002/ece3.3753

Morandi K, Lindholm AK, Lee DE, Bond ML. 2022. Phenotypic matching by spot pattern potentially mediates female giraffe social associations. J Zool. 318:147–157. https://doi.org/10.1111/jzo.13009

Morosse OJ, *et al*. 2025. North American barn swallows pair, mate, and interact assortatively. https://doi.org/10.5061/dryad.1g1jwsv8g

Munson AA, Jones C, Schraft H, Sih A. 2020. You're just my type: mate choice and behavioral types. Trends Ecol Evol. 35:823–833. https://doi.org/10.1016/j.tree.2020.04.010

Neff BD, Pitcher TE. 2008. Mate choice for non-additive genetic benefits: a resolution to the lek paradox. J Theor Biol. 254:147–155. https://doi.org/10.1016/j.jtbi.2008.05.019

Newman MEJ. 2003. Mixing patterns in networks. Phys Rev E Stat Nonlin Soft Matter Phys. 67:026126. https://doi.org/10.1103/PhysRevE.67.026126

Noë R, van Hooff JARAM, Hammerstein P, editors. 2001. Economics in nature: social dilemmas, mate choice, and biological markets. Cambridge UniversityPress.

Nolazco S, Delhey K, Nakagawa S, Peters A. 2022. Ornaments are equally informative in male and female birds. Nat Commun. 13:5917. https://doi.org/10.1038/s41467-022-33548-7

Oh KP, Badyaev AV. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. Am Naturalist. 176:E80–E89. https://doi.org/10.1086/655216

Pinter-Wollman N, *et al*. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav Ecol. 25:242–255. https://doi.org/10.1093/beheco/art047

Poirier NE, Whittingham LA, Dunn PO. 2003. Effects of paternity and mate availability on mate switching in house wrens. Condor. 105:816–821. https://doi.org/10.1093/condor/105.4.816

Ripperger SP, *et al*. 2020. Thinking small: next-generation sensor networks close the size gap in vertebrate biologging. PLoS Biol. 18:e3000655. https://doi.org/10.1371/journal.pbio.3000655

Rosenthal G. 2017. Mate Choice: The Evolution of Sexual Decision Making from Microbes to Humans. Princeton University Press. https://doi.org/10.1515/9781400885466

Safran RJ, *et al*. 2016. The maintenance of phenotypic divergence through sexual selection: an experimental study in barn swallows *Hirundo rustica*. Evolution. 70:2074–2084. https://doi.org/10.1111/evo.13014

Safran RJ, Levin II. 2019. The sexual and social behavior of the barn swallow. encyclopedia of animal behavior. 2nd edn. Academic Press. p. 173–180.

Safran RJ, McGraw KJ. 2004. Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American barn swallows. Behav Ecol. 15:455–461. https://doi.org/10.1093/beheco/arh035

Safran RJ, Neuman CR, McGraw KJ, Lovette IJ. 2005. Dynamic paternity allocation as a function of male plumage color in barn swallows. Science. 309:2210–2212. https://doi.org/10.1126/science.1115090

Saino N, *et al*. 2013. Sexual dimorphism in melanin pigmentation, feather coloration and its heritability in the barn swallow (*Hirundo rustica*). PLoS One. 8:e58024. https://doi.org/10.1371/journal.pone.0058024

Saino N, Primmer CR, Ellegren H, Møller AP. 1997. An experimental study of paternity and tail ornamentation in the Barn Swallow (*Hirundo rustica*). Evolution. 51:562–570. https://doi.org/10.2307/2411128

Scherer U, Kuhnhardt M, Schuett W. 2017. Different or alike? Female rainbow kribs choose males of similar consistency and dissimilar level of boldness. Anim Behav. 128:117–124. https://doi.org/10.1016/j.anbehav.2017.04.007

Schuett W, Dall SRX, Royle NJ. 2011. Pairs of zebra finches with similar "personalities" make better parents. Anim Behav. 81:609–618. https://doi.org/10.1016/j.anbehav.2010.12.006

Scordato ES, Safran RJ. 2014. Geographic variation in sexual selection and implications for speciation in the Barn Swallow. Avian Res. 5:8. https://doi.org/10.1186/s40657-014-0008-4

Secomandi S, *et al*. 2023. A chromosome-level reference genome and pangenome for barn swallow population genomics. Cell Reports. 42:111992. https://doi.org/10.1016/j.celrep.2023.111992

Shields WM. 1984. Factors affecting nest and site fidelity in adirondack barn swallows (*Hirundo rustica*). Auk. 101:780–789. https://doi.org/10.2307/4086904

Shizuka D, Farine DR. 2016. Measuring the robustness of network community structure using assortativity. Anim Behav. 112:237–246. https://doi.org/10.1016/j.anbehav.2015.12.007

Templeton AR. 2006. Population genetics and microevolutionary theory. John Wiley & Sons.

Tibbetts EA. 2014. The evolution of honest communication: integrating social and physiological costs of ornamentation. Integr Comp Biol. 54:578–590. https://doi.org/10.1093/icb/icu083

Van der Auwera GA, *et al*. 2013. From FastQ data to high confidence variant calls: the genome analysis toolkit best practices pipeline. Curr. Protoc. Bioinform. 43:11.10.1–11.10.33. https://doi.org/10.1002/0471250953.bi1110s43

Versluys TMM, Mas-Sandoval A, Flintham EO, Savolainen V. 2021. Why do we pick similar mates, or do we? Biol Lett. 17:20210463. https://doi.org/10.1098/rsbl.2021.0463

Village A. 1985. Spring arrival times and assortative mating of Kestrels in South Scotland. J Anim Ecol. 54:857–868. https://doi.org/10.2307/4383

Vitousek MN, Stewart RA, Safran RJ. 2013. Female plumage colour influences seasonal oxidative damage and testosterone profiles in a songbird. Biol Lett. 9:20130539. https://doi.org/10.1098/rsbl.2013.0539

Vitousek MN, Zonana DM, Safran RJ. 2014. An integrative view of the signaling phenotype: dynamic links between signals, physiology, behavior and social context. Curr Zool. 60:739–754. https://doi.org/10.1093/czoolo/60.6.739

Wang D, *et al*. 2019. Scrutinizing assortative mating in birds. Jennions MD, editor. PLoS Biol. 17:e3000156. https://doi.org/10.1371/journal.pbio.3000156

Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst. 34:365–396. https://doi.org/10.1146/annurev.ecolsys.34.011802.132439

Zahavi A. 1975. Mate selection—A selection for a handicap. J Theor Biol. 53:205–214. https://doi.org/10.1016/0022-5193(75)90111-3