

*Patterns and ecological predictors of age-related performance in female North American barn swallows, *Hirundo rustica erythrogaster**

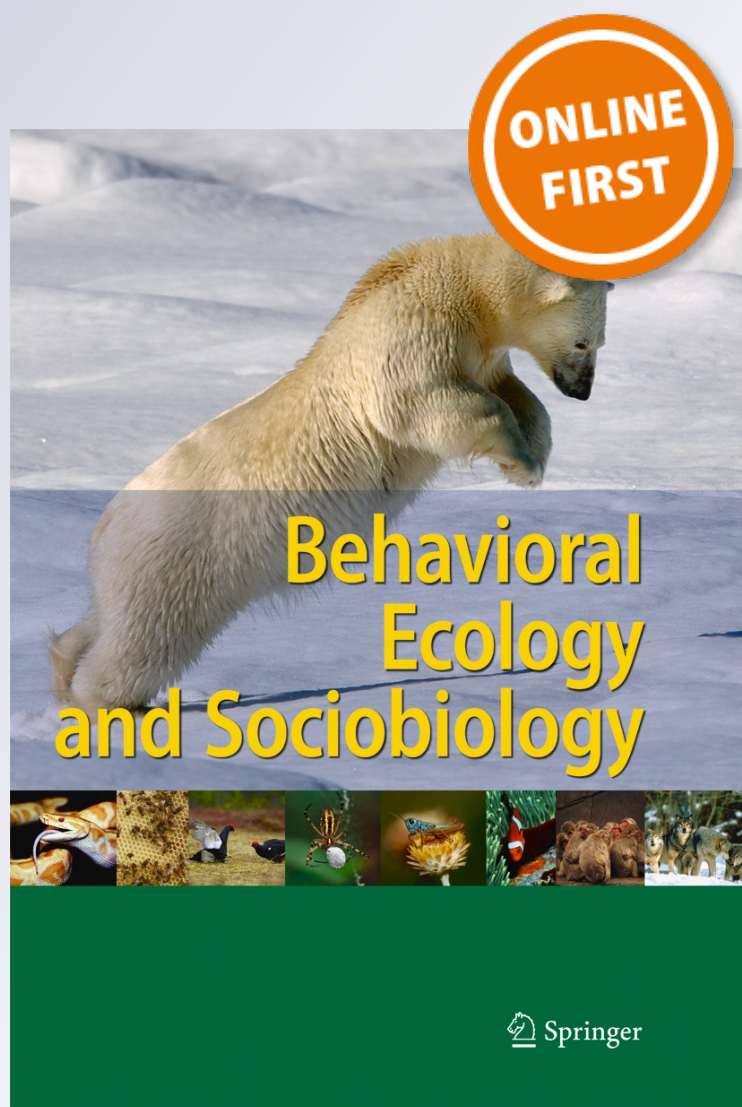
**R. J. Bradley, J. K. Hubbard,  
B. R. Jenkins & R. J. Safran**

**Behavioral Ecology and Sociobiology**

ISSN 0340-5443

Behav Ecol Sociobiol

DOI 10.1007/s00265-014-1797-5



**Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Patterns and ecological predictors of age-related performance in female North American barn swallows, *Hirundo rustica erythrogaster*

R. J. Bradley · J. K. Hubbard · B. R. Jenkins ·  
R. J. Safran

Received: 5 March 2014 / Revised: 12 August 2014 / Accepted: 13 August 2014  
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** Life history theory describes the optimization of important trade-offs within an individual's lifetime and predicts that an individual's reproductive performance (RP) will improve up until a point of senescence. Despite abundant evidence for this pattern, relatively few studies consider the mechanisms associated with age-related improvements in RP. In this study, we aimed to describe patterns of age-related RP (seasonal fledgling production) in female North American barn swallows (*Hirundo rustica erythrogaster*) using a longitudinal data set to test multiple hypotheses about the social, morphological, and ecological factors underlying this prominent life history pattern. To address these objectives, we used generalized linear mixed models in a three-step series of analyses in which we assessed (1) patterns of female age-related RP; (2) the influence of age on changes in social, morphological, and ecological factors; and (3) whether the changes in RP were concomitant with changes in these factors. We found that (1) females showed patterns of age-related reproduction, in which performance increased in the first 2 years of breeding and decreased thereafter, (2) female tail streamer length increased and the extent of breast coloration increased then decreased significantly with age, and (3) changes in morphological traits did not covary with changes in reproductive performance over time. Our within-individual results highlight the importance of considering explicit links between morphology and reproductive performance that are not easily captured by population-level analyses.

**Keywords** Avian · Generalized linear models · Life history · Longitudinal analyses · Reproductive performance · Social and ecological factors

## Introduction

Life history theory predicts that individuals will optimize the allocation of energy toward current and future reproduction, such that reproductive effort corresponds with reproductive gain as well as expected lifespan (Roff 1992). Trade-offs in reproductive effort lead to a widespread pattern across life history strategies whereby individuals increase in reproductive performance with age up to a point of senescence (e.g., olive baboon, *Papio anubis*, Packer 1979; barnacle goose, *Branta leucopsis*, Forslund and Larsson 1992; free-ranging moose, *Alces alces*, Ericsson et al. 2001). Because this pattern is pervasive, a deeper understanding of the mechanisms underlying within-individual, age-related changes in performance is of increasing interest (Lifjeld et al. 2011; Hayes et al. 2013; Bradley and Safran 2014).

Many aspects of an individual may change over time and any of these are likely to impact reproductive performance, such as age-related changes in resource quality, site fidelity, mate fidelity, breeding experience, and mate attraction cues (see Table 1 for hypotheses and predictions; Bradley and Safran 2014). Aspects of a species' life history, such as lifespan (e.g., Lombardo and Thorpe 2010) and reproductive strategy, inform the predictions for the role that these factors play in age-related performance. Short-lived species tend to allocate more energy toward current reproduction earlier in life, improving rapidly (Lombardo and Thorpe 2010), reaching a peak of reproductive performance and then rapidly declining thereafter (e.g., tree swallow *Tachycineta bicolor*, Robertson and Rendell 2001; Péron et al. 2010). Long-lived species, in contrast, are predicted to reserve energy for future

Communicated by S. Pruett-Jones

R. J. Bradley (✉) · J. K. Hubbard · B. R. Jenkins · R. J. Safran  
Department of Ecology and Evolutionary Biology,  
University of Colorado, Boulder, CO 80309, USA  
e-mail: rbradley810@gmail.com

R. J. Bradley  
Department of Zoology and Physiology, University of Wyoming,  
Laramie, WY 82071, USA

**Table 1** Hypotheses and predictions for factors that may co-vary with age and reproduction. Factors must be age-related to be considered as a potential correlate of age-related reproduction. Table adapted from Bradley and Safran 2014

Factor	Benefit	Variables measured	Prediction	Patterns found	Result
Site fidelity	Familiarity with local environment	Caught at the same breeding site as previous year? (yes/no)	Individuals that have bred at a site before (older individuals) reproduce better than individuals without experience at a site (Lombardo and Thorpe 2010)	< 2 % individuals captured switched sites between years. Site fidelity essentially fixed in the population	N/A
Resource quality	Access to higher-quality breeding territories	Nest status ("old" or "new"; Safran 2006)	Younger individuals tend to nest in new nests and older individuals in older nests, leading to age-related patterns of increased RS (Safran 2006)	Change in territory quality is not age-related	Change in territory quality is not age-related
Mate fidelity	Improve coordination of parental duties (Ens et al. 1993)	Pair status, given that mate was recaptured in population ("divorced" or "same")	Younger individuals divorce more often than older individuals, leading to age-related patterns of increased RS (Bradley et al. 1990)	Pair bond maintenance is not age-related	Pair bond maintenance is not age-related
Breeding experience	Increased parental competence	No appropriate variable to measure breeding experience	N/A	N/A	N/A
Mate attraction cues	Become more attractive as social and extra pair mates (Safran and McGraw 2004)	Ventral coloration (% reflectance) and tail streamer length (mm)	Older individuals have increased expression of ornaments and are more attractive as social and extra pair mates (Lubjuhn et al. 2007; Safran and McGraw 2004)	Older females are darker and have longer tail streamers	Changes in morphology do not influence female changes in RS

N/A not applicable

reproduction, both initiating reproductive behavior and senescing later in life (e.g., greater flamingo, *Phoenicopterus ruber roseus*, Devevey et al. 2009; Péron et al. 2010). Additionally, life history theory and variation in reproductive strategies yield different predictions for the sexes, as females are constrained to greater investment in fewer offspring compared to males (Roff 1992). Because of their greater investment in each breeding effort, especially in species with unequal parental care, females may have more detectable patterns of improvement and senescence when compared to males (Maklakov et al. 2009).

In this study, we examined and tested hypotheses about the patterns of within-individual age-related reproduction in females by using a 4-year longitudinal data set from a short-lived passerine, the North American barn swallow (*Hirundo rustica erythrogaster*). Barn swallows are insectivorous passerines that live on average for 2 to 3 years and lay two to three clutches of two to six eggs each breeding season (Brown and Brown 1999). Previous cross-sectional studies suggest that females increase fledgling production with age, but it is uncertain as to what factors predict changes in performance over an individual's lifetime and to what extent females show patterns of senescence (Møller and de Lope 1999; Møller et al. 2005). Several factors could affect changes in an individual's reproductive performance from 1 year to the next. Barn swallows are migratory and have the opportunity to change breeding sites and social mates each breeding season, although site fidelity is very common (Shields and Crook 1987; Galeotti et al. 2001; Saino et al. 2002; Safran 2004). While they are socially monogamous for the duration of the breeding season (April through September), individuals engage in extra-pair copulations, leading to high rates of extra-pair paternity (hereafter, "EPP") in the population; in central Colorado, EPP occurs at a rate of approximately 40 % across nests, ranging from 0 to 100 % for each nest (RJS et al. unpublished). Barn swallows breed in protected sites such as horse barns and culverts; breeding pairs will either occupy preexisting nests (those constructed during previous breeding seasons which remain intact over the winter) or construct new nests at the start of the breeding season. Construction of a new nest is time and energy intensive and often leads to a delay in lay date (Safran and McGraw 2004; Safran 2006). The female barn swallow also has two plumage-based traits that have previously been shown to predict measures of seasonal reproductive performance, such as clutch initiation date and number of fledged offspring: in North America, melanin-based ventral coloration predicts performance for females (Safran and McGraw 2004), whereas in European populations, manipulations of tail streamer length show a trade-off between long tail streamers and future performance (Cuervo et al. 2003). Tail streamer length is also known to increase and then decrease with age (Møller and de Lope 1999; Lifjeld et al. 2011).



Here, we used longitudinal data on reproductive performance and social, morphological, and ecological factors to investigate three major questions in this short-lived species: (1) Do females show patterns of age-related reproduction in either seasonal fledgling production or paternity allocation? Based on previous research, we predicted that females increase seasonal fledgling production over time (Møller and de Lope 1999) and that females decrease paternity allocation to extra-pair mates with age (Lubjuhn et al. 2007). (2) Do social, morphological, and ecological factors covary with age? (see Table 1 for factors and predictions). And (3) do changes in social, morphological, and ecological factors predict changes in age-related reproduction? (see predictions for questions 2 and 3, Table 1).

## Methods

### Data collection

Data were collected from May to September in four successive breeding seasons from 2008 to 2011. During this period, we gathered breeding data on 1,218 adult barn swallows and 3,263 of their offspring. Some adults were recaptured each year: in 2009, we recaptured 116 adults out of 491 total captured (23.6 %); in 2010, we recaptured 165 adults out of 426 (38.7 %); and in 2011, we recaptured 157 adults out of 419 (37.5 %). Using mist nets, we captured individuals during the first 2 weeks of each breeding season after pairs had formed; these captures took place across 17 different study sites located in Boulder, Jefferson, and Weld counties, Colorado. We uniquely marked the tail streamers of individuals with colored markers following Shields and Crook (1987), which does not affect measures of reproductive performance (Safran and McGraw 2004). We also applied numbered aluminum USGS rings and color bands to each individual. We then measured a variety of standard morphological variables (e.g., tail streamer length, wing length, mass) and collected feather samples in order to measure color (see description below, “Feather color”). These samples were stored in envelopes until they were taped to a card for objective color measurement. We checked nests at least every 4 days in order to determine clutch initiation dates (the day on which the first egg was laid), any predation events, and annual reproductive performance (total number of young fledged within the season). To assess paternity, we collected blood samples from adults and 12-day-old nestlings in the first brood (see “Paternity analyses” section for more detail) from the brachial vein using a microhematocrit capillary tube. Blood samples were stored in lysis buffer at room temperature until DNA extraction.

### Data organization

Using the database containing individuals caught from 2008 to 2011, we identified females that were recorded as breeding for at least two successive years during this period ( $n=53$ ). For many individuals, exact age was not known (less than 0.5 % of individuals born at our study site return as breeders); thus, “age” is the time since the first capture (e.g., a bird first captured in 2009 was considered as T+1 in 2010). However, at sites with excellent sampling coverage over successive years (in which most if not all breeding individuals were captured and accounted for at nests), we were able to identify immigrants (new birds at the site after our initial year of sampling) as first year breeders (e.g., a bird first captured at a site in 2010 where all of the breeding adults were previously captured at that site in 2009 was considered a first year breeding adult). Because so few adult barn swallows disperse from one breeding site to another, the assumption that new individuals arriving to our study site are in their first breeding season is conservative and has been made in previous studies of barn swallows (Galeotti et al. 2001; Saino et al. 2002; Safran 2004).

To measure whether there are patterns of age-related reproductive performance, we used seasonal fledgling production (SFP) and number and percentage of extra-pair young in the first brood of each season, as this may reflect age-based changes in reproductive strategy (Lubjuhn et al. 2007). Because seasonal fledgling reproduction was highly variable between years, we used within-year standardization (individual seasonal fledgling production—mean population seasonal fledgling production) so that we could determine individual seasonal fledgling production relative to the population mean within a given year and make comparisons between years. Some individuals were involved in experiments being conducted during the course of this study. Because such manipulations may have influenced measures of reproductive performance, reproductive performance measures were removed from the analyses for experimental individuals. Therefore, these individuals only had data entries for lay date (the only reproductive measure that was not manipulated in any experiment); morphological measurements; and changes in ecological, social, and morphological factors (see “Longitudinal analyses”). Note that not all analyses presented have equivalent sample sizes but were instead compiled to work with the most robust data set for each analysis (e.g., if we only had morphological data and not reproductive performance information for an individual, we included those individuals in the subset of analyses containing those variables).

We use the terms social, morphological, and ecological factors to refer to potential underlying mechanisms of patterns of age-related reproductive performance (see Table 1). In this study, per the natural history of our study system, we defined social factors in terms of mate fidelity between years and

ecological factors in terms of site fidelity and territory quality (measured as nest quality; Safran 2006). Because of the nature of breeding frequency in short-lived species, we were unable to measure breeding experience independent from age (Table 1; see “Discussion”). Morphological factors were defined by two ornamental traits in this species that have previously been shown to influence female reproductive performance in either North American or European populations of barn swallows: the tail streamer length (RTS; mm, Cuervo et al. 2003) and ventral coloration (average throat brightness, % reflectance, Safran and McGraw 2004).

#### Longitudinal analyses

To study within-individual change in reproductive performance, morphology, and features of the breeding environment, we analyzed data for two successive breeding seasons, hereafter referred to as a “sequence”. The sequences are defined as an individual’s year T to T+1 (sequence 1) and year T+1 to T+2 (sequence 2). Each individual in our data set had breeding data for at least one sequence or two consecutive breeding seasons. We compared change within sequences (“within-sequence change”) to determine whether the change in reproductive performance or a social, morphological, or ecological factor was significant from zero for each sequence (this analysis is similar to a one-sample *t* test). We also compared changes between sequences (“between-sequence difference”) to determine whether the rate of change in performance, ecological, social, or morphological factors differed between two sequences (this analysis is conceptually similar to a two-sample *t* test).

The final data set included measurements of reproductive performance, social factors, ecological factors, and morphological factors (see Table 1; “Data collection” section). For all birds assigned to a nest in each year, we calculated the change in each of these measurements across each sequence (e.g., measurement in year T+1 subtracted from measurement in year T). For measures of reproductive performance, we calculated the change in Julian lay date, total number of fledglings produced in the breeding season, standardized number of fledglings produced in the breeding season, and total eggs produced in the breeding season. For social factors, we recorded for each sequence whether a bird had reestablished a pair bond with the same mate (yes or no) and, if not, whether the bird was divorced (i.e., the previous mate was retained in the population but did not re-pair) or paired with a new bird (i.e., the previous mate was not retained in the population). For measurements of ecological factors, we recorded whether the individual changed nest type for each sequence and, if they changed, whether they moved from an old to a new nest or from a new to an old nest (old-new or new-old, respectively, which is associated with territory quality (Safran 2006)). We also included whether the bird had returned to the same

breeding site (yes or no) for each time. Lastly, for measurements of morphological factors, we calculated the change in streamer length and ventral feather coloration for each sequence.

#### Feather color

Feather sampling and analyses followed standard procedures (Jenkins et al. 2013). Briefly, we collected samples across a ventral transect of each bird and objectively measured color using an Ocean Optics USB4000 spectrometer (range 200–1,100 nm) using a fiber optic probe lit by a PX-2 Pulsed Xenon Light Source. We used average throat brightness as our measure of an individual’s ventral coloration, defined as the average reflectance (%) from 300 to 700 nm, after determining that the color descriptors (hue, chroma, brightness) and feather transect locations (throat, belly, breast, and vent) are all highly correlated.

#### Paternity analyses

Because of the high rate of EPP in this species, we performed paternity analyses for all nestlings in the first brood. We extracted DNA from nestling and adult blood samples that were stored in lysis buffer using DNEasy Blood and Tissue Extraction Kits (Qiagen, MD, USA). We then used polymerase chain reaction (PCR) to amplify six previously characterized microsatellite loci (*Escu6*, Hanotte et al. 1994; *Ltr6*, MacDonald and Potts 1994; *Pocc6*, Bensch et al. 1997; *Hir11*, *Hir19*, and *Hir20*, Tsyusko et al. 2007). Reaction conditions were optimized, with a pooled reaction for *Escu6*, *Ltr6*, *Hir20*, and *Hir11* primers (10- $\mu$ l solution with 50–100 ng of DNA, 0.12 mM each labeled forward and reverse primer, 200  $\mu$ M each dNTP, 3.25 mM magnesium chloride, 1X PCR buffer, and 0.15 units Taq polymerase (from New England Biolabs, MA, USA)); amplification protocol included an initial denaturation step, 94 °C for 1 min, 10 cycles with a denaturing phase at 94 °C for 30 s; an annealing phase at 55 °C for 30 s; and an elongation phase at 72 °C for 45 s, an additional 25 cycles starting at 87 °C for 30 s instead of 94 °C and a final extension at 72 °C for 3 min. *Pocc6* and *Hir19* were run in isolation, with modified reaction conditions and amplification schemes (modified from pooled reactions, *Pocc6* 1.25 mM magnesium chloride; *Hir19* 3 mM magnesium chloride and 0.2 mM each forward and reverse primer; amplification scheme was the same for both *Pocc6* and *Hir19*, where the pooled reaction was modified to have a 60 °C annealing temperature). Amplified PCR products with the fluorescently labeled forward primer were detected using an ABI3730 DNA analyzer (ABI, Inc.).

We genotyped 406 candidate parents and 477 offspring at all six loci using GeneMapper software (version 4.0, Applied Biosystems). We used CERVUS software (version 3.0.3) to

conduct paternity analysis; there was a first-parent exclusion probability of 0.922 for all six loci. Using the paternity exclusion protocol outlined in Neuman et al. (2007), we assigned paternity to 468 offspring, of these 169 offspring were sired by an extra-pair male. We used these analyses to determine the number and proportion of extra- and within-pair young in a given female's nest for the first brood.

Data analysis

All analyses were conducted using R (2.15.1, "Roasted Marshmallows") with the "nlme" and "lme4" packages. We utilized linear mixed models (LMM) and generalized linear mixed models (GLMM) to analyze (1) age-related patterns of performance (i.e., change in performance modeled by sequence), (2) patterns of age-relatedness in factors (i.e., change in factor modeled by sequence) as well as (3) the correspondence of these patterns (i.e., change in performance modeled by change in factor), with year and site as nested random effects, where each site was measured only once in a year. Year and site were included as random effects to control for natural variation between sites and years in reproductive performance as well as non-independence due to multiple breeding pairs at the same breeding site. We did not include individual identity as an additional random effect because each individual was measured only once within a site within a year. For the GLMMs, we used a binomial error structure with a logit link function. For both changes in mate fidelity and territory quality, there were more than two possible outcomes, so we analyzed the pairs of interest (i.e., old-new versus new-old and divorced versus same mates) and their relationship to sequence; the test statistic calculated was the Z statistic which is calculated as the parameter estimate divided by the standard error of the parameter estimate. P values from these models are calculated as an approximation of the loss of fit (i.e., increase in deviance) if the term was dropped from the model. For LMMs, the test statistics calculated were the t statistic (indicating within-sequence change) and the F statistic (indicating the difference between the sequences; see description above in "Longitudinal analyses"). We considered the analysis of each research question to be stepwise, where we proceeded to the next analysis only if a significant pattern was found in the current analysis (e.g., investigate age-related changes in factors only if there was age-related changes in performance).

Results

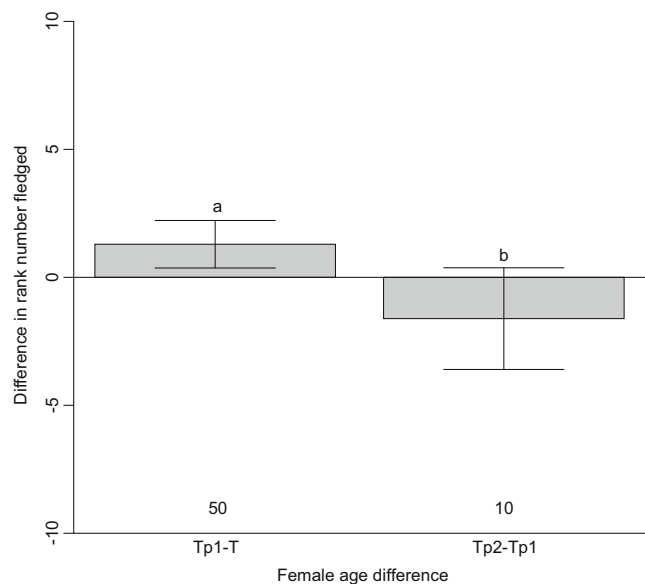
Patterns of age-related reproduction in females

Here, we examined differences in reproductive performance between and within sequences using longitudinal analyses to

examine within-individual changes for females, which revealed patterns of age-related reproduction.

Females show patterns of age-related reproductive performance in fledgling production, both within and between sequences. Females increased fledgling production within the first sequence: the change in number of fledged young that occurred between T and T+1 was significantly different from zero ( $t_{37}=2.794, P<0.01$ , Fig. 1), but did not change significantly within the second sequence (T+1 to T+2;  $t_{37}=-1.628, P=0.11$ , Fig. 1). Accordingly, the difference between sequences was significant (i.e., the rate of change within each of the two sequences was significantly different from one another: females had increased fledgling production in the first sequence compared to the second;  $F_{1,37}=7.235, P=0.01$ , Fig. 1).

Other indicators of seasonal performance including the onset of breeding (Julian lay date) and total egg production followed the same pattern as fledgling production between sequences (i.e., the rate of change between the two sequences was significantly different; onset of breeding tended to advance in sequence 1 and delay in sequence 2:  $F_{1,76}=4.616, P=0.03$ ; total egg production tended to increase in sequence 1 and delay in sequence 2:  $F_{1,96}=5.072, P=0.03$ ). However, there was not a significant difference within sequences in the onset of breeding and total egg production (i.e., the difference within each sequence was not significantly different from zero; onset of breeding: sequence 1:  $t_{76}=0.607, P>0.10$  and sequence 2:  $t_{76}=-1.64, P>0.10$ ; total egg production: sequence 1:  $t_{96}=-0.808, P>0.10$  and sequence 2:  $t_{96}=1.419, P>0.10$ ).



**Fig. 1** Patterns of age-related reproductive performance. Means are corrected for random effects. Time sequence notation (e.g., Tp1-T) indicates the individual change between the first and second years in sequence. Letters above bars indicate between-sequence differences; 95 % confidence intervals show whether the change within time sequences was significantly different from zero. Note sample sizes below each bar

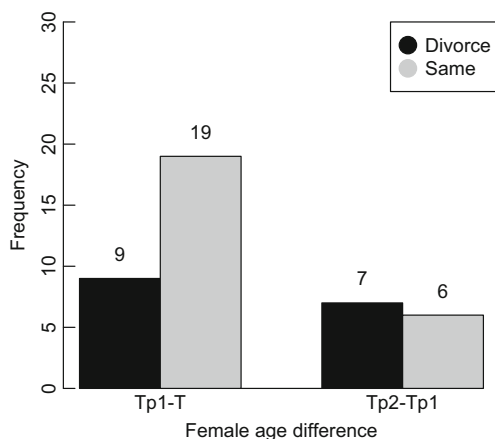
Females did not show any patterns of age-related changes in the number of extra-pair young in their nests either within sequence changes (time sequence 1:  $t_{15}=-0.604$ ,  $P=0.55$ ; time sequence 2:  $t_{15}=0.026$ ,  $P=0.97$ ) or between sequence differences ( $F_{1,15}=0.126$ ,  $P=0.73$ ).

Age-related changes in social, morphological, and ecological factors in females

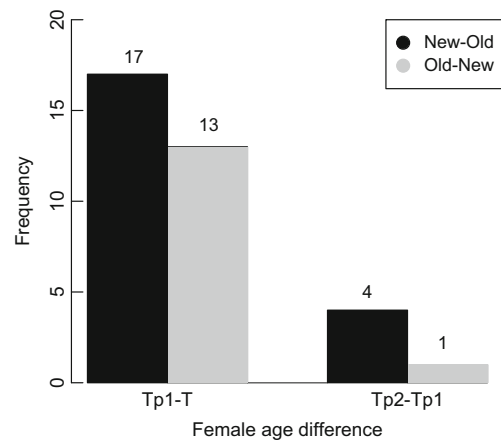
**Social factors** We did not find an age-related pattern with respect to divorce or mate fidelity; whether females divorced or retained their mate from the previous season was independent of sequence (i.e., the probability of divorcing or retaining was not significantly different between the first sequence (T to T+1) and the second sequence (T+1 to T+2);  $Z=-1.202$ ,  $P=0.23$ ,  $n_{obs}=41$ ; Fig. 2).

**Ecological factors** As the reuse of previously constructed (old) nests are associated with earlier clutch initiation dates and greater seasonal performance (Safran 2004, 2006), we predicted that returning (older) females should switch to older nests within breeding sites, when possible. Although some females changed territory quality between old and new nests, the females that changed to higher-quality nests (old nests) were not older, on average, than females that changed to lower-quality nests (new nests); the probability of “upgrading” to an old nest was not different between year sequences ( $Z=-0.0950$ ,  $P=0.34$ ,  $n_{obs}=35$ ; Fig. 3). Additionally, there were virtually no changes in site fidelity (out of 284 recaptures over 4 years, only four females changed site between seasons), and thus, we were unable to statistically test whether the benefits associated with site fidelity predict age-related performance.

**Morphological factors** There were significant age-related changes in female morphological variation related to tail



**Fig. 2** Age-relatedness of mate fidelity (*same*) or divorced (*divorce*) in females. Year sequence notation (e.g., Tp1-T) indicates the interval over which the fidelity or divorce occurred. Sample sizes are noted above each bar



**Fig. 3** Age-relatedness of territory quality changes. *Old-New* signifies a decrease in territory quality, *New-Old* indicates an increase in territory quality between years in sequence (e.g., Tp1-T). Sample sizes are noted above each bar

streamer length and ventral coloration. Females did not change in ventral brightness, measured as throat brightness, within the first sequence ( $t_{102}=-0.857$ ,  $P=0.39$ , see Fig. 4a), but decreased in brightness (i.e., became darker) within the second sequence ( $t_{102}=-2.688$ ,  $P<0.001$ , see Fig. 4a). The difference in the change in brightness between sequences was marginally significant ( $F_{1,102}=3.619$ ,  $P=0.059$ ; see Fig. 4a). Females increased tail streamer length in the first sequence ( $t_{99}=2.704$ ,  $P<0.01$ , see Fig. 4b), although not in the second sequence ( $t_{99}=1.643$ ,  $P=0.10$ ). The differences in tail streamer length between the sequences were not significant ( $F_{1,99}=0.32$ ,  $P>0.5$ , see Fig. 4b).

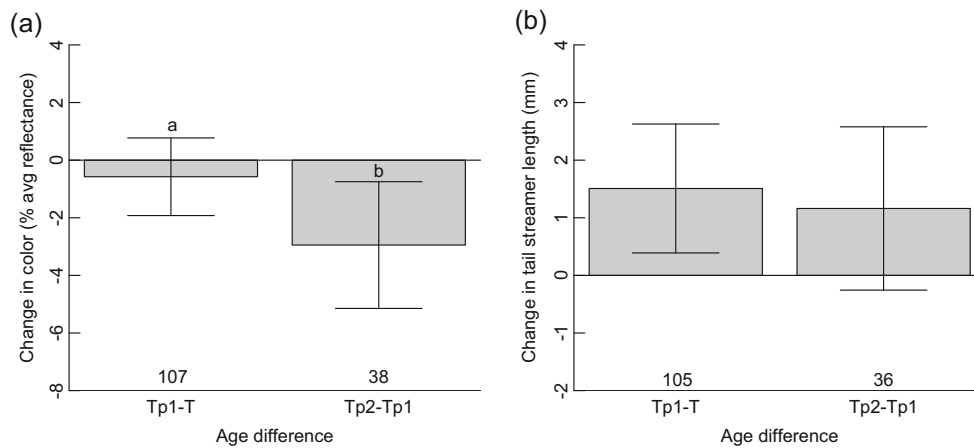
Concomitant changes between age-related performance and factors

To analyze whether age-related reproductive performance varied with social, morphological, or ecological factors that changed over an individual’s lifetime, we directly analyzed within-individual changes in performance as a function of within-individual changes in morphology. Per the previous section, this was the only factor among those we tested (Table 1) that changed significantly over the course of our study. In females, changes in morphology did not track with changes in fledgling production (tail streamer:  $F_{1,33}=0.16$ ,  $P=0.68$ ; ventral color:  $F_{1,35}=1.31$ ,  $P=0.26$ , Fig. 5a, b).

Discussion

We found that there are patterns of age-related reproductive performance, where females significantly increased their fledgling production relative to the population mean from T to T+1 (Fig. 1). Second, morphological trait variation changed over time: female tail streamer length increased at a





**Fig. 4** **a, b** Age-related changes in female morphology in **a** ventral color, where lower values indicate darker individuals, and **b** tail streamer length. Means are corrected for random effects. Time sequence notation (e.g., Tp1-T) indicates the individual change between the first and second years

stable rate over time and ventral plumage coloration darkened in later years (Fig. 4a, b). However, this age-related change in morphology did not predict changes in performance (Fig. 5a, b).

Patterns of age-related reproduction

Previous studies of age-related reproduction show patterns that are consistent with our results: an increase in reproduction until intermediate age and then a rapid senescent decline (e.g., male and female collared flycatcher, *Ficedula albicollis*, Gustafsson and Pärt 1990; female lesser snow geese, *Chen caerulescens*, Rockwell et al. 1993). These results corroborate the prevailing hypothesis that high investment in offspring production early in life corresponds with early senescence, particularly in short-lived birds (following Gustafsson and Pärt 1990; Péron et al. 2010).

We did not find that females allocated more or less to extra-pair paternity in their nests with age (contrasting patterns found in Lubjuhn et al. 2007), but it is likely that these decisions are based on male identity, as many studies have

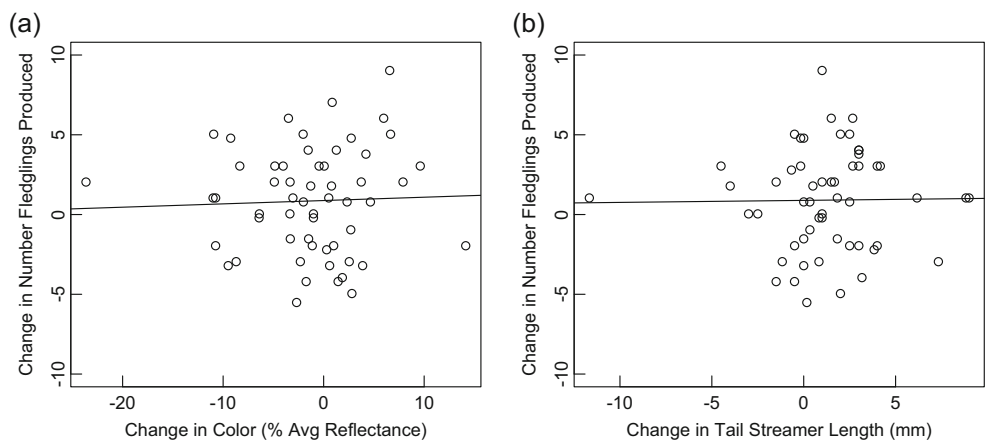
found a significant relationship between male age and extra-pair paternity (e.g., reed bunting, *Emberiza schoeniclus*, Bouwman et al. 2007; great tit, *Parus major*, Lubjuhn et al. 2007; pied flycatcher, *Ficedula hypoleuca*, Moreno et al. 2010; purple martin, *Progne subis*, Tarof et al. 2011).

Additionally, we did not find that individuals significantly advanced their breeding date (in either sequence) or significantly increased their clutch sizes (in either sequence). This contrasts with previous cross-sectional studies suggesting that breeding date advances with age (e.g., Robertson and Rendell 2001; Balbontín et al. 2007; Blas et al. 2009).

Social, ecological, and morphological factors over time in females

Of the five factors we investigated (Table 1), site fidelity, territory quality, and mate fidelity were not associated changes in performance over time. Regardless of age, the level of site fidelity in this population is consistent with what has been reported for most subspecies of *H. rustica* (Shields 1984; Galeotti et al. 2001; Saino et al. 2002; Safran 2004).

**Fig. 5** **a, b** Change in fledgling production by changes in morphology for females; **a** ventral coloration (n=56) and **b** tail streamer length (n=54). Fitted values, corrected for random effects, are shown



Because there was no variation in the degree of site fidelity among years, we could not evaluate its influence on changes in reproductive performance, although the lack of variation suggests that site familiarity is important for reproduction in short-lived species (as is the case for yellow warblers, *Dendroica petechia*, Lozano and Lemon 1999). While territory quality (defined here as nest age, see Safran 2006) is known to be an important predictor of performance in barn swallows, changes in territory quality were not found to be age-related in our population. Territory quality has been linked to age in studies of long-lived species that defend larger territories (e.g., Bonelli's eagle, *Hieraetus fasciatus*, Penteriani et al. 2003; black kite, *Milvus migrans*, Sergio et al. 2009). Likewise, we did not observe age-related changes in mate fidelity despite abundant supporting evidence in the literature, where older individuals remain with their mate longer and have higher performance up to a point, which may result from most studies examining these relationships in long-lived species (e.g., short-tailed shear water, *Puffinus tenuirostris*, Bradley et al. 1995; kittiwake, *Rissa tridactyla*, Naves et al. 2007). Because we found no evidence for adaptive divorce or mate fidelity, we suggest that divorce may be related more to age and sex differences in arrival time in this species, where older males typically arrive earlier than younger males and females of all ages (Møller and de Lope 1999; Ludwigs and Becker 2004; Balbontín et al. 2007).

We found that only one of several factors in our data set changed with sequence: morphology (see Table 1). Both tail streamer length and the darkness of ventral coloration increased with age in females in our population. Age-related morphology has been demonstrated in many studies and disparate species, although predominantly in males, such as house sparrows, *Passer domesticus*, (Nakawaga and Burke 2008); barn swallows, (Lifjeld et al. 2011); Jamaican field crickets, *Gryllus assimilis*, (Bertram and Rook 2011); and fiddler crabs, *Uca annulipes*, (Hayes et al. 2013).

#### Social and morphological factors influencing patterns of age-related reproduction

After determining that both reproductive performance and morphological variation changed within individuals over time, we explicitly addressed whether there are concomitant changes in streamer length or ventral color with changes in reproductive performance. While both morphology and reproduction are related to age, there is no evidence to suggest that changes in morphology and performance are related over time. This contrasts with previous studies, as some studies consider age-related morphology and age-related reproduction to be implicitly related and linked (sensu Lifjeld et al. 2011; e.g., tail length in male and female barn swallows, Balbontín et al. 2007; call characteristics in male Jamaican field crickets, Bertram and Rook 2011; mandible size in male

yellow-bellied marmots *Marmota flaviventris*, Cardini and Tongiorgi 2003). In studies that do consider the linkage between morphology and reproductive performance in an age-related context, often cross-sectional analyses are employed (Komdeur 2005; Bitton et al. 2008; Laskemoen et al. 2008; Nakawaga and Burke 2008; but see Bercovitch et al. 2003; Garamszegi 2005). We suggest that future studies of ornamentation and sexual signals explicitly test this relationship in a longitudinal framework in order to determine whether age-related changes in morphology can be evoked as an explanation for changes in an individual's reproductive performance.

#### Life history trade-offs and the role of experience

We were not able to consider breeding experience as a potential factor underlying patterns of age-related reproductive performance in this study, because no measure of experience could be fully independent from age as individuals breed every year after sexual maturation, and age is likely to covary with breeding experience in this short-lived species (Sanz-Aguilar et al. 2008). However, because breeding experience could be an important factor in producing patterns of age-related reproduction, as breeding experience is known to affect reproductive output, experimental studies should be designed to address this variable in short-lived species (Bradley et al. 1995; also see Bradley and Safran 2014).

#### Age-related performance: a longitudinal perspective

The results presented here demonstrate the utility of fully leveraging longitudinal data sets by asking whether changes in performance are concomitant with changes in social, ecological, and morphological factors using a longitudinal, within-individual analysis. The patterns and covariates of age-related performance are not easily detectable when using population-level analyses, as there may be many reasons for the given results such as progressive disappearance of inferior individuals over time (Forslund and Pärt 1995; van de Pol 2006). It is also important to consider the change in performance by sequence, instead of performance by age, as the goal of the within-individual analysis is to determine how much an individual changes between successive time intervals. Depicting performance at each age, while in some cases is more easily interpretable, does not fully take advantage of the paired analysis afforded by a longitudinal data set as it shows only population level age-related changes. In contrast, depicting changes in performance within and between year sequences demonstrates the within-individual change that occurs between successive years and is more informative when considering within-individual age-related improvements in performance. By examining changes in both performance and social and ecological factors, interpretation of results is more straightforward as it is within-individual analysis (e.g.,

females that have more breeding experience the previous season experience a subsequent decline in fledgling production the following year). This scheme for analyzing within-individual change may prove useful for other questions in evolutionary biology, such as those related to sexual selection (e.g., Bergeron et al. 2010; Lifjeld et al. 2011; Hayes et al. 2013).

**Acknowledgments** We acknowledge members of the Safran Lab at the University of Colorado, Boulder, for their comments and ideas throughout manuscript development as well as the field assistants that made collection of the data possible each summer: Matthew Wilkins, Conner Fitzhugh, Andrew Flynn, Maren Vitousek, Alexander Oesterle, Kate Gloeckner, Hayley Biddle, Tessa Warner, Stephen Alderfer, Audrey Tobin, and Ian Harold. We also acknowledge the Nevada Genomics Center for fragment analysis services. RJB was funded by the University of Colorado Boulder and Phi Beta Kappa. JKH and BRJ were funded by the University of Colorado Boulder Graduate School and the Ecology and Evolutionary Biology Department. RJS was supported by the National Science Foundation (IOS 0717421 and DEB-CAREER 1149942) and the University of Colorado.

**Ethical standards** The work done for this study has been approved by the University of Colorado's IACUC (permit no. 1004.01), the Colorado Division of Wildlife, and the United States Federal Bird-Banding lab.

## References

- Balbontín J, Hermosell IG, Marzal A, Reviriego M, de Lope F, Møller AP (2007) Age-related change in breeding performance in early life is associated with an increase in competence in the migratory barn swallow *Hirundo rustica*. *J Anim Ecol* 76:915–25
- Bensch S, Price T, Kohn J (1997) Isolation and characterization of microsatellite loci in a *Phylloscopus* warbler. *Mol Ecol* 6:91–92
- Bercovitch F, Widdig A, Trefilov A, Kessler MJ, Berard JD, Schmidtke J, Nürenberg P, Krawczack (2003) A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. *Naturwissenschaften* 90: 309–312
- Bergeron P, Grignolio S, Apollonio M, Shipley B, Festa-Bianchet M (2010) Secondary sexual characters signal fighting ability and determine social rank in Alpine ibex (*Capra ibex*). *Behav Ecol Sociobiol* 64:1299–1307
- Bertram SM, Rook V (2011) Jamaican field cricket mate attraction signals provide age cues. *Ethology* 117:1050–1055
- Bitton P, Dawson R, Ochs C (2008) Plumage characteristics, reproductive investment and assortative mating in tree swallows *Tachycineta bicolor*. *Behav Ecol Sociobiol* 62:1543–1550
- Blas J, Sergio F, Hiraldo F (2009) Age-related improvement in reproductive performance in a long-lived raptor: a cross-sectional and longitudinal study. *Ecography* 32:647–657
- Bouwman K, van Dijk R, Wijmenga J, Komdeur J (2007) Older male reed buntings are more successful at gaining extrapair fertilizations. *Anim Behav* 73:15–27
- Bradley RJ, Safran RJ (2014) Conceptual revisions and synthesis of proximate factors associated with age-related improvement in reproduction. *Ethology* 120:411–426
- Bradley J, Wooller R, Skira I, Serventy DL (1990) The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *J Anim Ecol* 59:487–496
- Bradley J, Wooller R, Skira I (1995) The relationship of pair-bond formation and duration to reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *J Anim Ecol* 37:31–38
- Brown CR, Brown MB (1999) Barn swallow (*Hirundo rustica*). The Birds of North America Online. <http://bna.birds.cornell.edu/bna/species/452>. Accessed 15 March 2014
- Cardini A, Tongiorgi P (2003) Yellow-bellied marmots (*Marmota flaviventris*) 'in the shape space' (*Rodentia, Sciuridae*): sexual dimorphism, growth and allometry of the mandible. *Zoomorphology* 122:11–23
- Cuervo JJ, Møller AP, de Lope F (2003) Experimental manipulation of tail length in female barn swallows (*Hirundo rustica*) affects their future reproductive success. *Behav Ecol* 14:451–456
- Devevey G, Bruyndonckx N, Houwald F, Studer-Thiersch A, Christe P (2009) Age-specific variation of resistance to oxidative stress in the greater flamingo (*Phoenicopterus ruber roseus*). *J Ornithol* 151: 251–254
- Ens BJ, Safrieli UN, Harris MP (1993) Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Anim Behav* 45:1199–1217
- Ericsson G, Wallin K, Ball JP, Broberg M (2001) Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* 82:1613–1620
- Forslund P, Larsson K (1992) Age-related reproductive success in the barnacle goose. *J Anim Ecol* 61:195–204
- Forslund P, Pärt T (1995) Age and reproduction in birds—hypotheses and tests. *Trends Ecol Evol* 10:374–378
- Galeotti P, Saino N, Perani E, Sacchi R, Møller AP (2001) Age-related song variation in male barn swallows. *Ital J Zool* 68:305–310
- Garamszegi L (2005) Age-dependent health status and song characteristics in the barn swallow. *Behav Ecol* 16:580–591
- Gustafsson L, Pärt T (1990) Acceleration of senescence in the collared flycatcher by reproductive costs. *Nature* 347:279–281
- Hanotte O, Zanon C, Pugh A, Dixon A, Burke T (1994) Isolation and characterization of microsatellite loci in a passerine bird: the reed bunting *Emberiza schoeniclus*. *Mol Ecol* 3:529–530
- Hayes CL, Booksmythe I, Jennions MD, Backwell PRY (2013) Does male reproductive effort increase with age? Courtship in fiddler crabs. *Biol Lett* 9:1–5
- Jenkins BR, Vitousek MN, Safran RJ (2013) Signaling stress? An analysis of pheomelanin-based plumage color and individual corticosterone levels at temporal scales in North American barn swallows, *Hirundo rustica erythrogaster*. *Horm Behav* 64:665–672
- Komdeur J (2005) Mutual ornamentation, age, and reproductive performance in the European starling. *Behav Ecol* 16:805–817
- Laskemoen T, Fosøy F, Rudolfson G, Lifjeld JT (2008) Age-related variation in primary sexual characters in a passerine with male age-related fertilization success, the bluethroat *Luscinia svecica*. *J Avian Biol* 39:322–329
- Lifjeld JT, Kleven O, Jacobsen F, McGraw KJ, Safran RJ, Robertson RJ (2011) Age before beauty? Relationships between fertilization success and age-dependent ornaments in barn swallows. *Behav Ecol Sociobiol* 65:1687–1697
- Lombardo MP, Thorpe PA (2010) Local breeding experience and the reproductive performance of tree swallows. *J Field Ornithol* 81: 294–301
- Lozano AGA, Lemon RE (1999) Effects of prior residence and age on breeding performance in yellow warblers. *Wilson Bull* 111:381–388
- Lubjuhn T, Gerken T, Brün J, Schmoll T (2007) Yearling male great tits, *Parus major*, suffer more strongly from cuckoldry than older males. *Zoology* 110:387–397
- Ludwigs J-D, Becker PH (2004) What do pairing patterns in common tern, *Sterna hirundo*, recruits reveal about the significance of sex and breeding experience? *Behav Ecol Sociobiol* 57:412–421

- MacDonald DB, Potts WK (1994) Cooperative display and relatedness among males in a lek-mating bird. *Science* 266:1030–1032
- Maklakov AA, Hall MD, Simpson S, Dessiman J, Clissold FJ et al (2009) Sex differences in nutrient-dependent reproductive ageing. *Aging Cell* 8:324–340
- 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
- Møller AP, de Lope F, Saino N (2005) Reproduction and migration in relation to senescence in the barn swallow *Hirundo rustica*: a study of avian “centenarians.”. *Age* 27:307–318
- Moreno J, Martínez J-G, Morales J, Lobato E, Merino S, Tomás G, Vázquez RA, Möstl E, Osorno JL (2010) Paternity loss in relation to male age, territorial behaviour and stress in the pied flycatcher. *Ethology* 116:76–84
- Nakawaga S, Burke T (2008) The mask of seniority? A neglected age indicator in house sparrows *Passer domesticus*. *J Avian Biol* 39: 222–225
- Naves LC, Cam E, Monnat JY (2007) Pair duration, breeding success and divorce in a long-lived seabird: benefits of mate familiarity? *Anim Behav* 73:433–444
- Neuman CR, Safran RJ, Lovette IJ (2007) Male tail streamer length does not predict apparent or genetic reproductive success in North American barn swallows *Hirundo rustica erythrogaster*. *J Avian Biol* 38:28–36
- Packer C (1979) Male dominance and reproductive activity in *Papio anubis*. *Anim Behav* 27:37–45
- Penteriani V, Balbontin J, Ferrer M (2003) Simultaneous effects of age and territory quality on fecundity in Bonelli's eagle *Hieraetus fasciatus*. *Ibis* 145:77–82
- Péron G, Gimenez O, Charmantier A, Gaillard J, Crochet P (2010) Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proc R Soc Lond B* 277:2849–2856
- Robertson RJ, Rendell WB (2001) A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. *J Anim Ecol* 70:1014–1031
- Rockwell R, Cooch E, Thompson C, Cooke F (1993) Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry. *J Anim Ecol* 62:323–333
- Roff DA (1992) The evolution of life histories: theory and analyses. Oxford University Press, Oxford
- Safran RJ (2004) Adaptive site selection rules and variation in group size of barn swallows: individual decisions predict population patterns. *Am Nat* 164:121–131
- Safran RJ (2006) Nest-site selection in the barn swallow, *Hirundo rustica*: what predicts seasonal reproductive success? *Can J Zool* 84:1533–1539
- 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
- Saino N, Ambrosini R, Martinelli R, Møller AP (2002) Mate fidelity, senescence in breeding performance and reproductive trade-offs in the barn swallow. *J Anim Ecol* 71:309–319
- Sanz-Aguilar A, Tavecchia G, Pradel R, Minguéz E, Oro D (2008) The cost of reproduction and experience-dependent vital rates in a small petrel. *Ecology* 89:3195–3203
- Sergio F, Blas J, Baos R, Forero MG, Donazar JA, Hiraldo F (2009) Short- and long-term consequences of individual and territory quality in a long-lived bird. *Oecologia* 160:507–514
- Shields W (1984) Factors affecting nest and site fidelity in Adirondack barn swallows. *Auk* 101:780–789
- Shields W, Crook JR (1987) Barn swallow coloniality: a net cost for group breeding in the Adirondacks? *Ecology* 68:1373–1386
- Tarof SA, Kramer PM, Tautin J, Stutchbury BJM (2011) Effects of known age on male paternity in a migratory songbird. *Behav Ecol* 23:313–321
- Tsyusko OV, Peters MB, Hagen C, Tuberville TD, Mousseau TA, Møller AP, Glenn TC (2007) Microsatellite markers isolated from barn swallows (*Hirundo rustica*). *Mol Ecol* 7:833–835
- van de Pol M (2006) Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (*Haematopus ostralegus*). *Behav Ecol* 17:982–991