Morphological Predictors and Genetic Consequences of Nest Predation in the North American Barn Swallow Hirundo Rustica Erythrogaster

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MORPHOLOGICAL PREDICTORS AND GENETIC CONSEQUENCES OF NEST PREDATION IN THE NORTH AMERICAN BARN SWALLOW *HIRUNDO RUSTICA ERYTHROGASTER*

by

ANDREW JAMES HABERSTROH FLYNN

B.A., University of Colorado, 2012

M.A., University of Colorado, 2012

A thesis submitted to the
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This thesis entitled:
Morphological predictors and genetic consequences of nest predation in the North American
barn swallow *Hirundo rustica erythrogaster*
written by Andrew James Haberstroh Flynn
has been approved for the Department of Ecology and Evolutionary Biology

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Dr. Rebecca Safran

__________________________________________
Dr. Michael Breed

Date April 19, 2012

The final copy of this thesis has been examined by the signatories, and we
Find that both the content and the form meet acceptable presentation standards
Of scholarly work in the above mentioned discipline.
Flynn, Andrew James Haberstroh (M.A., Ecology and Evolutionary Biology)
Morphological predictors and genetic consequences of nest predation in the North American barn swallow *Hirundo rustica erythrogaster*
Thesis directed by Assistant Professor Rebecca J. Safran

Nest predation is the primary cause of reproductive failure in most bird species, and thus is a powerful source of natural selection within populations. As nest predation is strongly tied to an individual’s reproductive performance – the currency of evolutionary change within populations – the ways in which parents respond to predation risk is likely shaped by natural selection. In particular, species that engage in multiple breeding attempts in a given season are able to modify their breeding strategies through extra-pair mating which might be influenced by predation events. Over a period of four consecutive years, I examined relationships between parental morphological variation, extra-pair mating, and nest predation in the North American barn swallow, *Hirundo rustica erythrogaster*, in order to examine morphological predictors and genetic consequences associated with nest predation in the wild. Males with darker plumage, a trait under sexual selection, experienced greater rates of nest predation. Female body mass was positively related to nest predation. Interestingly, molecular paternity analyses suggest that males with darker ventral plumage avoid the cost of reduced paternity in his social nest following a nest predation event. These findings suggest that parental morphology may play a significant role in nest predation risk and that females may alter the paternity of her offspring after a predation event based on features of her mate’s morphology.
ACKNOWLEDGMENTS

Special thanks to Rebecca Safran for countless hours of discussion, help with data analysis, and a great amount of support throughout the entirety of this study. For field assistance, I thank Connor Fitzhugh, Lori Fraser, Rachel Wildrick, Alex Oesterle, Brittany Jenkins, Maren Vitousek, Stephen Alderfer, Ian Harold, and Audrey Tobin. I thank Brittany Jenkins, Julie Marling, and Monica Brandhuber for color analysis. Thanks to Matthew Wilkins, Joanna Hubbard, Maren Vitousek, and Roi Dor for help in the field, with feather color measurements, and many comments that benefited this manuscript. Thanks to Barbara Demmig-Adams and Matthew Keller for serving on my Honors committee. Also, thanks to Michael Breed and Samuel Flaxman for serving on my Master’s committee. Many landowners across Boulder County, Colorado, graciously provided access to their populations of barn swallows. Funding was provided by the Undergraduate Research Opportunities Program (UROP) at CU-Boulder and the Howard Hughes Medical Institute Biosciences Research Grant.
CONTENTS

CHAPTER

I. INTRODUCTION ...........................................................................................................1

II. MATERIALS AND METHODS .............................................................................7
   Study Region and Field Methods .........................................................................7
   Plumage Color Measurements ...........................................................................7
   Paternity Analyses ...............................................................................................8

III. RESULTS ..................................................................................................................12
   Morphological Predictors of Nest Predation ......................................................12
   Extra-Pair Mating After Nest Predation .............................................................13

IV. DISCUSSION ............................................................................................................16

BIBLIOGRAPHY ...........................................................................................................20
TABLES

Table

1. Primer Sequences for Seven Polymorphic Microsatellite Loci ..................9
2. Correlation Matrix of Independent Variables ........................................11
3. Parental Morphology as a Predictor of Nest Predation ..........................13
4. Predation as a Predictor of Paternity Proportions ...............................15
FIGURES

Figure

1. Nest Fates by Year ................................................................. 10
2. Male and Female Morphological Predictors of Nest Predation .......... 12
3. Changes in Paternity Proportions by Nest Fate ............................... 14
4. Paternity and Color in Simulated Predation Events .......................... 14
CHAPTER I

Introduction

Understanding the factors that contribute to an individual’s survival and reproductive success is one of the principle goals of evolutionary biology. Nest predation, here defined as predation on dependent offspring in nests, is the principle cause of reproductive failure in the majority of bird species, accounting for 70%-95% of nest failures (Martin 1988, 1992, 1993), and is thus a strong source of natural selection within populations (Martin 1988, 1992, 1998). Engaging in multiple breeding attempts is a widespread reproductive strategy in a range of taxa (Verhulst, Tinbergen & Daan 1997). Extra-pair mating allows for the modification of individual mating decisions over the course of the breeding season and may be sensitive to previous nest failures due to predation. Therefore, the examination of relationships between nest predation, its predictors, and variation in female reproductive strategies within and between breeding seasons is an important part of understanding seasonal reproductive success within species, and thus how variables influencing nest predation are subject to evolutionary change.

Despite a great deal of interest in the factors that influence and predict nest predation, there are only a few studies which address interactions between parental morphological variation and nest predation risk. Indeed, while there is a large body of literature examining the relationship between adult morphology and adult predation risk (e.g., Darwin 1875, Møller 1994, Swaddle & Lockwood 1998, Nosil & Crespi 2006), the vast majority of studies on variation in nest predation have focused on the features of the nest and behaviors surrounding it, including parental and nestling behavior, nest size, and location (Lima 2009, Martin & Briskie 2009). It is likely that parental morphology may be a significant predictor of nest predation in some species but little information exists to test this hypothesis.
One of the putative costs of showy morphological variation in male birds is a possibility that traits like feather color make these individuals more visible to predators (Andersson 1994). Another intriguing pattern associated with ornamental male traits is that ‘top’ males frequently are inattentive parents who spend their time pursuing extra-pair mating opportunities instead of caring for their young (Møller 1992). Singing behavior of males, which might be positively correlated with ‘top’ male traits, has been shown to attract predators to courting and breeding locations (Mougeot & Bretagnolle 2000; Krams 2001; Hale 2004; Krama & Krams 2004). Body mass is another feature of morphology which may play a role in nest predation risk. Previous research has indicated that body mass might affect the ability of a parent to adequately defend its nest. For instance, Andersson and Norberg (1981) suggested that food provisioning by males for his brood may favor smaller male mass, as smaller males will have greater agility and skill in catching agile prey. Indeed, larger males that are unable to forage as efficiently for their nests and even themselves may travel to and from their nest less frequently, thereby failing to guard their nests. Additionally, parents of larger body mass may have difficulty defending their nests. A number of studies have predicted and documented the difficulty that heavy birds have when initiating flight (e.g. Blem 1975; Jones 1986; Hedenström & Alerstam 1992) as well as decreased maneuverability during flight (e.g. Blem 1975; Alerstam & Lindström 1990; Norberg 1990; Hedenström 1992). The hindrance of a larger body masses may reduce an individual’s ability to successfully maneuver when defending their nest, making the latter an easy target for predators.

Even as numerous studies have examined the effects of nest predation events on fitness, nesting choices, and adult behavior (reviewed by Lima 2009, Martin & Briskie 2009), I am currently unaware of any study examining the effects of nest predation on paternity allocation in post-predation breeding attempts. This gap in the literature is notable due to females’ potential to
significantly increase their fitness as a result of altered mating strategies, which may be loosely characterized as everything an individual does to determine when, how, and with whom it mates and to ensure that mating produces successful offspring. Additionally, it has long been known that adult morphology and mate choice are related (Darwin 1871). Assuming a relationship between nest predation and parental morphology, it is logical to explore a link between nest predation and mate choice. Indeed, it has been suggested that females will abandon the social pair-bond when the male of the pair bond has less attractive traits and there is increased genetic variability among locally breeding males (Shellman-Reeve and Reeve, 2000). A pair-bond does not preclude a female bird from participating in extra-pair copulations (EPCs) as she may benefit in terms of direct or indirect benefits. Direct benefits may include additional paternal care, while indirect benefits may include heritable features of sexual attractiveness (Saino et al., 2003) or genetic diversity (Neff and Pitcher, 2005) of offspring. To be sure, a male’s contribution of genetic material to the subsequent generation is typically directly dependent upon the number of copulations he obtains rather than the quality of his social brood (Kokko, Jennions, & Brooks 2006), while females are essentially wed to the nest and presumably must rely on her social mate for contributions to nest defense and parental care. Therefore, if females are capable of responding to the environmental and ecological pressures around her, one should predict that it is advantageous for her to maintain or enhance her original mating strategy after a successful first breeding attempt while it would only be advantageous for her to alter her overall strategy only subsequent to a failed breeding attempt.

As many species engage in extra-pair copulations (EPCs), one might expect a female to alter the social male’s level of paternity (paternity proportion) in a brood replacing another that failed due to nest predation. This modification could potentially lead to better genes for a
female’s offspring or enhanced parental care depending on whether EPCs increase or decrease. It has been suggested that EPCs are costly to females due to the reduction of paternal care given by their social mate (Arnqvist and Kirkpatrick, 2005). As a key prediction of the mate assistance hypothesis states that male parental care should increase the number of surviving young raised by a female bird, it seems probable that a female would rather rely on the pair-bond’s strength to ensure the survival of her offspring in high risk conditions. Thus, an overall decrease in EPCs may be advantageous to individuals breeding in areas with high nest predation rates if additional paternal care will be conferred. Alternatively, females may alter their reproductive strategy by increasing the number of EPCs in the second breeding attempt. This strategy might secure superior genes for her offspring that may provide them with increased survival and/or reproductive success, following the good genes hypothesis. If this occurs, males whose nests undergo higher rates of nest predation may experience a cost in terms of paternity in the second breeding attempt.

The primary objectives of this four-year field study were to investigate the possibility that nest predation events are related to adult morphological variation and whether females alter paternity allocation in second breeding attempts after the first underwent a nest predation event. I hypothesized that there is a relationship between nest predation and parental morphology. I examined whether females will adjust genetic mate choice by altering the number of extra-pair offspring (EPO) in their second broods. Note the propensity for females to either increase or decrease the number of EPO in the nest.

To assess whether phenotypic variation is associated with predation risk, I compared morphological variation of individuals whose nests had undergone a predation event and individuals whose nests did not. I compared traits previously shown to influence mate-selection
decisions in North American populations of barn swallows, namely ventral color (Safran et al. 2005), to determine if a potential cost of these traits is increased risk of predation to the nests cared for by individuals with exaggerations of both or either of these traits. Additionally, I compared other features of an individual’s morphology that are likely to influence parental care, including wing length and body mass, both of which influence foraging behavior in this aerial insectivore (Andersson & Norberg 1981). To examine paternity allocation in second breeding attempts, I compared the second-brood paternity from nests belonging to pairs that underwent nest predation in the first attempt and those belonging to pairs that successfully fledged young in the first attempt. As part of a larger experimental study, I simulated a nest predation event in 9 randomly selected nests to determine the effect of nest predation per se on the paternity of the social mate in a successive breeding attempt.

I utilized morphological, genetic, and behavioral data from a large breeding population of the North American barn swallow, *Hirundo rustica erythrogaster*, where nest failure due to predation is frequent (Fig 1). The barn swallow is a sexually dimorphic, insectivorous passerine, in which male ventral color is causally associated with his reproductive performance (Safran & McGraw 2004; Safran et al. 2005). Barn swallows breed in protected sites, such as horse barns and culverts, either in colonies or solitary pairs (Campbell et al. 1997). An open-cup nester, females lay two to three clutches, consisting of between two to six eggs each, during a given breeding season (Goodman 1982, Safran 2006). The nestlings are altricial and incapable of thermoregulation, feeding, and defending themselves for the first few weeks of life (Snapp 1976) during which males and females actively participate in the care of young within their shared nest. Female parental care is much greater during the two-week period in which eggs are being incubated; males participate in incubation about 5% of the time (Brown and Brown 1999).
Parental care in this subspecies is nearly equal in its distribution between social mates during the nestling stage (Maguire & Safran 2010). For adults, annual survival probabilities range from 30 – 60% (Brown and Brown 1999); individuals live on average two years. Site fidelity is extremely high in these long distance migrants (Shields 1984, Safran 2004). Of relevance to this study, extra-pair mating rates are high in barn swallow populations (e.g., Saino et al. 1997, Neuman et al. 2007).
CHAPTER II

Materials and Methods

Study Region and Field Methods

During the summers of 2008, 2009, 2010, and 2011, I studied a population of barn swallows from May to September in Boulder County, Colorado. Using nylon mesh nets, I captured individuals during the first two weeks of the breeding season after pairs had formed. I uniquely marked the tail streamers of individuals with colored markers following Shields and Crook (1987). I also applied numbered aluminum United States Fish and Wildlife Service rings and color bands to each individual. I 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 ventral plumage color. I checked nests at least every four days during the entire breeding season in order to determine clutch initiation dates, any predation events, and annual reproductive success. Additionally, during the summer of 2009 as part of a larger experiment I simulated nest predation events by removing clutches from 9 nests to determine changes in a male’s paternity after a predation event relative to his paternity in his first brood. I calculated paternity in a male’s first clutch by extracting genetic material from the embryos (following Safran et al. 2005).

Plumage Color Measurements

To objectively quantify plumage color, I collected 8 feathers from the breast region of males and females and mounted these on an index card to recreate the natural plumage appearance of the bird (Safran & McGraw 2004). These cards were stored in the dark until plumage-color scoring. The color of feather samples was scored along three traditional axes of color (hue, chroma, and brightness) using an Ocean Optics (Dunedin, FL) USB4000
spectrometer (range 200-1100 nm) with a fiber optic probe at an angle of 90° to the feather surface lit by a PX-2 pulsed xenon light source. Ambient light was excluded using a metal probe holder, which was placed against the feather sample; the probe was held at a constant distance from each sample, so that a 2.5 mm diameter of light hit the feather surface. Reflectance data were generated relative to a white standard (Ocean Optics WS-1) and a dark standard (all light excluded). Spectra were recorded with SpectraSuite software package (version 2.0.125, Ocean Optics Inc.). For each sample, 20 spectra were averaged to reduce noise from the spectrometer with an integration period of 200 ms. This procedure was repeated three times for each sample with the probe lifted between each scan. The three scans were performed at approximately the same location in the colored feather area. Because the measures of color (hue, chroma, brightness) across the ventral region of each individual are highly correlated, I used one metric of feather color (average breast brightness) which is representative of the overall color of an individual (Safran and McGraw 2004). Note that lower brightness scores (% reflectance) indicate plumage color which appears darker, redder, and more saturated compared to an individual with a higher % reflectance.

Paternity Analyses

I extracted DNA from parent and nestling blood samples, as well as nestling tissue samples, collected during breeding seasons using Qiagen’s (Valencia, CA) DNEASY Blood and Tissue kits. I used polymerase chain reaction (PCR) to amplify seven microsatellite loci, including Escu6, Ltr6, POCC6, Hir11, Hir19, Hir20, Hru6 (see Table 1). Individual PCR reactions were combined into multiplex mixes (Multiplex 1(M1); Escu6, Ltr6, POCC6, multiplex 2 (M2); and Hir11, Hir19, and Hir20. Hru6 was amplified as single locus). PCR amplification conditions were as following: initial denaturation at 95°C for 5 min; 35 cycles of denaturating at
95°C for 30 s, annealing at 50, 58, or 62°C for 30s (specific per multiplex PCR mix M1, M2, and Hru6, respectively), and extension at 72°C for 30s; and a final extension at 72°C for 30 min.

Products of PCR were genotyped on an ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA) with LIZ-500 as a size standard. Allele sizes were estimated using Genemapper v3.7 (Applied Biosystems) and scored by visual examination. Each marker was highly variable with a minimum and maximum of 11 and 60 alleles per locus. (see Table 1).

<table>
<thead>
<tr>
<th>Locus</th>
<th>Primer sequence (5’→3’)</th>
<th>$T_a$</th>
<th>$H_0$</th>
<th>$H_S$</th>
<th>$K$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Escu6¹</td>
<td>F: CATAGTGATGCCCTGCTAGG</td>
<td>50</td>
<td>0.89</td>
<td>0.903</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>R: GCAAGTGCTCCTTAATATTTGG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ltr6²</td>
<td>F: GCCATGCCACAGGAGTGAGTTC</td>
<td>50</td>
<td>0.663</td>
<td>0.639</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>R: AGTCATCTCCATCAAGGGCAT</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>POCC6³</td>
<td>F: TCACCTCAAAAAACACACACA</td>
<td>50</td>
<td>0.895</td>
<td>0.898</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>R: ACTTCTCTCTGAAAAAGGGGAGC</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hir 11⁴</td>
<td>F: AACACCTGAAACACCTACAC</td>
<td>58</td>
<td>0.814</td>
<td>0.859</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>R: CTTTGAGCAAATGAGTG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hir 19⁴</td>
<td>F: GTCACAACCAGCTAGAC</td>
<td>58</td>
<td>0.849</td>
<td>0.874</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>R: ATAGCCACAGGAAAGTCT</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hir 20⁴</td>
<td>F: GAAGTTGGAGAAGAGATTAG</td>
<td>58</td>
<td>0.849</td>
<td>0.819</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>R: TTATTGCTCTGGGTATGT</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hru6⁴</td>
<td>F: GCTGTGCTATTCTCATACATGAG</td>
<td>62</td>
<td>0.918</td>
<td>0.966</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>R: ACAGGGCAGTGTACTCTGC</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Table 1:* Primer sequences for seven polymorphic microsatellite markers in Barn Swallows, with their respective annealing temperatures ($T_a$), observed heterozygosity ($H_0$), expected heterozygosity ($H_S$), total number of alleles ($K$). References for primers: ¹Hanotte et al. 1994, ²McDonald and Potts 1994, ³Bensch et al. 1997, ⁴Tsyusko et al. 2006.

Paternity was assigned using Cervus V3 (Marshall et al. 1998). The combined exclusion probability of the seven loci for the first parent was 0.9987, for the second parent 0.99995, and for the parent pair 0.999999. Offspring were deemed extra-pair young (EPY) if at least two mismatches were detected between the offspring and putative father (male caring for offspring).

Statistical Analyses
Unless otherwise stated, data were analyzed using general linear models with ‘site name’ and ‘year’ as random effects to control for the lack of independence of nests within the same breeding site (Figure 1). Additionally, the fate of a nest was analyzed as a binary response variable, with successful nests receiving a value of one and nests that underwent predation receiving a value of zero. I used the Satterthwaite method to estimate the denominator degrees of freedom (Littell et al. 2002). All analyses were performed using SAS v. 9.2 (Cary, NC).

Figure 1: Plot detailing total nesting attempts and nest fates across the four years examined. Total attempts in 2008 through 2011 equal 255, 262, 125, and 168 respectively.

Trait Correlations

To use a size-corrected metric of body mass, I divided body mass by dividing mass by wing length (hereafter called body mass). I created a Spearman correlation matrix to determine
collinearity among independent variables, including breast coloration (% reflectance), intact tail streamer length (mm), and body mass (g/mm) within each sex. Correlations among these variables indicate that tail streamer length is strongly related to both corrected body mass and ventral plumage coloration (Table 2) and accordingly, I analyzed the effect of tail streamer length in a model separate from color and corrected body mass.

A male’s paternity was calculated as a proportion: the number of extra-pair offspring over the number of total offspring produced in the focal nest.

<table>
<thead>
<tr>
<th></th>
<th>Streamer Length</th>
<th>Ventral Brightness</th>
<th>Body Mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Streamer Length</td>
<td>X</td>
<td>-0.108*</td>
<td>-0.347*</td>
</tr>
<tr>
<td>Ventral Brightness</td>
<td>-0.129*</td>
<td>X</td>
<td>0.0446</td>
</tr>
<tr>
<td>Body Mass</td>
<td>-0.674*</td>
<td>0.0056</td>
<td>X</td>
</tr>
</tbody>
</table>

*Table 2:* Spearman correlation matrix of independent variables, with significant relationships in italics and marked by an asterisk. Males are represented in blue, while females are represented in red. (*) indicates a ϱ-value less than 0.05.
CHAPTER III

Results

Morphological Predictors of Nest Predation

*Males*

Controlling for site and year effects, nests that underwent a predation event belonged to
darker males compared to those that did not undergo a nest predation event; body mass was not
significantly related to nest predation (Figure 2, Table 3). In second breeding attempts no
relationship between nest predation and morphology were (Figure 2, Table 3).

*Females*

Nests belonging to females with higher body mass values underwent higher rates of nest
predation in both first and second breeding attempts while ventral plumage color was not a
predictor of nest predation events (Figure 2, Table 3).

*Figure 2:* Differences in male and female morphology between individuals whose nests underwent a nest predation
event and those whose did not, including body mass and average brightness. Sample sizes are indicated at the base
of each bar. (***) indicates a p-value less than 0.05.
Table 3: Mixed models examining the relationship between the fate (successfully fledged or predated nestlings) of first nesting attempts and the fate of second nesting attempts sorted by sex.

Extra-Pair Mating After Nest Predation

Males who successfully rear their first brood experience no significant change in paternity in their second breeding attempt (Figure 3, Table 4). Moreover, I found no statistically significant difference in paternity proportions between the paternity proportions of second broods for males whose first nests underwent a nest predation event compared to males whose first breeding attempts were successful, (Figure 3, Table 4). Nests that underwent a simulated predation event (i.e., those nests for which male paternity can be compared before and after a
predation event) experienced a significant decrease in overall paternity in their second breeding attempts (Figure 4, Table 4).

Figure 3: (A) Change in paternity over the course of a breeding season after a successful first breeding attempt. N = 51. (B) Differences in second attempt paternity proportions following a successful first breeding attempt (N = 51) and a predation event (N = 12) during the first breeding attempt.

Figure 4: (A) Differences in second attempt paternity proportions in nests that experienced a predation event in the first breeding attempt (N = 12) and those nests that underwent a simulated predation event in the first attempt (N = 9). (B) Difference of average male plumage brightness whose nests underwent a simulated predation event (N = 9) and those whose nest underwent a predation event in 2009 (N = 52). (**) indicates a p-value less than 0.05.
Table 4: Mixed models examining the relationships between a number paternity proportions. These models include: (A) the relationship between paternity proportions in successful first breeding attempts and paternity in successful second breeding attempts, (B) the relationship between the second breeding attempt paternity proportions of pairs that suffered a nest predation event in their first breeding attempt and those of pairs that successfully fledged young in their first breeding attempt, and (C) the relationship between paternity proportions in successful first breeding attempts and paternity in successful second breeding attempts of birds whose nests underwent a simulated nest predation event during their first attempt.

Upon comparing the ventral plumage color of those males whose nests underwent a simulated predation event to that of the general breeding population that year, I found that those males randomly chosen to undergo a simulated nest predation event have significantly lighter ventral plumage than those that underwent a nest predation event in the 2009 breeding population (breast color: mean difference male breast color ± SD: simulated predation = 32.79 ± 2.39, predation in 2009 = 27.89 ± 0.97; t-test: N = 60, t(9.49) = -1.904, P = 0.0438, Figure 6).
Consistent with my predictions, I found a previously unknown positive relationship between male ventral plumage coloration and nest predation rates. This is noteworthy because male mates are chosen by females based on plumage color, where males with darker ventral plumage have greater reproductive benefits compared to males duller in color (Safran & McGraw 2004; Safran et al. 2005). Indeed, sexually selected traits are expected to show a relationship (either positive or negative) with various measures of reproductive success (Andersson 1994). In examining the relationship between plumage and nest predation, it should be noted that the plumage itself is most likely not attracting predators to individuals’ nest – rather it is most likely behaviors associated with the plumage that is predisposing nests to predation. Barn swallows’ feathers contain melanin-based pigmentation (McGraw et al. 2004), and that melanin-based pigmentation has been characterized as testosterone-dependent – the more circulating testosterone at the time of molting, the darker the plumage that is developed (Evans, Goldsmith & Norris 2000). Indeed, this relationship has been shown in barn swallows, with darker individuals exhibiting higher levels of testosterone than brighter conspecifics during the breeding season (Safran et al. 2008). Further suggesting a link between high testosterone and nest predation risk is the lack of an effect of ventral plumage color on second breeding attempt predation events as testosterone levels decrease over the course of the breeding season (Safran et al. 2008). In other avian taxa (e.g., dark-eyed juncos), elevated levels of testosterone in males have been significantly associated with increased nest predation rates (Cawthorn, Ketterson & Nolan 1998), decreased parental care in some cases (McGlothlin, Jawor & Ketterson 2007, Lynn 2008), and increased metabolic demands (Buchanan et al. 2001). These studies suggest that it is
not the males’ plumage coloration \textit{per se}, but the behavioral traits (e.g., low parental care, pursuit of EPCs, singing rates) associated with high levels of testosterone that may be associated with lower parental care behavior and thus, greater risk of nest predation. One should expect that males with high levels of testosterone in other taxa to undergo similarly high rates of nest predation. Traits indicative of higher levels of testosterone might be examined in other taxa if similar relationships are to be discovered.

Body mass was found to be positively related to nest predation events only in females. This finding is consistent with my previous suggestion that larger individuals may be unable adequately defend their nests. This failure to successfully care for their young may be due to their own metabolic demands keeping them from the nest assuming they are intent on maintaining their own physical quality. Alternatively, these individuals may be unable to adequately defend their nest or due to lack of mobility or agility due to their larger body mass. In either case, it is interesting that male body mass was unrelated to nest predation risk. This perhaps suggests that females provide either a higher level of care or are more present at the nest. Indeed, previous findings have indicated that females provide higher levels of care when mated to males with darker ventral plumage (Maguire & Safran 2010).

Examining possible changes in female reproductive strategies indicates that females most likely do alter their reproductive strategies through manipulation of the number of EPO produced following a nest predation event. Comparing paternity proportions in second breeding attempts indicated that there was no difference between those broods belonging to males whose first nest underwent a predation event and those males whose first nest were successful. This suggests that the females typically do not alter their social mate’s paternity as the season progresses. Despite this finding, I did detect a change in paternity proportions after a simulated nest predation event.
Here, with the knowledge of paternity proportions in the first and second breeding attempts of these individuals, I was able to determine that the social male’s genetic paternity significantly decreases following a predation event. Interestingly, those individuals whose nests underwent simulated predation events displayed significantly brighter ventral plumage coloration than those individuals whose nests underwent a nest predation event during the 2009 breeding season. Since natural predation events typically affect males with dark ventral plumage and the simulated predation events affected males with significantly brighter ventral plumage, it is possible that darker males may be able to mediate the costs of nest predation events and that brighter males are unable to do so. Considering females are losing approximately half of the total broods produced in a breeding season, it is possible that darker males provide some sort of benefit to females. As a past examination of male provisioning behavior indicated no difference between dark males and bright males (Maguire & Safran 2010), it is likely that darker males provide some sort of indirect benefit to their mates (e.g., good genes) that brighter individuals are incapable of offering.

Future studies examining the morphological predictors of nest predation and changes in EPO after a nest predation event should focus on traits related to testosterone and female mate choice. For instance, a potential future examination of testosterone-related traits may alter the morphology of males with the trait desired by female conspecifics. Indeed, color manipulations, previously shown to increase testosterone levels in male barn swallows (Safran et al. 2008), may be an interesting way to determine a causal relationship between male color and increased predation risk. Even if such a causal relationship cannot be replicated in other taxa, enhancing a sexually selected trait may mediate the number of EPO in second breeding attempts following a predation event. Furthermore, behavioral observations of nest defense and nestling provisioning
rates in combination with experimentally elevated perceived predation risk has the potential to expose the intricate relationships between parental care, morphology, and mate choice in a great number of taxa.

Overall, my findings suggest that male plumage coloration not only predicts nest predation, but potential mediates the costs of such events. Additionally, female body mass was a significant predictor of nest predation across the breeding season and could indicate that females are incapable of both maintaining high physical quality and providing care to their offspring. This study provides strong evidence that adult morphological variation is a significant factor in the occurrence of nest predation and might mediate its potential fitness costs.
Bibliography


