Morphological Changes Predict Inter-Seasonal Reproductive Performance
In the North American Barn Swallow

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ABSTRACT

Differential allocation between providing costly parental care and self-preservation is a well-known trade off in evolutionary theory. Across a variety of vertebrate taxa, a pattern exists where younger individuals tend to produce less offspring than older individuals after the onset of reproduction. I present data from a three-year study in a population of North American barn swallows Hirundo rustica erythrogaster to determine whether there is a pattern of age-related increases in reproduction and analyze how within-individual (1) site fidelity, (2) social mate, and (3) changes in morphology affect patterns of seasonal reproductive success, defined as the total number of young fledged in a given breeding season. Over the course of this study, I did not detect a clear pattern of increases in reproduction with age. Interestingly, significant changes in morphology between years predicted reproductive performance; females that minimized growth in tail streamers between 2008 and 2009 had greater reproductive performance. Males that became darker had greater reproductive performance only between 2008 and 2009. These relationships were not detected in the years between 2009 and 2010. I did not find that site fidelity or mate familiarity significantly impacted reproductive performance, in contrast to what was concluded in previous work. These analyses of intrinsic, morphological changes within individuals indicate that there are important underlying age-related mechanisms of reproductive performance.
INTRODUCTION

Differential allocation between providing costly parental care and self-preservation is a well-known trade-off described by evolutionary theory (Roff 1992, Stearns 1992). Interestingly and in support of this theory, there is a prevalent pattern among vertebrate taxa where younger individuals tend to produce less offspring than older individuals, up to a point (Forslund and Larsson 1992, Nussey et al. 2006, Hamel et al. 2009, Ericsson et al. 2001, Bercovitch et al. 2003, Packer 1979). For long-lived taxa, patterns towards the end of life are indicative of senescence with declining reproductive performance begins to decline over time. Because birds present such a diverse and well-studied group much research has been devoted to examining life history patterns related to age and reproductive performance using long-term descriptive data as well as experimentation (Curio 1983, Balbontín et al. 2007, Bradley et al. 1995, Hatch and Westneat 2007, Komdeur 1996, Cichoñ 2003).

A growing body of literature is focused on the ecological mechanisms that underlie age-related reproductive performance and addresses predictors that are highly correlated with age including: 1) the accumulation of breeding performance or experience, 2) social pair bond duration, 3) fidelity to a particular breeding location, 4) resource or territory quality, or 5) other extrinsic effects including abiotic events such as highly inclement weather and prey resource fluctuations (Martin 1995, Lozano and Lemon 1999, Lombardo and Thorpe 2010, Laaksonen et al. 2002). However, there has been limited investigation of intrinsic changes that an individual may experience with age, such as changes in morphology or physiological factors (Angelier et al. 2007) although these variables themselves have been the subject of investigation for age-related reproduction within a breeding season (e.g., Safran et al. 2010) and may also vary within individuals over time. Indeed, there are a number of morphological traits thought to vary with age, (see Table 1). Some of these changes have been
found to significantly impact reproductive performance, such as in the American bighorn sheep *Ovis canadensis*, where older individuals grow longer horns with age and have a greater probability of winning contests over mates (Coltman *et al.* 2002).

While extrinsic changes, such as accumulation of pair bond experience, breeding experience, and local site experience, have been studied in relation to their effect on reproductive performance, the effect of within-individual changes in morphological traits and their effects reproductive performance are less well understood. Using a three-year data set on a short-lived passerine bird, I adopt longitudinal approaches to analyze directly within-individual changes in behavior, morphology and performance, where reproductive performance is defined as the number of fledgling produced in a breeding season. I hypothesize that 1) there are age-related patterns in reproductive performance, based on previous work that has shown that many bird species increase fledgling production with age (Forslund and Pärt 1995), 2) there are changes in morphology that positively predict fledgling production, as there are morphological characteristics that predict performance in this system (Safran and McGraw 2004), and in other populations these characteristics change through time (Balbontín *et al.* 2007), and 3) that mate retention between years leads to greater performance, as this trend has been seen in many species, and was found to be significant across avian taxa in a meta-analysis by Cezilly and Dubois (2002); for predictions, see Table 2. Here, I characterize age-related changes in reproductive performance to determine whether they follow the predominant pattern of increased productivity over time and test hypotheses about the role of extrinsic and intrinsic factors for predicting age-related patterns of performance.

**METHODS**

*Study System*

The barn swallow *Hirundo rustica erythrogaster* is a migratory, insectivorous passerine bird that breeds throughout North America. It is one of six sub-species of the Holarctic-distributed barn swallow species complex (Brown
and Brown 1999). Barn swallows are a short-lived species, living on average for two to three years (Møller and De Lope 1999). Barn swallows are also a model species for sexual selection and two ornamental traits, tail streamers and ventral coloration. These traits have been studied extensively to determine their role in predicting reproductive success in North American and European barn swallows (Neuman et al. 2007, Safran and McGraw 2004, Møller and Tegelström 1994). It appears that tail streamer length is under strong sexual selection in European populations (Saino et al. 1997) and ventral color is a signal used in mate-selection in North American populations (Safran et al. 2005). Barn swallows breed in protected sites in horse barns and culverts either in colonies or solitary pairs, and are highly philopatric, returning to the same site year after year (Møller 1994). They are socially monogamous, and commonly pair for the entirety of the breeding season (April through September). However, extra-pair copulations occur at high rates in barn swallow populations (Safran et al. 2005, Neuman et al. 2007). Breeding pairs will either occupy preexisting nests or construct new nests at the start of the breeding season (Safran 2004, Safran 2006). In each breeding season, females lay two to three clutches, each consisting of two to six eggs. The nestlings are altricial, incapable of feeding themselves for the first few weeks of life; both parents care for the young during the nestling stage, and females perform most of the parental care during the two-week egg incubation period.

Over three breeding seasons, from 2008 to 2010, we studied a population of barn swallows from May to September in Boulder County, Colorado. In all, we gathered breeding data on over 350 adult barn swallows and data on over 500 of their offspring each season. My longitudinal analyses take advantage of a reduced data set, which is comprised of individuals who were tracked for part of or the entirety of the sampling period from 2008 to 2010. Additional details about this data set are found below in the section on Data Organization.
**Data Collection**

Using mist nets, we captured individuals during the first two weeks of the breeding season after pairs had formed, across 17 different study sites located in and around Boulder County, Colorado. We uniquely marked the tail streamers of individuals with colored markers following Shields and Crook (1987), which do not affect reproductive performance (Safran 2004). We also applied numbered aluminum USFWS 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 from the ventral portion of the bird in order to objectively measure color. We checked nests at least every four 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).

**Feather Color**

To analyze color, we taped samples of feathers from each plumage patch (throat, breast, belly and vent) to a standard white card background, in the way they lay on the bird. We analyzed the prepared samples with an Ocean Optics USB4000 spectrometer (range 200-1100 nanometers (nm)) using a fiber optic probe at an angle of 90˚ to the feather surface lit by a PX-2 pulsed xenon light source. We excluded ambient light by using a metal probe holder, placed against the feather sample at a constant distance from each sample, so that a 2.5 millimeter (mm) diameter of light hit the feather surface. To standardize our samples, reflectance data were generated relative to a white standard (Ocean Optics WS-1) and a dark standard (all light excluded). We collected these data with SpectraSuite software package (version 2.0.125, Ocean Optics Inc., Dunedin, FL). To reduce noise from the spectrometer, we generated 20 spectra per individual with an integration period of 200 milliseconds (5 spectra per plumage patch) and averaged the values. This procedure was repeated three times for each sample, and between each scan we lifted the probe. The three scans were performed in approximately the same location in the colored feather
area. We used average brightness as our measure of an individual’s coloration, defined as the average reflectance (%) from 300 nm to 700 nm. I used average throat brightness as the metric for darkness (lower values mean a darker bird), as there is a strong correlation between other well-known color descriptors including hue (color purity) and chroma (color intensity), as well as the three other ventral areas where feather samples are collected (throat, belly, breast and vent; Safran and McGraw 2004).

Data Organization

Using the database gathered from individuals caught in 2008 to 2010, I identified individuals that returned for at least two successive years during this period. Because an individual’s exact age was not known (less than 0.5% of individuals born at our study site return as breeders), and not every individual returned for all three years, I analyzed data from 2008-2009 and 2009-2010 as separate data sets, so that analyses would reflect individuals in year (t) and year (t+1) for each data set.

Reproductive performance is defined as the total number of young fledged in each given breeding season. For analyses that required comparisons between years, I used a standardized measure of total reproductive performance, so that all values were relative to the population mean standardized to zero. In 2008, mean population reproductive performance (RS) was 4.65 fledglings (n=144), in 2009 mean RS was 3.35 (n=183), and in 2010 mean RS was 0.897 (n=175). In 2009 and 2010 there were ongoing manipulative experiments which involved removing clutches from experimental birds and manipulating brood sizes, respectively. As a result, breeding data for birds that were used in experiment years were excluded for all standardizations and analyses . For this reason and because there may have been some circumstances in which some birds may not have had all morphological measures taken in every year, not all analyses presented below have equivalent sample sizes. Instead, I compiled datasets to maximize our sample sizes for each analysis.
The final data compilation included all morphological measurements available for each bird including right wing length (RWL; mm), right tail streamer (RTS; mm), mass (grams) and average throat brightness (% reflectance). For all birds assigned to a nest in each year, I recorded Julian lay date, total reproductive performance, standardized reproductive performance, whether the bird had re-mated, was mated with a new bird, or experienced a divorce (i.e., previous mate was retained in the breeding population, but was not associated with the individual). To analyze between-year changes and their impact on reproductive performance, I calculated changes in morphology by subtracting the second year from the first year (e.g., average throat brightness in year 2 minus average throat brightness in year 1). This allowed me to determine whether age-related changes in morphology affect reproductive performance.

Data Analysis: Changes within individuals over time

Using the statistical packages JMP 9 (version 9.0.0, SAS institute) and SAS (version 9.2.0, SAS institute), I used paired analyses to determine whether individual changes in reproductive performance were different between years 2008-2009 and 2009-2010. I also used paired analyses to determine whether any features of morphological variation changed over time within individuals. I applied Wilcoxon signed rank analyses to determine whether individual performance and morphological variation was consistent between years. I report all mean difference values expressed ± standard deviation in Table 3.

Data Analysis: Mixed Linear Models

To determine whether changes in morphology explained reproductive performance, I used general linear mixed models (GLMM) with site and Julian lay date as random effects, and morphological variables as fixed effects that changed significantly between years (i.e. change in mass, throat brightness, and tail streamer). I did not include changes in wing length, as they were highly correlated with the other morphological variables including mass and streamer length in both males and females. In mixed linear models, random effects control for variation due to sampling design or environmental variation that could
confound my results. Site was included as a random effect to control for natural variation between sites that may lead to differing reproductive performance. I also included Julian lay date as a random effect to control for seasonal effects that may play a role in predicting total RS, where earlier breeders may have more performance due to environmental changes. Males and females were analyzed in separate models as they are sexually dimorphic in size and color (Safran and McGraw 2004).

Additionally, I constructed a GLMM to analyze whether pair status affected breeding performance in order to address whether being paired with a previous or new mate affected reproductive performance compared to the previous year. I defined pair status in two ways. First, “new” pairs are those in which individuals did not pair with their mate from the previous year. I included both birds that were forced to re-mate (i.e. their mate from the previous year did not return to our study area) as well as birds that divorced (i.e. their mate was still present in the breeding population) as “new” to indicate that the individual was unfamiliar with their current mate. Second, “same” pairs are comprised of members who were paired in the previous year. To eliminate the problem of pseudo-replication (analyzing both members of the same pair bond), I did not include males whose mate was present during the season’s breeding biology. In the model, I used pair status (new or same) as a fixed effect, with site and Julian lay date random effects as functions of the response variable, total reproductive performance in the second year, excluding experimental individuals. I repeated this analysis for both 2008-2009 and 2009-2010.

RESULTS

Age-related changes in reproduction

In both 2008-2009 and 2009-2010, neither males nor females significantly changed their reproductive performance (Figure 1, Table 3). Females tended to increase their performance relative to the population mean and males tended to decrease, but neither trend was statistically significant in either pair of years.
Age-related changes in morphology

In both males and females, individuals tended to become larger (wing length), darker (decreased brightness) and heavier over time (Table 3, Figures 2 through 5), although these trends were not always statistically significant.

Between 2008 and 2009, females that were successful in the first year, tended to be again successful in the second year (Wilcoxon signed rank, S = 94.50, p = 0.04), but this was not true in 2009-2010 (Wilcoxon signed rank, S = 55.00, p = 0.22). Males were not consistent in fledgling production during either set of years (Wilcoxon signed rank, S_{08-09} = -48.50, p = 0.09; S_{09-10} = -26.50, p = 0.26). Both females and males were consistent in 2008-2009 and 2009-2010 for tail streamer length (females: S_{08-09} = 422.50, p < 0.01, S_{09-10} = 656.5, p < 0.01; males: S_{08-09} = 410.00, p < 0.01, S_{09-10} = 674.00, p < 0.01). Only males were consistent in wing length in both year sets, although the relationship changed between years, from a negative relationship in the first set to a very positive relationship in the 2009-2010 year set (S_{08-09} = -246.50, p < 0.01, S_{09-10} = 434.50, p < 0.01). Females were consistent in mass for both year sets (S_{08-09} = 242.50, p < 0.01, S_{09-10} = 553.50, p = 0.05).

Changes in morphology as predictors of reproductive performance

For females in 2008-2009, only changes in right tail streamer predicted reproductive performance, and changes in mass did not (Table 4). Females that lengthened their tail streamers between years tended to have lower reproductive performance than females whose streamers either shortened or remained similar over time. In males in 2008-2009, only changes in throat brightness were significantly related to reproductive performance, where darker males had greater reproductive performance (Table 4). However, in 2009-2010, such trends were not observed, and no morphological changes significantly predicted reproductive performance (Table 4).

Change in mate as a predictor of reproductive performance
Pair status in 2008-2009 and 2009-2010 did not significantly predict reproductive performance in either year ($F_{08-09} = 1.92$, $p = 0.19$; $F_{09-10} = 0.76$, $p = 0.39$; Figure 6).

**DISCUSSION**

*Age-related changes in reproduction*

There was no clear age-related pattern of reproductive performance in barn swallows. There were suggestive trends, in which females tended to increase reproductive success over time whereas males tended to decrease over time but these trends were neither statistically significant nor consistent within an individual between years; i.e., an individual’s reproductive performance in year (t) was not indicative of their performance in year (t+1). This may have been due to decreased sample sizes for each year, and the effects of widespread predation in our study area, particularly in 2010. Additionally, as we do not know exact age of the individuals, there may potentially be an obscured effect of senescence in these results (Saino 2002). However, as individual barn swallows tend to live two to three years, it is unlikely that there are a significantly large number of senescing old-aged birds (> 4 years of age) that would skew results in this study (Saino 2002, Balbontín *et al.* 2007). Also, unlike previous work that grouped individuals into age cohorts, the present study utilized a unique longitudinal, within-individual approach that uses paired analyses to control for aspects unique to each individual that do not change over time (e.g., genetic variation). The absence of an increase in reproduction over a three-year period in this study, contrasting Balbontín *et al.* (2007), suggests additional factors, such as predation and inclement weather that may be affecting North American swallows and obscure normal age-related patterns. Additionally, previous studies suggest that age may play a role in extra-pair copulations (EPC) where older males are more likely to obtain EPCs, as well as protect paternity in their own nest, such that paternity to this study of reproductive performance might yield different results, especially for males (Schmoll *et al.* 2007, Budden and Dickinson 2009).
Age-related changes in morphology

Barn swallow morphology changes over time. Males and females increase tail streamer length between seasons, males become darker between years, and females became heavier. Individuals were morphologically consistent between years (e.g., individuals that were darkest in year (t) were also darkest in year (t+1)). These changes are consistent with findings with European barn swallows, Hirundo rustica rustica (Balbontín et al. 2010, Galván and Møller 2009). Not all morphological trends were consistent between the year sets analyzed, however. Females became darker, and males became heavier only in 2009-2010. Males also decreased their wing length significantly in 2008-2009, yet increased in 2009-2010. These differences may be a product of changes in environment, both in the breeding grounds and in the over-wintering grounds. In the 2010 breeding season, fledgling production declined severely, apparently as a result of virulent predation by magpies and other predators, as well as inclement weather that plagued the season (noted by personal observation). Additionally, the over-wintering grounds of these birds are unknown, and so changes in morphology may thus reflect the availability of food and other resources of these latter areas more than an individual’s intrinsic and programmed rate of change. Our future work on stable isotopes, analyzing isotope signatures found in birds’ feathers, will allow us to infer the migratory distance of individuals within our population and to some extent, their nutritional state during the non-breeding season, which may be a significant predictor of seasonal reproductive performance (Norris 2005).

Changes in morphology as predictors of reproduction

Some changes in morphology significantly predicted reproductive performance in 2008-2009, but not in 2009-2010. Females that minimally increased their tail streamer length had better performance, which might indicate a physiological cost of growing streamers, although this was not seen in both year sets. This result differs from studies with H.r. rustica in Europe, which demonstrate that individuals with longer tail streamers have greater reproductive success (Møller and Tegelström 1997). In the first two years in this study, males
that became darker between years performed better. Based on previous showing a causal relationship between male ventral coloration and reproduction in North American barn swallows (Safran and McGraw 2004), males would be expected to increase in darkness with age and reproduce more as a result. Such a trend could indicate that females are sexually selecting, or “choosing” males that are darker as an indication of age, which could in turn indicate some measure of quality or good genes (Freeman-Gallant et al. 2010). The inconsistencies between year sets may be due to the stochastic breeding and over-wintering environments mentioned previously.

Changes in mate as a predictor of reproduction

Whether or not an individual was familiar with their mate did not affect reproductive success in either year set. This finding contrasts with the results of previous studies with H.r. rustica and other birds, in which age per se and pair bond length were significant predictors of reproductive performance (Balbontín et al. 2007, Dubois and Cezilly 2002). This may be related to how pair status was considered, as a binary variable, where in other studies pair status is expressed as the number of years a pair has bred together (Clum 1995, Dubois and Cezilly 2002). However, as barn swallows only tend to survive to two or three years old, pair bond length is unlikely to have an effect on these findings. Additionally, as noted previously, pair bond status may be overridden by strong stochastic changes in the physical environment. The “mate familiarity” hypothesis predicts that individuals in pair bond are able to coordinate their provisioning efforts at the nests, significantly increasing fledgling production (Cezilly and Dubois 2002). When there are extreme fluctuations in temperature or predation as in this population of barn swallows, mate familiarity may not actually increase reproduction (Fowler 1995). Alternatively, research would suggest that some species’ mate fidelity may be due more to site fidelity and synchronous return to the nest site than to the mate’s ability to contribute to nest productivity (Møller 2007, Møller et al. 2009). Mate fidelity may simply be a result of synchronized migration and philopatry in swallows, and there may not be a benefit to remaining in a pair bond.
Conclusions

There was no a widespread pattern of age-related reproduction in this population of barn swallows, but there were marked changes in morphology that correspond with age. Interestingly, these changes impacted reproductive performance, in some, but not all years. My results corroborate previous work on changing morphology, although as suggested by Neuman et al. (2007), tail streamer length does not play a role in reproduction in this population of North American barn swallows. Male ventral coloration is associated with an increase in performance in some years, which supports previous work in North American barn swallows (e.g., Safran and McGraw 2004 and Safran et al. 2005). Additionally, pair bond maintenance between two breeding seasons does not appear to impact reproductive performance, which is in contrast to work by Balbontín et al. (2007). Differences between years analyzed indicate the presence of important environmental factors which influence reproduction. While the present study was able to focus on intrinsic morphological change and mate familiarity within an individual, there are numerous other ecological changes that occur in an individual’s lifetime. These include over-wintering and breeding environment, changing levels of predation between years, and weather during migration. In summary, important morphological changes take place between breeding seasons, which may have an effect on reproductive performance, but their effect depends on the changing environment in which individuals breed.
Table 1. Examples of age-related morphological variation in a wide range of vertebrate taxa.

<table>
<thead>
<tr>
<th>Genus and Species</th>
<th>Common name</th>
<th>Study</th>
<th>Age-dependent trait</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Marmota flaviventris</em></td>
<td>Yellow-bellied marmot</td>
<td>Cardini and Tongiorgi 2003</td>
<td>Increasing mandible strength and size</td>
</tr>
<tr>
<td><em>Sialia Mexicana</em></td>
<td>Western bluebirds</td>
<td>Budden and Dickinson 2009</td>
<td>Increasing head plumage brightness</td>
</tr>
<tr>
<td><em>Geothlypis trichas</em></td>
<td>Common yellowthroat</td>
<td>Freeman-Gallant et al 2010</td>
<td>Increasing facial mask size, bib brightness</td>
</tr>
<tr>
<td><em>Sturnus vulgaris</em></td>
<td>European starling</td>
<td>Komdeur et al 2005</td>
<td>Increasing throat feather iridescence</td>
</tr>
<tr>
<td><em>Luscinia svecica</em></td>
<td>Bluethroat</td>
<td>Laskemoen et al 2008</td>
<td>Increasing testes size, seminal glomera size, cloacal protuberance size</td>
</tr>
<tr>
<td><em>Otis tarda</em></td>
<td>Great bustard</td>
<td>Alonso et al. 2010</td>
<td>Increasing body size</td>
</tr>
<tr>
<td><em>Ursus americanus</em></td>
<td>American black bear</td>
<td>Costello et al. 2009</td>
<td>Increasing body size</td>
</tr>
<tr>
<td><em>Capreolus capreolus</em></td>
<td>European roe deer</td>
<td>Vanpé et al. 2009</td>
<td>Increasing antler size</td>
</tr>
<tr>
<td><em>Ovis Canadensis</em></td>
<td>Bighorn sheep</td>
<td>Coltman et al. 2002</td>
<td>Increasing horn length</td>
</tr>
</tbody>
</table>
Table 2. Summary table of research questions with hypotheses and predictions that will be addressed in this study.

<table>
<thead>
<tr>
<th>Question</th>
<th>Hypothesis</th>
<th>Predictions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Do individuals reproduce better with age?</td>
<td>There are age-related patterns in reproductive performance in barn swallows</td>
<td>1) Individuals will significantly increase reproductive performance over time.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2) Variables that co-vary with age will be significantly related to reproduction</td>
</tr>
<tr>
<td>Does morphology change with age, and does this impact reproductive performance?</td>
<td>Morphology changes with age and significantly impacts subsequent reproductive performance</td>
<td>1) Individuals’ morphological measurements will significantly change between years</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2) Changes in these measurements will significantly explain reproductive performance</td>
</tr>
<tr>
<td>If an individual retains its mate between years, does this increase reproductive performance?</td>
<td>Mate retention between years leads to greater reproductive performance.</td>
<td>1) Reproductive performance will be related to pair status, whether an individual is paired with the same or a new bird than the year prior</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2) Birds that paired with a new bird will have significantly lower reproductive performance than those that stayed with the same mate</td>
</tr>
</tbody>
</table>
Table 3. Changes in within-individual performance and morphology between pairs of years. Significant results (p < 0.05) are denoted by bolded text and asterisk (*). Note that a decrease in color indicates that individuals get less bright or visually ‘darker’ over time. Mean differences are expressed ± standard deviation; sample sizes are reported beside the trend directions.

<table>
<thead>
<tr>
<th>Term</th>
<th>Sex</th>
<th>2008-2009</th>
<th>2009-2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2008-2009</td>
<td>2009-2010</td>
</tr>
<tr>
<td>Standardized Reproductive Performance</td>
<td>Males</td>
<td>Decrease (21)</td>
<td>Decrease (18)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-1.475 ± 3.755</td>
<td>-0.991 ± 3.92</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>Increase (29)</td>
<td>Increase (28)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.525 ± 0.832</td>
<td>1.131 ± 3.611</td>
</tr>
<tr>
<td>Wing Length</td>
<td>Males</td>
<td>Decrease (48)*</td>
<td>Increase (72)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-1.667 ± 2.39</td>
<td>0.672 ± 2.48</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>Increase (54)</td>
<td>Increase (70)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.895 ± 1.49</td>
<td>0.246 ± 3.01</td>
</tr>
<tr>
<td>Tail Streamer Length</td>
<td>Males</td>
<td>Increase (44)*</td>
<td>Increase (65)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.62 ± 2.77</td>
<td>2.138 ± 4.69</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>Increase (50)*</td>
<td>Increase (67)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.26 ± 3.23</td>
<td>1.36 ± 2.73</td>
</tr>
<tr>
<td>Throat Brightness</td>
<td>Males</td>
<td>Decrease (48)*</td>
<td>Decrease (71)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-2.27 ± 5.67</td>
<td>-3.38 ± 5.87</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>Decrease (47)</td>
<td>Decrease (69)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-1.48 ± 8.43</td>
<td>-1.86 ± 6.53</td>
</tr>
<tr>
<td>Mass</td>
<td>Males</td>
<td>Increase (48)</td>
<td>Increase (71)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.21 ± 1.22</td>
<td>0.792 ± 1.20</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>Increase (54)*</td>
<td>Increase (69)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.94 ± 2.60</td>
<td>1.23 ± 2.51</td>
</tr>
</tbody>
</table>
Table 4. Results from the general linear mixed model for females and males (2008-2009, 2009-2010). These models portray morphological changes ($\Delta$) as a function of total reproductive performance in the second year.

<table>
<thead>
<tr>
<th>Term</th>
<th>Estimate</th>
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Figure 1. Changes in standardized reproductive success ± standard error bars (number of fledglings produced per year) for 2008-2009 and 2009-2010 for males and females. These relationships were not significant.
Figure 2. Changes in wing length ± standard error in 2008-2009 and 2009-2010 for males and females. Males significantly changed in both year sets.
Figure 3. Changes in tail streamer length ± standard error bars in 2008-2009 and 2009-2010 for males and females. Males and females changed significantly in both year sets.
Figure 4. Changes in throat brightness ± standard error in 2008-2009 and 2009-2010 for males and females. Lower values indicate darker individuals; negative changes in color indicate that individuals become darker in appearance over time. Males significantly changed in both year sets; females only changed significantly in 2009-2010.
Figure 5. Changes in mass ± standard error bars in 2008-2009 and 2009-2010 for males and females. Females became significantly heavier in both year sets; males only became significantly heavier in 2009-2010.
Figure 6. Average least square mean differences in reproductive performance ± standard error for newly and same mated individuals in 2008-2009 and 2009-2010.
REFERENCES


