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Plumage characteristics, reproductive investment and assortative mating in tree swallows *Tachycineta bicolor*

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Abstract Elaborate ornamental plumage has been associated with various measures of individual quality in many species of birds. Male plumage characteristics, which have been relatively well studied, have been shown to reflect past reproductive investment, as well as the potential for reproductive investment in the current breeding attempt. In contrast, the signalling functions of female traits remain largely unexplored. In this study, we investigated the relationship between plumage attributes of breeding adult tree swallows and past reproductive investment, current reproductive investment and social mate pairing strategy. Both males and older females possess metallic green to metallic blue iridescent plumage on their dorsal surface, making this a suitable species for this type of investigation. We did not find any effects of past reproductive investment and success on the plumage attributes of returning breeders. In contrast, female plumage hue covaried with fledging success, and female plumage brightness was positively associated with mean clutch egg mass. In addition, we found that social pairs mated assortatively with respect to plumage brightness. We argue that since plumage characteristics vary with age in both male and female tree swallows, plumage attributes in this species are indicative of breeding experience and may be honest signals of quality. Positive assortative pairing could be the result of mutual mate choice or intra-sexual competition for nest sites by both males and females.

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Introduction

The feathers of birds can be coloured by deposition of pigments, such as carotenoids and melanins, or through the physical interaction between light and the nanostructures of barbs and barbules (Prum 2006). Carotenoids are mainly responsible for the production of red, orange and yellow feathers, while melanins produce most blacks and browns. In contrast, structural elements of the feathers can produce blue, violet, ultraviolet and iridescent plumage. These colours are produced when light strikes the quasi-ordered matrix of keratin and air within feather barbs or alternating layers of material with different refractive indices such as keratin, melanin and air in feather barbules (Doucet et al. 2006).

While the cost of incorporating pigments in feathers to produce saturated and bright plumage has been relatively well studied both in the wild and in aviaries (Hill 2006), the cost of producing brilliant structural plumage is poorly understood. Indeed, there is considerable variation among species in the nanostructure arrangement in feathers; therefore, it is difficult to generalise the costs associated with producing quality plumage (Prum 2006). Nonetheless, experimental evidence suggests that producing fine nanostructures within feathers is costly (Hill 2006), and, therefore, these traits have the potential to be honest signals of individual quality (Kodric-Brown and Brown 1984). For example, structural plumage characteristics have been shown to be affected by endoparasites (Hill et al. 2005) and nutritional stress (McGraw et al. 2002). In males, plumage attributes have also been associated with differences

in age (Delhey and Kempenaers 2006) and body condition at the time of moult (Keyser and Hill 1999). Past reproductive effort could also entail a cost on the production of structural plumage as experimental increase in parental effort during brood rearing has been shown to influence plumage characteristics following moult in eastern bluebirds (*Sialia sialis*; Siefferman and Hill 2005a).

Although much work has focussed on the ecological and behavioural importance of elaborate ornamentation in males, the signalling potential of plumage in females has, until recently, largely been ignored (Amudsen and Pärn 2006). Plumage characteristics of females have often been considered a by-product of selection on males, uninfluenced by the pressures of sexual selection (Amundsen 2000). Recent studies, however, have presented strong evidence, suggesting that plumage attributes of females may also honestly signal quality. Variation in structural plumage characteristics in females have been associated with age (Komdeur et al. 2005), and various indices of individual quality such as body condition (Siefferman and Hill 2005b) and immunological status (Hanssen et al. 2006). In addition, there is evidence for mate choice of elaborately ornamented females by males (Griggio et al. 2005). Clearly, our understanding of the functions of female plumage warrants more attention.

Tree swallows (*Tachycineta bicolor*) are rather unique among North American passerines, as it is females, not males, which display delayed plumage maturation. Sub-adult females in their second year (SY) of life are capable of breeding but possess dull brown plumage on their dorsal surface that usually contains less than 50% bright iridescent feathers (Hussell 1983). In contrast, third-year (TY) and after third-year (ATY) females display male-like metallic green to metallic blue iridescent feathers. The ecological reasons for this delay in plumage maturation are unclear, but it has been hypothesised that in the context of competition for nest sites, dull brown plumage may allow younger females to suffer less aggression from older females (Robertson et al. 1992). This explanation, however, does not preclude the possibility that female plumage characteristics also serve as inter-sexual signals.

In this study, we investigated the relationship between plumage attributes of breeding adult tree swallows and past reproductive investment, current reproductive investment, and social mate pairing strategy. More specifically, we investigated (1) the influence of past reproductive investment and success on the plumage characteristics of returning breeders, (2) the relationship between breeding adult plumage characteristics and reproductive investment and success within the same breeding season and (3) whether pairs mated assortatively based on plumage characteristics.

Materials and methods

Study area and field procedures

We conducted this study on a population of tree swallows breeding in nest boxes near Prince George, BC, Canada (53° N, 123° W). The study area consists of open agricultural fields mixed with patches of coniferous and deciduous forest and several small wetlands. The site had 125 nest boxes mounted on fence posts, placed approximately 20–30 m apart. During the breeding seasons of 2002 to 2004, we started visiting nest boxes every other day in early May, keeping track of the nest-building progress until the first egg was laid. From then on, all nests were visited daily, and we recorded the clutch initiation date and, upon completion of egg laying, clutch size. In 2002 and 2003 (but not 2004), each egg was weighed on the day it was laid using an electronic balance (nearest 0.01 g) and numbered with a non-toxic permanent marker according to laying sequence.

Soon after the eggs had hatched, we captured male and female adults in the nest using a swing-door trap. Females were aged as either SY subadults or older (TY and ATY adults) based on plumage characteristics (Hussell 1983) and previous banding records. All adults were banded, and a blood smear was made from a drop of blood extracted by puncturing the brachial vein (Bennett 1970). Blood smears were subsequently fixed in 100% ethanol and stained with Wright-Giemsa. Counts were made of heterophils, eosinophils, basophils, monocytes and lymphocytes by scanning for a minimum of 100 white blood cells at ×1,000 magnification, and we subsequently calculated the ratio of heterophils to lymphocytes (*H*/*L*). Nests were monitored throughout the brood-rearing period to determine how many nestlings fledged.

Plumage characteristics

For birds captured in 2003 and 2004, we colleted feather samples from the rump and mantle of all males and from the rump of TY and ATY females. The feathers were kept in envelops at room temperature until analysis (described in Bitton et al. 2007). In short, four feathers (of the same area and individual) were taped to a black piece of cardboard in an overlapping pattern that reproduced how the feathers would naturally have been positioned on the bird, creating a continuous surface from which measurements could be obtained. Spectral data were collected using an Ocean Optics USB2000 spectrometer (Dunedin, Florida, USA) with a deuterium tungsten halogen light source (Avantes, Broomfield, Colorado, USA). We used a bifurcated probe held in a cylindrical sheath that excluded ambient light and kept the probe tip at a 90° angle, 6 mm from the feather

surface. We took readings at three arbitrary locations on the feathers; spectral data were recorded between wavelengths of 300–700 nm as the proportion of light reflected relative to the reflectance of a WS-1 pure white standard (Ocean Optics). We summarised the spectral curves of each body region by quantifying measures of brightness, hue and chroma. Average brightness (R_{av}) was calculated as the average percent reflectance between 300 and 700 nm (Doucet 2002). As an index of hue, we used the wavelength of maximum reflectance (λR_{Max}). For chroma, since the iridescent plumage of tree swallows peaks in the blue range of the spectra, we calculated blue chroma as the relative contribution of the blue range as a percentage of the overall brightness ($R_{400-512\ nm}/R_{300-700\ nm}$). We also calculated ultraviolet (UV) chroma ($R_{300-400\ nm}/R_{300-700\ nm}$).

For males, since the rump and mantle feathers did not differ within individuals for any of the four plumage descriptors that were measured, we used the average values of both types of feathers for all analyses (Doucet 2002). The four plumage characteristics were entered in a principal components analysis to adjust for the multiple correlations among the measures. This was done separately for males and females because the relationship between the four descriptors was slightly different for each sex. For males, the first principal component, PC1, explained 52.0% of the total variance and was heavily weighted by the hue, blue chroma and UV chroma but very little by brightness (rotated matrix values: −0.98, 0.56, 0.90 and −0.08, respectively); PC1 was therefore interpreted as a measure of hue. The second component, PC2, explained 25.5% of the total variance and was heavily loaded by brightness (rotated matrix values: 0.09, 0.33, −0.19 and 0.93 for hue, blue chroma, UV chroma and brightness, respectively); PC2 was therefore interpreted as a measure of brightness. For females, the first principal component explained 61.1% of the total variance and was also heavily weighted by the hue, blue chroma and UV chroma but very little by brightness (rotated matrix values: −0.97, 0.89, 0.83 and 0.15 for hue, blue chroma, UV chroma and brightness, respectively); PC1 was interpreted as a measure of hue. The second component, which accounted for 26.5% of the variance, was heavily loaded by brightness (−0.16, 0.04, 0.25 and 0.98 for hue, blue chroma, UV chroma and brightness, respectively); PC2 was interpreted as a measure of brightness.

Statistical analysis

We investigated the influence of past reproductive investment and success on the plumage characteristics of returning breeders, separately for males and females, with analysis of covariance (ANCOVA). Using data from TY and ATY females only ($n=24$), we conducted two tests, one with plumage hue (PC1) as the dependent variable and a second with plumage brightness (PC2) as the dependent variable. In both cases, we included reproductive variables collected the previous year as independent predictors, using data from individual females only once. These predictors included clutch initiation date (standardised for each year separately by defining the date that the first egg was laid in the population as day "0"), mean egg mass, clutch size and number of young fledged. In these models, we also included female age (TY or ATY), the year the feathers were collected (2003 or 2004) and the interactions between age and all other factors as independent variables. For males ($n=28$), we also conducted two tests with plumage hue (PC1) and plumage brightness (PC2) as dependent variables. Because males should not be affected by female-related investments such as clutch size and egg mass, we did not include these variables in the models. Instead, these models included, from the previous year, clutch initiation date, number of young fledged, the year the feathers were collected (2003 or 2004) and all first order interactions as independent variables. For these analyses, we used a backward-stepwise procedure to eliminate interactions and variables that did not approach significance ($P>0.10$).

We also used ANCOVA to investigate the relationship between plumage characteristics of breeding adults and reproductive investment and success (clutch size, mean egg mass and fledging success) in the same year. Since male characteristics have been shown to influence female investment in some species (e.g. Uller et al. 2005), we included both male and female attributes for each nest in these analyses. The models for investment in clutch size ($n=96$ nests) and mean egg mass ($n=20$ nests) as dependent variables included year the feathers were collected (2003 or 2004), female age, clutch initiation date, male and female plumage hue (PC1), male and female plumage brightness (PC2) and all interactions between year and the other factors as independent variables. When testing for the influence of parental attributes on fledging success ($n=53$ nests), we also included male and female H/L ratio (log-transformed to correct for non-normal distribution) in the analysis. The H/L ratio is a measure of stress in birds and has been shown to correlate with reproductive success in some species (Friedl and Edler 2005). This variable was not significant in any of the models and, therefore, is not reported or discussed further.
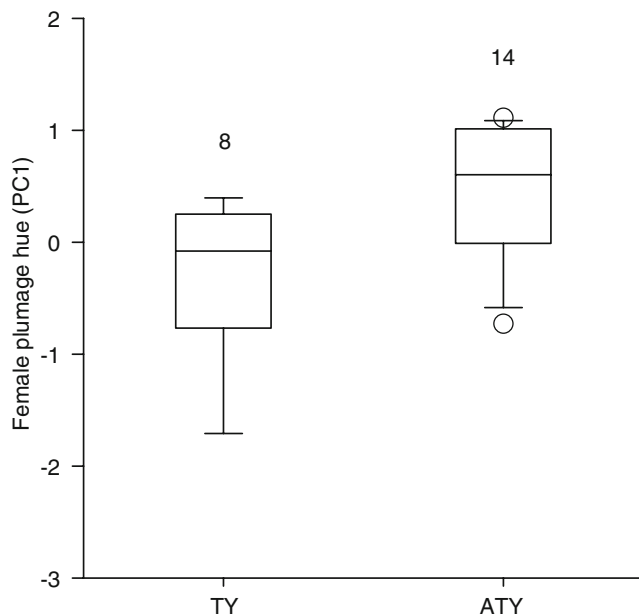
Finally, we used correlations to compare plumage hue (PC1) and brightness (PC2) between social mates ($n=49$ pairs). Tree swallows will sometimes remain paired over more than one breeding season. In such cases, we used only the initial pairing when testing for assortative pairing. For the other tests, we included birds that bred in both years, considering the data points independent from one another. All statistical analyses were performed using SPSS (Norušis

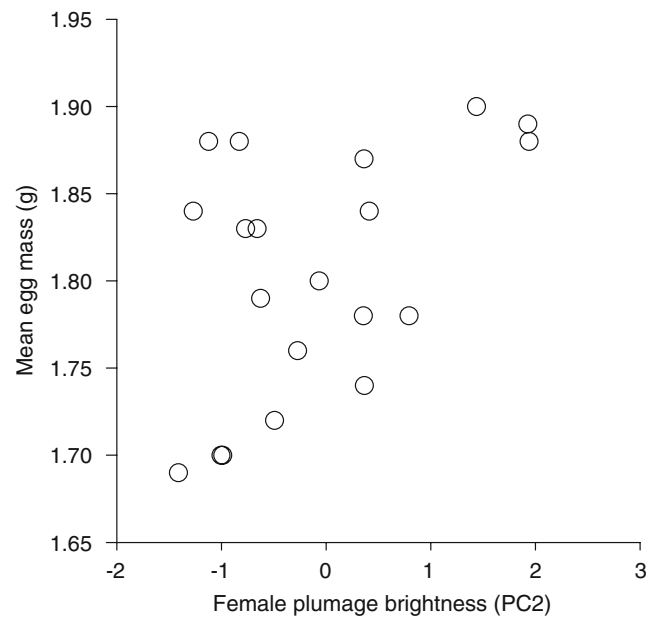2000). Results were considered significant at the 0.05 level, and we present means ± 1 SE, unless stated otherwise.

Results

We did not find any effects of past reproductive investment or past reproductive success on female plumage hue (PC1; all Ps>0.10) and plumage brightness (PC2; all Ps>0.10), or on male plumage hue (PC1; all Ps>0.10) and plumage brightness (PC2; all Ps>0.10). Female plumage hue was influenced by female age ($F_{1,20}$=5.61, P=0.03, R^2=0.22), with ATY individuals displaying bluer plumage than TY conspecifics (Fig. 1).

When investigating the relationship between adult characteristics and current reproductive effort and success (as measured by clutch size, mean egg mass and fledging success), we found that females that laid earlier in the season had larger clutches ($F_{1,94}$=6.89, P=0.01, R^2=0.07), but adult plumage characteristics were unrelated to clutch size (all Ps>0.10). We did, however, find relationships between female plumage characteristics and current invest-ment in egg mass and reproductive success. There was a significant positive association between female plumage brightness (PC2) and mean egg mass ($F_{1,18}$=5.27, P=0.03, R^2=0.26; Fig. 2). In addition, females reflecting light maximally at shorter wavelengths (i.e. bluer) were more

Fig. 2 Mean egg mass in relation to plumage brightness of female tree swallows (*n*=20). Plumage brightness is a unitless score (*PC2*) from a principal components analysis, with brighter birds receiving larger scores

successful at fledging young in both years of our study (PC1: $F_{1,49}$=6.61, P=0.01; R^2=0.24; Fig. 3). In this model, year was also a significant factor as more young were fledged in 2004 than in 2003 ($F_{1,49}$=12.74, P<0.001). In contrast, neither of the two male plumage attributes included in these models were significant predictors of
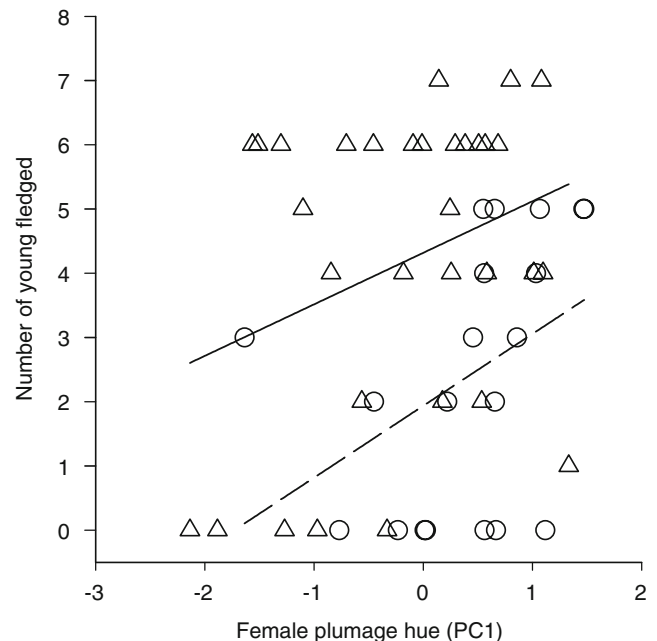

Fig. 1 Plumage hue in relation to age in female tree swallows (*TY* third year, *ATY* after third year). Plumage hue is a unitless score (*PC1*) extracted from a principal components analysis with higher scores representing shorter wavelength hues (i.e. bluer). *Boxes* show median (50th percentile) and interquartile range (25th to 75th percentile), and *whiskers* indicate the 95% confidence intervals. *Open circles* are data points outside the 95% confidence range, and sample sizes are shown *above each box*

Fig. 3 Number of young fledged in relation to plumage hue of female tree swallows (2003: *open circles* and *dashed line*, *n*=20; 2004: *open triangles* and *solid line*, *n*=32)

female reproductive investment or the pair's reproductive success (all Ps>0.10).

When testing for assortative pairing, we found no significant relationship between plumage hue in mated pairs of tree swallows (PC1; $r=-0.13$, $P=0.38$, $n=49$); however, plumage brightness was positively correlated within pairs (PC2; $r=0.39$, $P<0.01$, $n=49$; Fig. 4), suggesting assortative mating.

Discussion

Our results show that plumage hue of females reflects age in tree swallows (at least between TY and ATY) and that this plumage characteristic is associated with the ability to successfully fledge young (Fig. 3). Females displaying bluer feathers were generally older and, in both years of this study, fledged more young than relatively green females.

Plumage attributes are reliable signals of age in many species. Older female bluethroats (*Luscinia svecica*), for example, are brighter than juveniles (Rohde et al. 1999; but see Amundsen et al. 1997), and a similar pattern has been observed in European starlings (*Sturnus vulgaris*; Komdeur et al. 2005). In tree swallows, at the population level, older males are also bluer than younger conspecifics (Bitton and Dawson 2008). Our present results show that plumage hue of females of this species is related to age and seems indicative of their ability to raise young. It is possible that older, more experienced birds are more efficient at feeding and caring for their nestlings. Although there is little evidence to suggest that nestling feeding rates are different

Fig. 4 Relationship between plumage brightness of male and female tree swallows in social pairs ($n=49$)

among age groups in tree swallows (Lombardo 1991), older females may still be able to provide better care. For example, female tree swallows whose condition was influenced by feather clipping fed their young at lower frequencies (Winkler and Allen 1995); however, nestlings raised by clipped after-second year (ASY) females performed just as well as those raised by intact ASY females. In contrast, nestlings raised by SY females that had been clipped did not fair as well as nestling raised by unclipped SY females (Ardia and Clotfelter 2007). This may indicate that older, bluer females are better able to cope in stressful situations or that they preferentially allocate energy to raising their nestlings. Indeed, it is hypothesised that birds should increase their reproductive effort as they age since their prospects of surviving and reproducing declines (Clutton-Brock 1984; Velando et al. 2006). Bluer females may therefore be investing more in raising their nestlings than relatively green females.

Our results also show that brighter females laid heavier eggs (Fig. 2). In tree swallows, mean egg mass is highly heritable (Wiggins 1990), but this measure of reproductive investment has also been found to be influenced by female age (Ardia et al. 2006; De Steven 1978). Again, this may indicate that older females are in better condition or that they strategically invest more in reproduction than younger females. Although we did not find age-related differences in female plumage brightness, male tree swallows do increase in brightness with age (Bitton and Dawson 2008). Longitudinal analyses of plumage attributes would be required to determine if this is also the case in females. Nonetheless, our results do suggest that plumage brightness in females may also signal individual quality.

Perhaps surprisingly, we did not detect any effects of past reproductive investment and success on the plumage characteristics of returning breeders. Adult tree swallows begin moulting their feathers while still on the breeding grounds (Robertson et al. 1992), suggesting that if plumage is reflective of condition at the time of moult, birds that raised or fledged larger broods should bear these costs while producing feathers. As such, experimental increase of the number of young raised by male eastern bluebirds was shown to reduce the ability of these males to invest in bright plumage (Siefferman and Hill 2005a). However, large-scale experimental studies in tree swallows have found evidence suggesting that there is no phenotypic cost of reproduction for adults of this species (Shutler et al. 2006 and references therein). Survival rates of nestlings and adults in enlarged broods were no different than those from reduced broods, and increased parental care did not influence subsequent year investment in reproduction. Therefore, our results concur with other studies of tree swallows concluding that there is little or no phenotypic cost of reproduction for adults of this species.
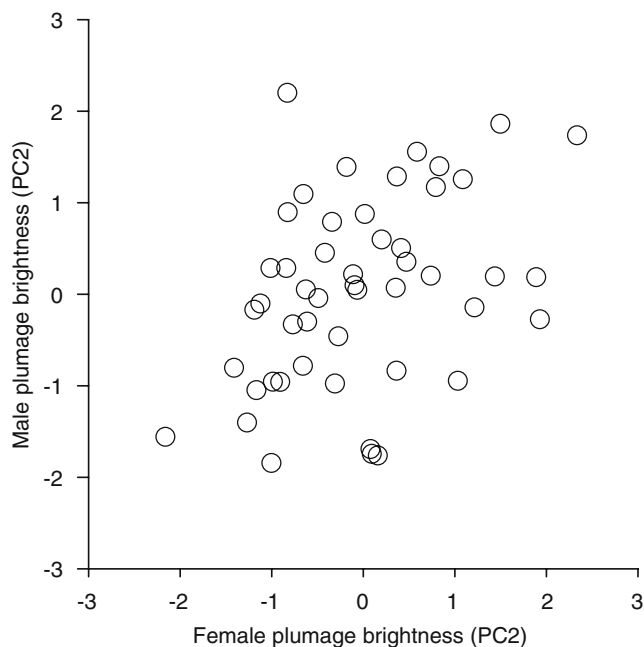
In this study, we did not find any influence of male plumage attributes on female reproductive investment, although there are obvious advantages for females to assess male colour displays. Quality plumage in males has been found to signal the holding potential of larger and higher quality territories (Keyser and Hill 2000), greater nestling provisioning effort (Siefferman and Hill 2003) and good genes for offspring (Sheldon et al. 1997). As such, in various species, male plumage attributes are known to influence female investment in reproduction. In some species for example, females mated to attractive males lay heavier eggs (Rutstein et al. 2004; Uller et al. 2005) and may invest more antioxidants (Williamson et al. 2006; Szigeti et al. 2007) and testosterone (Gil et al. 1999) in their yolks. In tree swallows, older males display bluer and brighter plumage (Bitton and Dawson 2008). Females could therefore be expected to vary their investment in reproduction based on male plumage attributes. The fact that we did not detect such trends does not imply that females are incapable of adjusting their reproductive effort. When there is a perceived risk of high parasitism in the nest, for example, female tree swallows have been demonstrated to reduce their clutch size (O'Brien and Dawson 2005). In addition, females in good body condition will skew the sex ratio of their broods towards a higher proportion of sons (Whittingham and Dunn 2000). It is possible that females did not adjust their reproductive investment in relation to the social mates' plumage attributes because of the high rate of extra-pair paternity found in this species. Tree swallows are socially monogamous yet exhibit among the highest rates of extra-pair paternity identified in passerines. About 50–89% of females produce at least one extra-pair young, and at the population level, between 38% and 69% of all offspring are the result of extra-pair mating (Lifjeld et al. 1993, Barber et al. 1996, O'Brien and Dawson 2007). Since more than half of the offspring contained in a brood are often extra-pair young, investment in reproduction by females might be more dependent on their own quality rather than that of their social mate.

In this study population, social pairs of tree swallows are paired assortatively by plumage brightness (Fig. 4). This type of pairing has been observed in other structurally coloured species (Andersson et al. 1998; Komdeur et al. 2005) and can theoretically occur by a variety of behavioural mechanisms. First, social pairing can be driven by the mutual preference of individuals with similar phenotypes along a continuum of available phenotypes (Burley 1983). This behaviour has been observed in a number of taxa and seems mostly attributed to the greater compatibility of "like" individuals (e.g. morphological compatibility: Brown 1993; personality compatibility: Buston and Emlen 2003). Alternatively, assortative pairing can occur when there is mutual

mate choice for similar ornaments (Johnstone et al. 1996). In this scenario, both males and females prefer to mate with individuals that possess certain characteristics (e.g. bright plumage). Although all individuals strive for the highest quality mates, lower quality individuals are competitively excluded from mating with high-quality mates. Finally, assortative pairing can be driven by intra-sexual competition for nest sites, with high-quality individuals gaining access to the best territories and pairing with higher quality mates (Creighton 2001; Ferrer and Penteriani 2003). In tree swallows, competition for nest sites is thought to be a major influence on their breeding behaviour (Robertson et al. 1992). Males arrive on the breeding ground early in the spring and start defending cavities several days prior to arrival of females. Even after pairing has occurred, females will visit other males for several days and nest usurpation takes place (Leffelaar and Robertson 1985). Both sexes are known to ferociously defend their territories against conspecifics, and this level of aggression often leaves one of the combatants dead or seriously injured (Lombardo 1986). Indeed, it is not uncommon for dead male or female tree swallows to be found in nest boxes (Robertson et al. 1986). It is possible, therefore, that the positive assortative pairing observed in this population was driven by intra-sexual competition for nest sites. Supporting this hypothesis, in a 25-year study of reproductive performance in tree swallows, Robertson and Rendell (2001) found evidence for assortative pairing by age. Older individuals in many species are more aggressive and win territorial contests more often than juveniles (Landmann and Kollinsky 1995; Hyman et al. 2004). By gaining access to good-quality territories, both males and females would find themselves mated to individuals sharing similar phenotypic traits that honestly signal quality. It is also possible for the pattern of assortative pairing observed in this study to be driven by mutual mate choice. Female mate choice is known to occur (Amundsen et al. 1997; Hunt et al. 1999) and should be expected when both sexes provide parental care (Burley 1977). Studies in tree swallows suggest that males spend much time feeding the nestlings, removing fecal sacs and defending the territory against intruders (Lombardo 1991; McCarty 2002). Males could be choosing to mate with females based on certain phenotypic characteristics such as plumage brightness. As our data do not allow us to distinguish whether assortative pairing is driven by mutual mate choice or intra-sexual competition for nest sites, future studies should attempt to determine which of these two behaviours, if not both, lead to the pattern of paring observed in this study. Nonetheless, our results are important because we are the first to show that in tree swallows, plumage characteristics of ASY females is related to age and has the potential of being an honest signal of individual quality.

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