Testing the mediating role of female-male social interactions on the relationship between age and reproductive success.

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Word count: 3,497 – (allowed = 3,500)
 # Tables: 3 – (allowed = 3)
 # Figures: 3 – (allowed = 3)
 # References: 67

Running head: Testing the mediating role of social interactions

Key words: social network, causal inference, mediation, reproductive success, age

ABSTRACT – 191 words – (allowed 200)

Differential reproduction is a key driver of evolution that is determined by individual characteristics and mating opportunities, including mate choice. Social interactions between conspecifics are hypothesized to be important in facilitating mate choice and reproductive success but are difficult to measure. Using data from 52 adult barn swallows (*Hirundo rustica erythrogaster*) whose social interactions were measured via proximity tags, we tested the hypothesis that opposite sex social interactions mediate the relationship between age (a proxy for experience) and condition-dependent plumage traits, and their associations with reproductive success. We found that older female barn swallows have higher fecundity and that older males have higher reproductive success. Darker ventral plumage coloration was not associated with higher reproductive success in either sex, even among experimentally darkened males. We also observed that older birds appear to be less social, as indicated by weaker interaction strength and degree, though these associations only approach statistical significance in males. Finally, despite a robust effect in which older barn swallows have higher reproductive success, we found no evidence of mediation by social interactions. Our results suggest that older, more experienced birds can produce more offspring while being less social.

INTRODUCTION

Annual reproduction is a key component of Darwinian fitness that is determined by characteristics inherent to the individual and mating opportunities that are influenced by interactions with conspecifics [1]. Individuals that are in better condition or more experienced typically produce more and healthier offspring than animals in poor condition or lacking experience [2–5]. Condition and experience change with age and are often associated with expression of secondary sexual traits [6], and as a result, age and condition-dependent traits influence reproductive success. Reproduction is also influenced by social interactions, including intrasexual competition and intersexual mate choice [1]. Non-random mate choice based on traits that reliably convey information about partner attributes, including experience, is predicted to lead to higher reproductive success [7–9].

A mechanism through which individuals can sample and select a mate is social interaction. There are numerous examples wherein members of the opposite sex assess potential mates as part of their mate selection process. A conspicuous example is lek mating [10–12]. If social interactions allow individuals to assess potential mates' traits, then more extensive interactions should optimize mate selection and increases reproductive success [13].

We used data from North American barn swallows (*Hirundo rustica erythrogaster*) to ask: are age and/or plumage traits associated with reproductive success, and to what extent are these relationships mediated by female-male social interactions? Barn swallows are migratory passerines that breed in North America each summer. Reproductive success in this subspecies has been found to be positively associated with age [14] and ventral plumage darkness [15]

First, we hypothesized that older barn swallows and swallows with darker ventral plumage coloration would have higher reproductive success. Second, we hypothesized that older swallows would have darker plumage. Third, we hypothesized older and darker swallows would have a greater quantity of social interactions with members of the opposite sex. Fourth, we hypothesized that more social individuals would produce more offspring. Fifth, we hypothesized that the effect of age and ventral plumage coloration on reproductive fitness would be mediated by social interactions with members of the opposite sex.

To test these hypotheses, we conducted a mediation analysis. Briefly, mediation models involve decomposition of the total effect of the explanatory variable on the outcome into its direct and indirect effects [16,17]. The direct effect is the effect of the explanatory variable on the outcome that is independent of the mediator, while the indirect effect is the effect that passes through the mediator. The sum of the direct and indirect effects equals the total effect. To explore mediation, the total effect of age and/or plumage traits on reproductive success can be decomposed into the direct and indirect effects in scenarios involving varying strengths of mediation by social interactions (**Figure 1, a-d**).

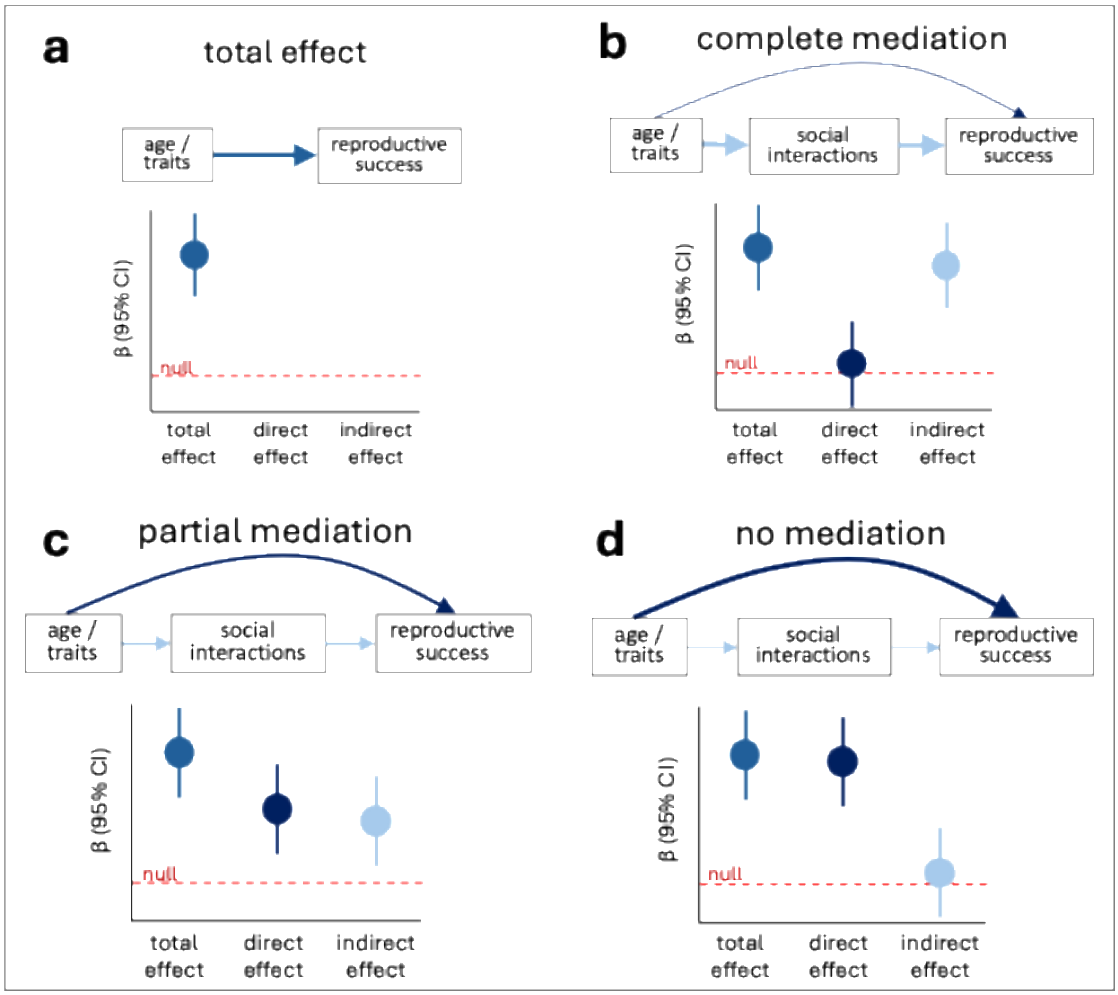

Figure 1. Directed Acyclic Graphs (DAG) of the hypothesized biological mechanism in which age and/or morphological traits affect reproductive success, and social interactions mediate these relationships. The predicted decomposition of **a)** the total effect into the direct and indirect effects under scenarios of **b)** complete, **c)** partial, or **d**) no mediation. Total effect = direct effect + indirect effect.

METHODS

Study population.

We studied 61 wild adult barn swallows at a farm during the breeding season by monitoring nests between 1 May – 9 September 2015 in Boulder County, CO, USA. Using mist nets, we first captured 58 of the 61 (95%) adult birds on June 11 or June 13 and fit each bird with a U.S. Geological Survey numbered aluminum leg band and a unique combination of 2 plastic color bands. We dichotomized continuous age as a two-level categorical measure corresponding to

‘second year’ (SY) birds in their first breeding season, and ‘after second year’ (ASY) which included any birds with prior breeding season experience. During the initial capture we also measured morphology, collected feathers for plumage assessment, sampled blood for paternity analyses, and attached a proximity logger for quantifying social interactions. See **Figure S1** for a description of our sampling timeline.

Trait assessment and experimental manipulation

To measure plumage color, we plucked 15-20 feathers sampled across a transect from the ventral surface and focus on two regions previously shown to be associated with reproductive success and/or mate assortativity [15,18] (**Figure S1, b**). Feathers were stored in opaque envelopes until feather brightness was quantified via spectrometry. We used an Ocean Optics USB4000 spectrometer (Dunedin, FL) and a pulsed xenon light (PX-2, Ocean Optics) to measure breast and belly brightness. In addition to measuring both female and male natural plumage brightness, we also quantified male breast brightness after manipulating ventral plumage color using PrismaColor Light Walnut (#3507) marker to artificially darken the breast feathers of 14 randomly assigned males. Additional information about quantifying plumage brightness is in the supplemental material and Levin et al. 2018.

Social interactions

Social interactions between female and male swallows were recorded from Encounternet proximity loggers (tags) [20,21]. Tags were set to collect interaction data from 29 female and 29 male barn swallows between approximately 6:00 - 9:00 am before and after the plumage

manipulation experiment. Pre-manipulation interaction data were collected between June 13-15, while post-manipulation data were available from June 19-20. Pre- and post-manipulation adjacency matrices of all opposite sex interactions were used to calculate node level social network metrics. We included interactions at or less than a maximum distance of ~0.1m based on filtering the minimum average receiver signal strength indicator (RSSI) values to ≥ 20 [20]. We focused on degree, the total number of opposite sex conspecifics that an individual interacts with, and strength, the sum of the total number of opposite sex interactions [22].

Several of the originally tagged birds (n=58) were removed from our final pre-manipulation and post-manipulation analyses. One female left the site and two additional females lacking complete social interaction data were removed from analyses (n = 26). Similarly, two males were removed because they lacked reproductive success data, and another male lacked complete social interaction data (n = 26). We retained the social interaction data for birds with incomplete reproductive success data before removing them from the final data sets because they contribute to the strength and degree of other birds. For post-manipulation networks, six additional males and five females were removed due to tag battery failure.

Reproductive success

We monitored nests every 3 days throughout the breeding season to record reproductive measures for each nest. We counted the total number of eggs each female laid (fecundity) for up to three clutches over the duration of the breeding season. For males, we measured reproductive success by estimating his within pair (offspring sired with his social mate) and extra-pair paternity and summing these paternity measures. We assigned paternity to eggs

sired by each male from the first clutch, while paternity from second and third broods was determined using DNA from nestlings. Details on paternity assignment are in the supplemental material.

Statistical analysis

To test our hypotheses, we implemented a causal mediation analysis that extends the conditional linear regression approach through the estimation of natural direct and indirect effects, even in the presence of an interaction between the explanatory and mediator variables [23–25]. This entailed four primary steps, 1) establishing a relationship between explanatory and outcome variables, 2) estimating the association between the explanatory and mediator variable, 3) fitting a model that includes the explanatory, mediator, and outcome variables, and 4) using the causal mediation functions in the '*mediation*' package to estimate the natural direct and indirect effects [26].

First, we used linear regression to estimate the associations between each pair of explanatory and outcome variables. Among females, we began by assessing the effect of categorical age on total fecundity. Breast and belly brightness were considered as both explanatory variables as well as potential mediators, since we hypothesized that age may be a determinant of plumage color, and both may influence reproductive success. Therefore, we also ran separate female models in which both standardized values of breast and belly brightness were explanatory variables and total fecundity was the outcome.

For males, we ran additional linear regression models to accommodate the experimental plumage manipulation and multiple measures of reproductive success. We

assessed the association between male age and first clutch, second clutch and total (summation of all breeding attempts) reproductive success as outcomes in separate models. In separate models, males' natural breast and belly brightness were included as explanatory variables and first and total clutch reproductive success were included as outcome variables. We also modeled the effect of breast brightness after the experimental darkening treatment on second clutch reproductive success, which was the reproductive event following the treatment.

Second, we used linear regression to estimate the associations between categorical age and interaction strength and degree, from the pre- and post-manipulation social networks. Among females, we also modeled the association between belly and breast brightness and each social network metric as separate outcomes. For males, we investigated associations between natural breast brightness and pre-manipulation social network metrics as well as models of the relationships between artificially enhanced breast brightness and post-manipulation network metrics. We also investigated the relationship between male belly brightness and pre- and post-manipulation social network metrics.

Third, we ran a set of linear regression models in which we considered plumage traits as a mediator. For both sexes, we assessed the association between categorical age and plumage brightness. Fourth, we ran linear regression models to assess the associations between the social interactions and reproductive success to understand the relationship between mediator and outcome. Finally, we proceeded with the causal mediation models, which we implemented using the mediate() function in the '*mediation*' package in R [26]. We tested for interactions between our explanatory variables and mediators in models where reproductive success was

the outcome and included interactions terms in our final mediation models when those estimates were statistically significant.

All data management and analyses were conducted in in R, version 4.4.2 (R Core Team 2024) using '*tidyverse'* [28], and '*igraph'* packages [29,30]. In all models, α = 0.05 was set as the threshold for statistical significance.

RESULTS

Background characteristics.

Among 26 female and 26 male barn swallows included in our final data, 23% were SY females, 27% ASY females, 23% SY males, and 27% ASY males (**Table S1**). The average (± SD) breast brightness was 38.18 (± 10.75)% for females, 32.52 (± 8.78)% for males' natural plumage, and 23.57 (± 5.48)% for experimentally darkened males. Female belly brightness was 39.65 (± 10.51)% and for males 33.72 (± 7.59)%. In pre-manipulation social networks, average female strength was 44.69 (± 20.21) interactions, and average degree was 13.12 (± 5.58) unique social partners. For males, pre-manipulation strength was 41.12 (± 22.26) and degree was 12.19 (± 4.92). In post-manipulation social networks (n=43), average strength and degree were approximately 2.25 and 3 times lower in both sexes, respectively (**Table S2**). Female total fecundity was on average 9.85 (± 3.18) eggs (**Table S3**). The average number offspring males sired in the first nesting attempt was 3.27 (± 2.72), in the second nesting attempt, 3.29 (± 2.53) nestlings, and average number of nestlings for males based on the sum of all three nesting attempts was 7.85 (± 4.97).

Step 1: Trait associations with each other and reproductive success.

Older females produced 2.50 (95% CI: 0.20, 4.80) more eggs than younger females (**Table 1**). Similarly, older males consistently sired more offspring than younger males during the first nesting attempt 2.82 (95% CI: 1.00, 4.64) and over the duration of all three nesting attempts 5.91 (95% CI: 2.79, 9.02 eggs/nestlings). Older males also sired more nestlings during their second nesting attempt, but this association only approached significance 1.86 (95% CI: -0.22, 3.95 nestlings). Breast and belly brightness were not associated with total fecundity in females (**Table 1**), nor was natural or experimentally darkened plumage associated with any measure of male reproductive success (**Table 1**). Age was not associated with ventral plumage color in either sex (**Table S4**).

Table 1. Associations between barn swallow age and plumage traits and reproductive success.

	Female Reproductive Success	Male Reproductive Success		
	Total fecundity	**Total paternity first clutch**	**Total paternity second clutch**	**Total paternity all clutches**
	β (95% CI)	***β (95% CI)*** *	***β (95% CI)*** *,†	***β (95% CI)*** *
Categorical age	*n = 26*	*n = 26*	*n = 21*	*n = 26*
Second year	0.00 (Reference)	0.00 (Reference)	0.00 (Reference)	0.00 (Reference)
After second year	**2.50 (0.20, 4.80)**	**2.82 (1.00, 4.64)**	*1.86 (-0.22, 3.95)*	**5.91 (2.79, 9.02)**
Plumage traits (separate models)	*n = 26*	*n = 26*	*n = 21*	*n = 26*
Breast brightness (z-score)	-0.43 (-1.69, 0.83)	0.49 (-0.58, 1.56)	-0.59 (-1.70, 0.52)	-0.48 (-2.62, 1.65) ‡
Belly brightness (z-score)	-0.12 (-1.40, 1.15)	-0.41 (-1.49, 0.66)	-0.74 (-1.83, 0.35)	-1.01 (-2.96, 0.93)

* Among males, reproductive success includes eggs/nestlings the male sired with their social mate and via extra pair paternity.

† Sample size is restricted to birds who are included in the post-manipulation social networks.

‡ In this model, we include the treatement effect, a categorical variable for received color manipulation, yes vs. no, as a covariate.

Beta estimates (95% CI) are from linear models.

There are up to three clutches throughout the breeding season.

Bold estimates are significant at $P < 0.05$, and italicized estimates are significant at $P < 0.10$.

Step 2: Trait associations with social interactions.

In both females and males, older birds had lower interaction strength in pre-manipulation networks, -11.87 interactions (95% CI: -27.05, 3.31) and -14.80 interactions (95% CI: -31.29,

1.69), respectively, although this association only approached significance in males. In post-manipulation networks, older females and older males had lower degree, but again this association only approached significance among males. The associations between age and pre-manipulation degree and post-manipulation strength for both females and males were in the same direction, with older birds interacting less and with fewer members of the opposite sex, but these association were not significant (**Table 2**). Ventral plumage was not associated with pre- and post-manipulation social interactions (**Table 2**).

Table 2. Associations between barn swallow age and plumage traits with social interactions both pre- and post- plumage manipulation experiment.

	Pre-manipulation social interaction metrics		**Post-manipulation social interaction metrics**	
	Strength *β (95% CI)*	**Degree** *β (95% CI)*	**Strength** *β (95% CI)*	**Degree** *β (95% CI)*
Female categorical age	*n = 26*	*n = 26*	*n = 22*	*n = 22*
Second year	0.00 (Reference)	0.00 (Reference)	0.00 (Reference)	0.00 (Reference)
After second year	-11.87 (-27.05, 3.31)	-2.26 (-6.56, 2.04)	-2.82 (-12.03, 6.40)	-1.64 (-3.57, 0.30)
Male categorical age	*n = 26*	*n = 26*	*n = 21*	*n = 21*
Second year	0.00 (Reference)	0.00 (Reference)	0.00 (Reference)	0.00 (Reference)
After second year	*-14.80 (-31.29, 1.69)*	-0.88 (-4.74, 2.98)	-3.33 (-14.30, 7.63)	*-2.03 (-4.05, -0.01)*
Female plumage traits *	*n = 26*	*n = 26*	*n = 22*	*n = 22*
Breast brightness	2.11 (-5.93, 10.15)	0.80 (-1.41, 3.01)	-3.07 (-7.63, 1.49)	-0.31 (-1.36, 0.74)
Belly brightness	2.67 (-5.35, 10.68)	0.58 (-1.64, 2.80)	2.04 (-2.63, 6.71)	0.74 (-0.26, 1.75)
Male plumage traits *	*n = 26*	*n = 26*	*n = 21*	*n = 21*
Breast brightness - original	-4.74 (-13.45, 3.96)	-1.61 (-3.47, 0.25)	-	-
Breast brightness - experimental	-	-	0.61 (-4.99, 6.22)	-0.37 (-1.48, 0.74)
Belly brightness	-0.32 (-9.23, 8.59)	-0.40 (-2.37, 1.56)	1.57 (-4.00, 7.14)	0.35 (-0.77, 1.46)

* Traits are z-score standardized and each trait is assesed in separate models.
Beta estimates (95% CI) are from linear models.
Bold estimates are significant at $P < 0.05$, and italicized estimates are significant at $P < 0.10$.

Step 3: Social interaction associations with fitness and exploring mediation assumptions.

Female barn swallows that more frequently interacted with males in pre-manipulation networks, had lower total fecundity (-1.33 [95% CI: -2.48, -0.17), but the association between post-manipulation strength and female fecundity only approached significance (**Table 3**). We observed no association between female degree and fecundity. We also observed no

relationship between male interaction strength or degree and any measures of reproductive success.

We tested for an interaction between age and pre-manipulation strength and post-manipulation degree based on step 2, where associations between age and these social interaction metrics approached significance and were of similar direction, magnitude and precision in both sexes. The only significant interaction was male age by pre-manipulation strength ($p < 0.01$; **Table S5**).

Table 3. Associations between barn swallow social interactions and reproductive success.

	Female Reproductive Success	Male Reproductive Success		
	Total fecundity	Total paternity first clutch	Total paternity second clutch	Total paternity all clutches
	β (95% CI)	*β (95% CI)* *	*β (95% CI)* *,†	*β (95% CI)* *
Pre-manipulation social network metrics (separate models)	*n = 26*	*n = 26*	-	*n = 26*
strength (z-score)	**-1.33 (-2.48, -0.17)**	-0.01 (-1.10, 1.08)	-	-0.13 (-2.12, 1.85)
degree (z-score)	-0.69 (-1.94, 0.55)	0.45 (-0.62, 1.53)	-	1.20 (-0.73, 3.13)
Post-manipulation social network metrics (separate models)	*n = 22*	-	*n = 21*	-
strength (z-score)	*-1.37 (-2.68, -0.06)*	-	0.51 (-0.60, 1.63)	-
degree (z-score)	-0.95 (-2.33, 0.42)	-	0.33 (-0.80, 1.46)	-

* Among males, the count includes eggs/nestlings the male sired with their social mate and via extra pair paternity.

† Sample size is restricted to birds who are included in the post-manipulation social networks.

Beta estimates (95% CI) are from linear models.

There are up to three clutches throughout the breeding season.

Bold estimates are significant at $P < 0.05$, and italicized estimates are significant at $P < 0.10$.

Step 4: Causal mediation by social interactions

We ran causal mediation models focusing on age and pre-manipulation strength and post-manipulation degree based on associations from steps 1-3. In the causal mediation model involving female age, pre-manipulation strength, and total fecundity, the total effect of older age was 2.50 (95% CI: 0.17, 4.62) more eggs, the natural direct effect of older age was 1.89 (95% CI: -0.31, 3.97), and the natural indirect effect of older age through strength was 0.61

(95% CI: -0.15, 1.80; **Figure 4, a; Table S6**) more eggs, respectively. We saw no evidence of mediation of the effect of female age on fecundity by post-manipulation degree (**Figure 4, b; Table S6**).

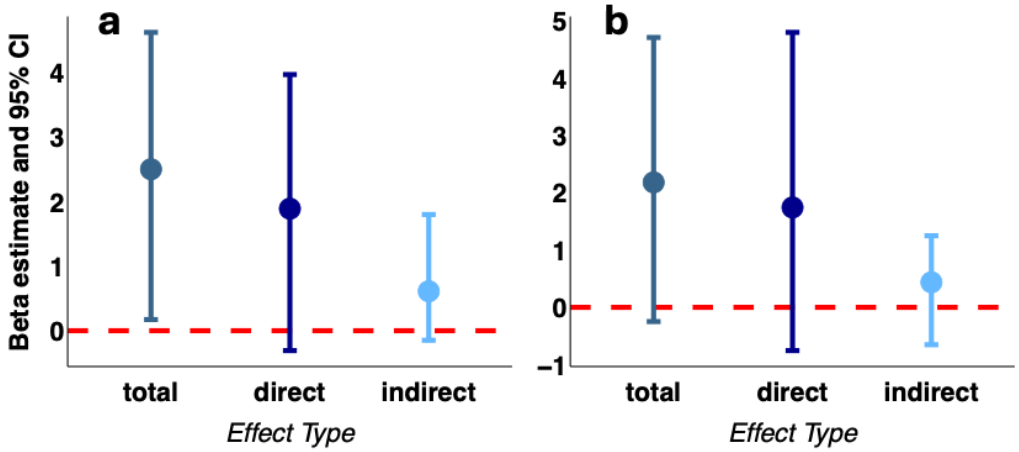

Figure 4. Estimates from the female barn swallow causal mediation models for the effect of age on total reproductive success and mediation by **a)** pre-manipulation strength and by **b)** post-manipulation degree. Estimates include the total effect estimated from each model and its decomposition into the natural direct effect (average direct effect; ADE) and the natural indirect effect (average causal mediation effect; ACME).

Among males, the total effect of older male age was 2.82 (95% CI: 0.94, 4.87) greater reproductive success from the first clutch. The corresponding average natural direct effect was 3.63 (95% CI: 1.42, 6.09), and the average natural indirect effect involving pre-manipulation strength was -0.81 (95% CI: -2.15, 0.12; **Figure 5, a; Table S6**) reproductive success. The total and natural direct effects of male age on total reproductive success were similar (total effect, 5.91 [95% CI: 3.31, 9.19] and natural direct effect, 6.57 [95% CI: 3.66, 10.55]), eggs/nestlings sired while the natural indirect effect that was mediated by pre-manipulation strength (-0.70 [95% CI: -2.69, 0.11]; **Figure 5, c; Table S6**) was small. Like females, male post-manipulation

degree did not mediate the effect of male age on second brood reproductive success (**Figure 5, b; Table S6**).

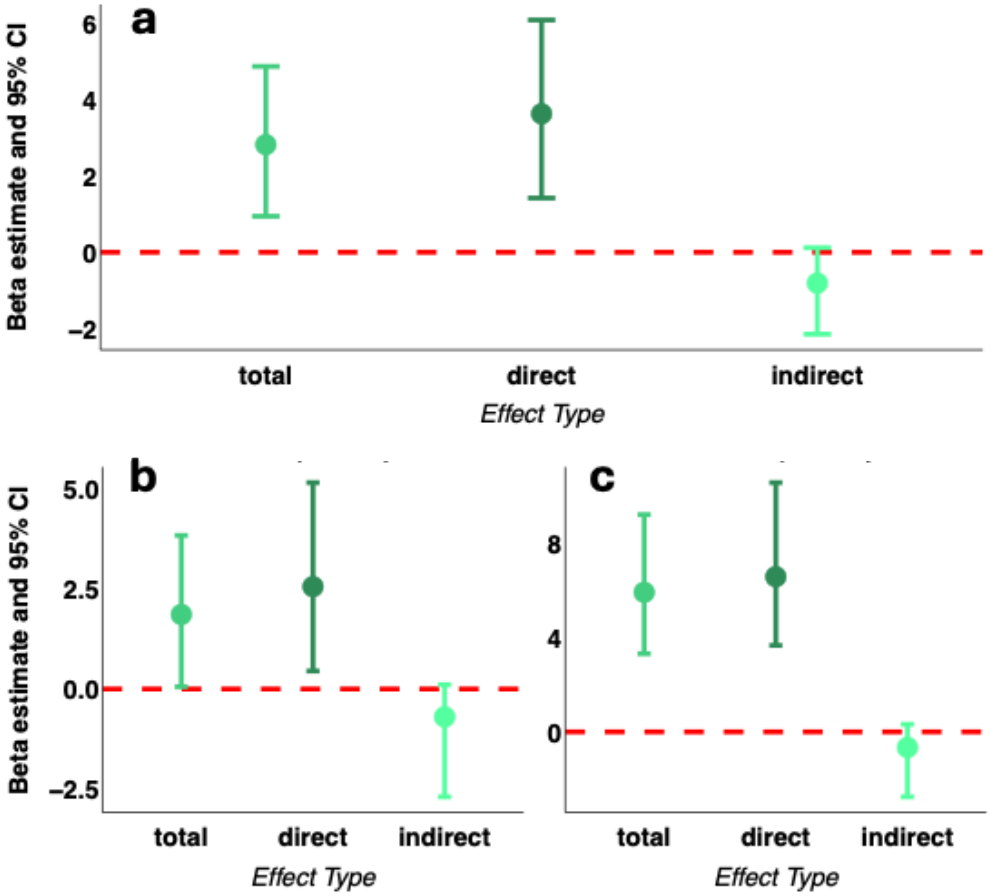

Figure 5. Estimates from the male barn swallow causal mediation models looking at the effect of age on **a)** first clutch reproductive success and mediation by pre-manipulation strength, **b)** second clutch reproductive success and mediation by post-manipulation degree, **c)** all total reproductive success and mediation by pre-manipulation strength Estimates include the total effect estimated from each model and its decomposition into the natural direct effect (average direct effect; ADE) and the natural indirect effect (average causal mediation effect; ACME).

DISCUSSION

We conducted a mediation analysis to determine if age and plumage traits affect reproductive fitness and the extent to which those effects are mediated by social interactions. Using data from 52 adult barn swallows that co-occupied a single breeding site, we found that both older females and males had higher reproductive success. However, darker breast and belly plumage

were not associated with higher reproductive success, even among males that had their breast feathers artificially darkened. We found some evidence that older birds are less social, as indicated by weaker strength and degree observed in older females and males, though these associations only approach statistical significance in males. Finally, evidence of mediation by social interactions was lacking.

Age but not plumage coloration affects fitness.

In our population, older birds with at least one or more prior years of breeding experience produce more offspring than first time breeders. An increase in annual reproductive success with increasing age prior to senescence is common among many passerine species [31–35], including in barn swallows [36,37]. Two non-mutually exclusive hypotheses that might explain these results, include 1) that individuals improve their reproductive competence with age or 2) there is selective disappearance of certain phenotypes at the population level [38].

According to the competence hypothesis, more experienced individuals are better able to locate and secure resources, including nest sites, food, or mates. In an experimental study of captive zebra finches (*Taeniopygia guttata)* more experienced females laid more eggs and initiated their clutches earlier than inexperienced females [39]. Whether higher reproductive success is due to experience *per se* or some other age-associated residual confounding remains unknown in our population. Nevertheless, greater experience leading to improved reproductive outcomes independent of age has been found in several wild birds, including both male and female Seychelles warbler (*Acrocephalus sechellensis*) [40], female collared flycatchers (*Ficedula albicollis*) [5], and western gulls (*Larus occidentalis*) [41].

In addition to experience, high-condition individuals typically have higher reproductive success [42,43], since those in better condition can pay higher costs to produce more offspring [44–46]. Information about condition is often conveyed through expression of signals that are displayed during social interactions and used to assess potential mates [7]. In North American barn swallows, ventral plumage coloration is a condition dependent [47], sexually selected signal, and males with darker ventral plumage have higher reproductive success [15,18]. We assessed natural plumage coloration in both sexes, as well as experimentally darkened breast plumage in males, but observed no effects on fitness. By collecting initial cultches to synchronize breeding, we may have inadvertently altered the mate selection process. We also did not find that older birds have darker ventral plumage. Contrary to our results, other studies have found age related change in the expression of condition dependent signals that influence reproductive success [6,48,49]. Our null findings may reflect a context dependence that decouples the signal from age related condition and fitness [50–53].

An alternative to the competence hypothesis, selection pressure imposed by migration may remove poor-condition individuals from our population as has been found in European barn swallows [54], thus confounding the relationship between age and reproductive success. Still, we have previously found that females increase their reproductive success and increase expression of condition dependent plumage traits as they age [14]. Empirical support for both the improvement of individual competence [55] and the selection hypotheses [56] have been found in studies of wild birds but require longitudinal data to disentangle population from individual level effects [33,57]. If an age-related increase in individual performance is coupled

with selective removal of poor-condition swallows from our study population, then our estimate for the effect age on reproductive success may be biased away from the null.

Age is weakly associated with social interactions

We found that older swallows tended to have lower interaction strength early in the breeding season, and to interact with fewer different members of the opposite sex later in the season. Several recent studies have found a decrease in social interactions with age that is attributable, in part, to within individual change in social behavior and not just selective disappearance. In griffon vultures (*Gyps fulvus*) older individuals have lower interaction strength [58], a finding like in forked fungus beetles (*Bolitoherus cornutus*) that experience decreased strength and betweenness with increasing age [59]. Older and more experience birds might be more selective in their social interactions or prospect less for mating opportunities. A qualitative decrease in the population mean interaction strength and degree as the breeding season advances hints that with increasing experience and familiarity there is a decrease in sociality in barn swallows (see **Table S2**). Still, demographic processes, including the appearance and disappearance of individuals and changes in population age structure, can influence the pool of individuals available for interactions [60–62], and contribute to age related differences in social connectedness, which we cannot rule out.

Social interactions do not mediate the effect of age on fitness.

Despite older swallows exhibiting higher reproductive success and appearing to be less social, we did not find evidence that social interactions mediate the relationship between age

and annual reproduction. In wild baboons (*Papio cynocephalus* and *P. anubis*) social bonds are not strong mediators of the relationship between exposure to adversity early in life and health and fitness outcomes [63,64]. Consistent in both species is a lack of mediation by social interactions, strong direct effects of the exposure to outcome, and notable independent effects of exposure to mediator and mediator to outcome. For example, we find that females who had fewer social interactions had higher fecundity. Unlike our results, positive selection on social connectivity has been observed in forked fungus beetles [13,65], although the relationship between social connectedness and fitness may vary depending on the size, age structure, and sex ratio of the group [66,67].

Conclusion

Older barn swallows produce more offspring but whether this association reflects individual condition or selective removal requires further investigation. Our results do not support our original prediction that more social interactions with members of the opposite sex are part of the mechanistic pathway by which older individuals optimize mating opportunities to increase fitness. Rather, older birds seem less social, and among females, less social birds have higher fecundity, possibly because they invest time in accruing resource instead of prospecting for mates. Our mediation models do not provide strong support that social interactions are on the causal pathway between age and reproduction. A better understanding of how age, condition, and social interactions influence fitness requires future studies to track animals across their life course to assess within vs between individual change.

Ethics. Research was approved by University of Colorado IACUC no.1303.02.

Data and Code accessibility. All data and analysis code used in this paper are available at this this GitHub repository (https://github.com/laubach/bs_trait_dtrmnts_repro_success_mediation) and will be permanently archived at Zenodo upon final review.

Authors' contributions. Z.M.L., K.P.K., R.J.S. and I.L.L. conceptualized this study; I.L.L. R.J.S. and T.T. collected data; Z.M.L. conducted analyses with input from K.P.K.; Z.M.L. drafted the manuscript; All authors reviewed and edited the drafts and gave final approval for publication.

Competing interest. We declare no competing interests.

Funding. This work was supported by NSF-IOS awards 1856229 (K.P.K.), 1856254 (I.I.L), 1856266 (R.J.S.), NSF-DEB award 1149942 (R.J.S.) and NSF DBI-1306059 to I.I.L.

Acknowledgements. We thank Matt Aberle and Amanda Hund for help with fieldwork and Heather Kenny-Duddela for thoughtful feedback on early drafts of this manuscript. We thank Colorado Horse Rescue who gave us access to their property where barn swallows nest.

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