

Age-related differences in plumage characteristics of male tree swallows *Tachycineta bicolor*: hue and brightness signal different aspects of individual quality

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Age-related differences in plumage characteristics of birds can be the result of differential survival of more ornamented individuals, within-individual changes in plumage attributes with age, or a combination of both. In this study, we investigated age-class related differences in plumage attributes of male tree swallows *Tachycineta bicolor* by performing both cross-sectional and longitudinal analyses. Male tree swallows in their first breeding season do not display delayed plumage maturation, and possess, like experienced breeders, metallic green to metallic blue iridescent plumage on their dorsal surface. Our results showed that, at the population level, older males were brighter and reflected light maximally at shorter wavelengths (i.e. were more blue). Differences in plumage brightness were most likely caused by changes within individuals as males increased in brightness between the first time they were captured and the subsequent year. Differences in hue, however, were not due to within-individual changes, but rather appear to be the result of greener individuals having lower survival and/or nest site fidelity. Indeed, relatively dull, greener birds had a lower probability of being recaptured the subsequent year. In contrast, we found that if birds captured in their first year as breeding adults were relatively bright, hue was not related to the probability of recapture. These results suggest that plumage attributes in male tree swallows have the potential of being honest signals of quality. Furthermore, plumage brightness and plumage hue might signal different aspects of male quality in this species.

Many theoretical models predict that the expression of secondary sexual characters is dependent on condition, and that such characters can honestly signal individual quality (e.g. Kodric-Brown and Brown 1984). In birds, these traits are usually more developed in older individuals (Andersson 1994) because they may be more efficient at foraging and in better condition at moult (Keyser and Hill 1999a, Doucet and Montgomerie 2003). If females prefer mating with older individuals because they hold better territories (Keyser and Hill 1999b), provide better parental care (Siefferman and Hill 2005), or because they can provide good genes for their offspring (Brooks and Kemp 2001), females could use plumage attributes of males to help them choose older mates.

In several species of birds, adult males progress through distinct age-specific plumages; males breeding for the first time have delayed plumage maturation and display dull, often female-like, plumage. These individuals can be sexually mature but are usually less successful at securing a mate (Thompson 1991). In most species, however, plumage characteristics vary in a continuous manner as individuals age, with younger birds often displaying drabber or less elaborate plumage in comparison to older birds. In general, the greatest change in ornamentation occurs

between the first year and second year (e.g. Delhey and Kempenaers 2006); whether plumage changes in hue, brightness, or both seems to be species-specific (e.g. Komdeur et al. 2005, Siefferman et al. 2005). At the population level, age-related differences in plumage characteristics can also be caused by differential survival of more ornamented individuals. Males that display more elaborate traits may have higher survival rates (Jennions et al. 2001), and be over-represented in the older portion of the population (Forslund and Pärt 1995). However, if the production of secondary sexual characteristics is too costly, the expression of these traits could be negatively correlated with survival (Hunt et al. 2004).

In this study, we investigated age-related differences in plumage attributes of male tree swallows *Tachycineta bicolor*. Males and mature females of this species possess bright iridescent contour feathers on their dorsal surface that range in colour from metallic green to metallic blue. Although females in their second year display brown dorsal plumage (Hussell 1983), males do not exhibit this delayed plumage maturation. However, whether the plumage characteristics of younger males differ significantly from those of older males is unknown. To determine if there are age-class related differences in plumage attributes at the

population level in male tree swallows, we performed cross-sectional analyses on data collected during two field seasons. We also investigated whether plumage attributes changed with age within individuals by conducting longitudinal analyses. Furthermore, we tested the idea that plumage characteristics can be used as predictors of survival or dispersal probability by comparing the plumage attributes of males that returned to the study area in years following capture to those that did not.

Methods

Study area and field procedures

We conducted this research on a population of tree swallows breeding in nest boxes near Prince George British Columbia, Canada (53°N, 123°W). Our study area consists of open agricultural fields mixed with patches of coniferous and deciduous forest, and small wetlands. The site holds 125 nest boxes mounted on fence posts, and placed approximately 20–30 m apart. During the breeding seasons of 2002 to 2004, when this study was conducted, we captured adult males in the nest using a swing-door trap as soon as possible after eggs had hatched. Birds were banded with standard U. S. Fish and Wildlife Service aluminum leg bands.

Male tree swallows cannot be aged using morphological measurements. However, since adult male tree swallows have relatively high rates of fidelity to nest sites (Robertson et al. 1992), and fewer than 5% of all breeding males change breeding sites during their lifetime (Winkler et al. 2004), males breeding on the study area for the first time are probably relatively young individuals in comparison to males banded as adults in previous years. Therefore, we used capture status (relatively young or “newly captured” versus relatively old or “recaptured”) as a surrogate for age in our analyses (see also Bitton et al. 2007).

Plumage characteristics

At the time of capture, we collected feathers from the rump and mantle of all males. Feathers were stored in small opaque envelopes at room temperature, and spectral analyses were performed as 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. Unlike some species where spectral data are difficult to obtain from feather samples due to the plumaceous nature of the contour feathers (see Quesada and Senar 2006), the vanes of rump and mantle feathers of tree swallows have abundant barbicels and so four feathers were sufficient to create a continuous surface from which measurements could be obtained. Spectral data were collected using an Ocean Optics USB2000 spectrometer (Dunedin, FL, USA) with a deuterium tungsten halogen light source (Avantes, Broomfield, 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 summarized 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 nm 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 ($R_{400-512\text{ nm}}/R_{300-700\text{ nm}}$). We also calculated ultraviolet (UV) chroma ($R_{300-400\text{ nm}}/R_{300-700\text{ nm}}$). Although the plumage of tree swallows does not peak in the ultraviolet range of the spectrum (Bitton et al. 2007), studies in other species have shown that UV chroma of male plumage can influence female mate choice (Bennett et al. 1997, Hunt et al. 1999) and that ultraviolet reflectance may be a biologically and ecologically relevant signal in birds (Hausmann et al. 2003).

Since the rump and mantle feathers did not differ within individuals for any of the four plumage descriptors that were measured (unpubl. data), we used the average values of both feather types for all analyses (Doucet 2002). The four plumage characteristics were entered in a principal components analysis to eliminate the multiple correlations among the measures. The first 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 the 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 strongly represented differences in brightness among individuals (rotated matrix values: 0.09 , 0.33 , -0.18 , and 0.93 for hue, blue chroma, UV chroma, and brightness, respectively).

Statistical analysis

To investigate the influence of age on plumage characteristics, we performed both cross-sectional and longitudinal analyses. For the cross-sectional analyses, we used data from birds captured in 2003 and 2004. For birds captured in both years, we randomly selected one of the observations to include in the analysis. We used general linear models with plumage characteristics (either PC1 or PC2) as the dependent variables, capture status (newly captured or recaptured) and year as fixed factors, and the first-order interactions in both models. For these analyses, we used a backward-stepwise procedure to eliminate interactions and variables that did not approach significance ($P > 0.10$).

For longitudinal analyses, we used data from 2002 to 2003 for newly captured birds that were subsequently captured in the next breeding season (2003 and 2004). We analysed changes in plumage characteristics (PC1 and PC2) between the two years using repeated-measures ANOVA, with plumage characteristic in year x and $x+1$ as the within-subject factor, and year as a between-subjects factor. To assess whether the pattern of change within individuals was consistent, or whether it was influenced by the years the

data were collected (either 2002 to 2003, or 2003 to 2004), we included the interaction between the within-subject factor and year in the models. Inter-year repeatability, which can be used to set an upper limit on heritability of a trait, was also estimated for each plumage attribute (PC1 and PC2) using the interclass correlation coefficient (Lessells and Boag 1987).

To test whether plumage characteristics at the population level could be influenced by differential survival and/or dispersal of individuals based on plumage attributes, we used a logistic regression model with a binary dependent variable (returned/did not return), and plumage hue (PC1), plumage brightness (PC2), and the interaction as explanatory variables. For this analysis, we included data from all newly captured birds that were recaptured the subsequent year, and an identical number of randomly selected newly captured birds that never returned to breed on the study site. To control for year-to-year differences in plumage characteristics (Table 1), we standardized the four measures extracted from the original spectra for each year using z-scores (mean = 0, SD \pm 1). These new scores were reduced to measures of hue (PC1) and brightness (PC2) using principal components analysis as described above.

All statistical analyses were performed using SPSS (Norušis 2000). Results were considered significant at the 0.05 level, and we present means \pm 1 SE unless stated otherwise.

Results

Older male tree swallows were bluer and brighter than newly captured males, which were generally greener (PC1; $F_{1,86} = 5.94$, $P = 0.02$; Fig. 1a) and duller (PC2; $F_{1,86} = 5.42$, $P = 0.02$; Fig. 1b). Year effects were not significant in these analyses (all $P_s > 0.10$). Longitudinal analyses of male plumage attributes revealed that plumage hue (PC1) was highly correlated between the first capture and the subsequent year capture ($r = 0.74$, $P < 0.001$, $n = 19$), and that this plumage characteristic did not change within individuals from one year to the next (repeated measures ANOVA, $F_{1,17} = 0.22$, $P = 0.65$; Fig. 2a). In addition, repeatability within-individuals between years for this plumage characteristic was also significant ($r = 0.75$,

$F_{18,19} = 7.00$, $P < 0.001$). These results suggest that plumage hue (PC1) is a trait partially inherent to individuals. In contrast, although plumage brightness (PC2) between the first capture and the subsequent year capture were correlated ($r = 0.48$, $P = 0.038$, $n = 19$), males became brighter with age (repeated measure ANOVA, $F_{1,17} = 16.76$, $P = 0.001$; Fig. 2b). As a result, this characteristic did not show significant repeatability within individuals sampled over consecutive breeding seasons ($r = 0.24$, $F_{18,19} = 1.62$, $P = 0.15$). Together, these results suggest that while individual males become brighter with age, the brightness of any particular male relative to other individuals also remains consistent across years.

The analysis of returns to the study area suggested that neither plumage hue (PC1; Wald = 0.01, $df = 1$, $P = 0.98$, $n = 44$) nor plumage brightness (PC2; Wald = 0.43, $df = 1$, $P = 0.51$, $n = 44$) alone were significant predictors of probability of returning; however, the interaction between these two terms was significant (Wald = 6.56, $df = 1$, $P = 0.01$, $n = 44$). To investigate the nature of this interaction, we separated the data into two groups based on whether plumage brightness was greater than average (bright) or lower than average (dull), and analysed the effects of hue (PC1) on probability of returning. The model for dull birds fit the data acceptably ($\chi^2_1 = 6.792$, $P < 0.01$, $n = 22$), with hue (PC1) as a valid predictor of probability of returning (Wald = 3.82, $df = 1$, $P = 0.05$), suggesting that relatively dull, greener birds were less likely than bluer birds to be recaptured in the subsequent year. In contrast, the model for bright birds did not fit the data acceptably ($\chi^2_1 = 0.11$, $P = 0.74$; $n = 22$) suggesting that hue did not influence the recapture probability of bright birds (Fig. 3).

Discussion

In this study, we showed that at the population level, plumage hue and brightness of male tree swallows were influenced by capture status, a surrogate measure of age. Relatively older individuals reflected light maximally at shorter wavelengths (Fig. 1a) and were brighter (Fig. 1b) than younger males. Patterns of age-related plumage characteristics were influenced by both year to year changes within individuals, and hue-biased return rate. Individual

Table 1. Plumage characteristics of male tree swallows captured near Prince George (British Columbia, Canada) in 3 different years.

Plumage characteristic	n	Year	Mean	\pm SD	F	df	P
Average brightness	20	2002	10.52	1.42	1.17	105	0.32
	38	2003	10.77	1.38			
	50	2004	11.09	1.60			
Blue chroma _(400–512 nm)	20	2002	42.31	1.99	1.28	105	0.28
	38	2003	42.97	1.65			
	50	2004	42.41	1.81			
Hue (λ Rmax)	20	2002	458.04	13.53	4.43	105	0.01†
	38	2003	468.65	12.08			
	50	2004	466.13	13.57			
Ultraviolet chroma _(300–400 nm)	20	2002	18.84	3.28	5.15	105	0.01†
	38	2003	16.34	2.76			
	50	2004	17.33	2.66			

†Post-hoc tests revealed that 2002 values were significantly different than 2003 values ($P = 0.01$), but that all other pairwise comparisons were not significant (Bonferroni corrections applied).

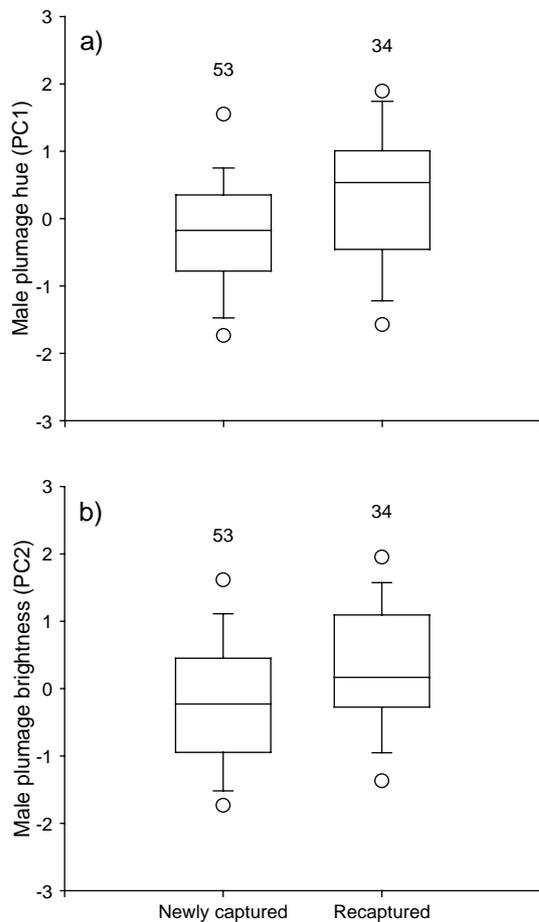


Figure 1. Plumage hue (a) and plumage brightness (b) in relation to capture status in male tree swallows. Plumage hue is a unitless score (PC1) extracted from a principal components analysis of four spectral curve descriptors (see Methods), with higher scores representing shorter wavelength hues and greater UV chroma. Plumage brightness is a unitless score (PC2) extracted from a principal components analysis of four spectral curve descriptors, with brighter birds receiving larger scores. Capture status is a surrogate measure of age; newly captured birds are relatively young individuals, recaptured birds are relatively older individuals. Boxes show median (50th percentile), interquartile range (25th to 75th percentile) and whiskers indicate the 95% confidence intervals. Open circles are the data points from the extremes of the data set when. Sample sizes are shown above each box.

birds increased in overall brightness from one year to the next (Fig. 2b), but did not seem to change significantly in hue (Fig. 2a). Instead, plumage hue was related to the probability of returning to the study area in subsequent years; among males that were relatively dull, greener individuals were less likely to return as breeders than bluer individuals. In contrast, if the males were relatively bright, hue did not influence probability of returning (Fig. 3).

Iridescent colours of feathers are produced by the coherent scattering of light from alternating layers of materials that have different reflective indices (Prum 2006). These colours are known to be produced mainly at the interfaces between air, keratin and melanin. Unlike non-iridescent structural colours that are produced by the feather barbs, iridescent colours are produced by the barbules (Doucet et al. 2006, Prum 2006). Although the

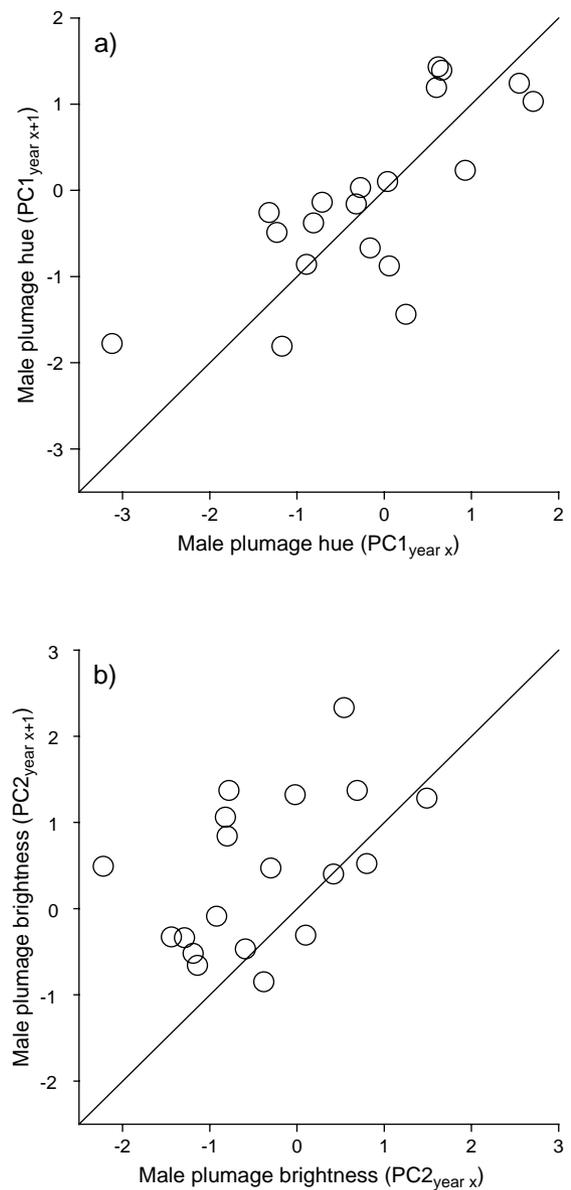


Figure 2. Relationship between a) plumage hue (PC1) and b) plumage brightness (PC2) of individual male tree swallows between the first year of capture (year x) and the following year (year $x + 1$). Solid line represents 1:1 reference line.

cost of producing quality iridescent plumage is poorly understood, general trends have been emerging from recent research on structural colours. Differences in hue within species have been attributed to variation in feather cortex thickness, while differences in UV chroma have been attributed to the percentage of melanin found below the keratin (Doucet et al. 2006). In contrast, variation in brightness is thought to be related to the number or condition of barbules (Shawkey et al. 2003, Doucet et al. 2006). Hence, susceptibility to feather damage, abrasion, and even keratinolytic bacteria could influence variability in brightness (Osorio and Ham 2002, Shawkey et al. 2007). Together, these lines of evidence suggest that, if the production of quality barbules is influenced by genetic quality or physiological stress during feather development, iridescent colours may honestly signal individual quality.

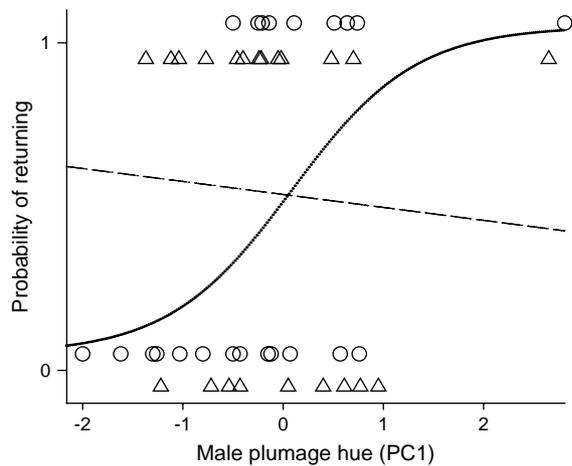


Figure 3. The probability that a newly captured male tree swallow will return to the study area in the subsequent year is related to plumage hue (PC1) when individuals are dull (low PC2 score; open circles and solid line), but not when individuals are bright (high PC2 score; open triangles and dashed line). Removal of the 2 extreme data points did not qualitatively change the results and therefore were kept in the analyses.

Within-individual changes in plumage attributes

We found evidence that suggests plumage characteristics in tree swallows are partly inherent to the individual. Plumage hue showed significant repeatability between the first time a bird was captured and its subsequent recapture, and did not significantly change from one year to the next (Fig. 2a). Plumage brightness, however, did increase from one year to the next, but, as with hue, was also correlated between the first and second capture (Fig. 2b). These results show that birds that were relatively dull when they were first captured were still relatively dull as returning breeders, albeit brighter than the first time they were captured.

Age-related differences in structural plumage attributes are not consistent among species. In both European starlings *Sturnus vulgaris* and blue tits *Cyanistes caeruleus*, hue and brightness have been shown to change with age (Komdeur et al. 2005, Delhey and Kempenaers 2006). In eastern bluebirds *Sialia sialis*, however, the structurally coloured rump increases in brightness over the lifetime of an individual but does not change in hue (Siefferman et al. 2005). It is therefore possible that changes in structural plumage characteristics with age are species-specific. Although all structural colours are produced by coherent scattering of light, the physical composition and structural arrangements of feather barbules are very different among species (Prum 2006). There is a large variety of developmental and physiological mechanisms that produce various feather structures, and so colour production may be more flexible in some species than in others. As such, it is not surprising that plumage hue has been found to change with age in certain species, but not in others. If plumage brightness is primarily a function of density and quality of barbules, however, this structural plumage attribute may be more variable among individuals of the same species. Developmental mechanisms may limit the ability of individuals to vary plumage hue from year to year, but investment in feather barbules may be more flexible. If this

is the case in tree swallows, increase in plumage brightness with age might simply indicate, as in other species, that older birds are more adept at foraging (e.g. Heise and Moore 2003, Limmer and Becker 2006), and are therefore in better condition during moult. The fact that plumage brightness from one year to the next was correlated among birds, however, may indicate that plumage brightness could also signal inherent qualities of the individual (see also Senar and Quesada 2006). Indeed, newly captured birds that were relatively dull were also relatively dull the subsequent year. This suggests that by comparing plumage brightness among individuals, it would be difficult to differentiate dull, experienced breeders from bright inexperienced individuals. If brightness is partially indicative of inherent quality, young birds would be able to convey that information.

Plumage hue and return rate

Our results also suggested that the age-related differences in plumage hue were partially driven by biased return rates of bluer males; however, not all relatively green individuals had a lower probability of returning. When including only relatively dull birds in our model, greener birds were less likely to return. In contrast, when considering only relatively bright birds, we did not find any evidence of hue-biased return rates (Fig. 3). Whether or not a bird was recaptured could have been influenced by a variety of factors including the ability to capture them, breeding site fidelity, and overwinter survival. Since birds were captured in the nest soon after the eggs had hatched, a few of the returning birds may not have been captured if their clutch did not successfully hatch. If this is the case, our results would suggest that greener males may have been mated to females of lower quality, since the ability to incubate eggs is related to female age and condition in tree swallows (Ardia and Clotfelter 2007). This further implies that greener individuals may themselves be of lower quality, as there is evidence for assortative mating in this population (Bitton et al. 2008) and in other populations of this species (Robertson and Rendell 2001). It is also possible that greener individuals may disperse to different breeding sites more readily than bluer individuals. This seems unlikely, however, as male tree swallows have very high nest site fidelity and rarely disperse after having bred at one location (Winkler et al. 2004). More probable is the possibility that plumage hue reflects individual quality and the likelihood of surviving from one year to the next. Overwinter survival has been associated with quality structural plumage (Sheldon et al. 1999, Griffith et al. 2003), melanin-based plumage (Bize et al. 2006), and carotenoid-based plumage (Hörak et al. 2001). Even in species that exhibit specific morphs, plumage attributes have been shown to influence adult survival (Brommer et al. 2005). If elaborate sexual ornaments are costly to produce, current sexual selection theory predicts that the expression of these ornaments can be negatively correlated with survival (Kokko et al. 2002). In many cases, however, plumage attributes have been shown to correlate positively with some aspect of individual quality, and thus covary with apparent survival. In tree swallows, overwinter survival has been positively associated

with individual immunocompetence (Ardia et al. 2003) and longer telomeres (Hausmann et al. 2005). In both cases, the ability to survive from one year to the next was argued to reflect the capacity of individuals to fair well in high-stress situations.

The fact that greener individuals had lower return rates than relatively bluer individuals may suggest that plumage hue, at least among dull birds, could be an indicator of individual quality. Our results from the longitudinal analyses strongly suggested that plumage hue in this population is largely inherent to the individual, however, making it more difficult for this trait, compared to plumage brightness, to honestly reflect current condition of the individual. Although seemingly contradictory, the lack of environmental influence on a plumage attribute does not preclude its possible signalling function. The study of the evolution and function of colour traits has mostly focused on traits that are condition-dependent and that can be influenced by environmental conditions, arguing that these traits are more likely to honestly signal quality. It is also possible, however, for genetically inherited traits to reveal information about individual quality (reviewed in Roulin 2004). For example, different colour morphs are associated with different life-history strategies, which may, to a certain extent, influence survival. Although some species have plumage dimorphism within a sex, plumage characteristics that vary on a continuous spectrum can also be under genetic control (Bize et al. 2006, Py et al. 2006). If plumage attributes are co-inherited with either behavioural or physiological traits that can increase the likelihood of an individual surviving over winter, plumage attributes may convey information about individual quality. Unfortunately, there is no information currently available on colour-specific behaviour or the heritability of plumage characteristics in tree swallows, making it difficult to strongly infer the signalling value of plumage hue in this species.

Overall, our results suggest that both plumage hue and plumage brightness have the potential to signal quality in male tree swallows. Plumage brightness seems to reflect an individual's age, suggesting that bright birds may be in better condition at time of moult. Conversely, plumage hue may be indicative of an individual's inherent quality; however, the exact mechanisms that would make this possible are uncertain. Future studies on plumage coloration of tree swallows should investigate the proximate mechanisms that influence plumage hue, so that a better link may be established between an individual's hue and its ability to survive. Furthermore, there is a need for a better understanding of the costs associated with developing the structures that produce colour. This might require an extensive survey of the light reflecting structures found among birds since the diversity of feather nanostructures makes it difficult to generalise the cost of producing them.

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