Plumage colour is associated with partner parental care in mutually ornamented tree swallows

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Sexually selected traits can signal an individual's ability to contribute offspring care. Differential allocation theory posits that when these same traits also influence brood value, it may be adaptive for partners to adjust care in response to their mates' traits. Evaluating the strength and direction of parental quality signalling and differential allocation is thus essential to understand selection on ornamental traits. We examined relationships between plumage colour and parental care in tree swallows, *Tachycineta bicolor*, a mutually ornamented species in which plumage colour is related to male and female reproductive performance. Using a model of avian vision to quantify parental colour trait variation, we found that male and female tree swallows that were paired to partners with greener, more saturated plumage colour fed offspring at higher rates. Among tree swallow pairs where both partners were in their second year of breeding or older, individuals with greener, more saturated plumage colour also fed their offspring at higher rates. We show that offspring of males that provisioned more often tended to achieve greater body mass independent of the colour traits of their parents. Our results suggest a role for partner parental care in selection on female ornamentation in this species.
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Differential allocation theory predicts that when partner traits influence brood value, parents should adjust investment accordingly (Burley, 1986, 1988; Ratikainen & Kokko, 2010). This principle is supported by studies of many species showing that females often adjust maternal behaviour in response to male traits (Horváthová, Nakagawa, & Uller, 2012; Sheldon, 2000). These traits can signal a male's heritable genetic contribution to offspring quality, survival and/or reproduction, or they may be condition-dependent indicators of a male's ability to contribute parental care (e.g. Hill, 1991; Siefferman & Hill, 2003).

While there is ample evidence that females adjust care in response to male traits, the role of mutual ornamentation is less clear (Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007). In species where both sexes contribute care, there is limited evidence that males also adjust paternal care in response to partner traits (Burley, 1988; Limbourg, Mateman, & Lessells, 2013; Mahr, Griggio, Granatiero, & Hoi, 2012; Roulin, 1999). To date, only one study

has evaluated the relative importance of an individual's own traits (as signals of parental quality) versus those of its partner (via differential allocation) in determining parental care (Limbourg, Mateman, & Lessells, 2013b). That study of blue tits, *Cyanistes caeruleus*, reported that partner traits (but not a bird's own traits) were related to parental provisioning rate, and that partner ultraviolet (UV) coloration had opposing effects on males and females, such that females paired to males with greater UV reflectance fed offspring more often, whereas males paired to females with greater UV reflectance fed less often (Limbourg et al., 2013b).

We compared the ability of own and partner traits to explain variation in parental provisioning rate in tree swallows, *Tachycineta bicolor*, a mutually ornamented species with ample variation in the extent of care provided by both sexes (Leffelaar & Robertson, 1986; McCarty, 2002). Both male and female tree swallows have blue-green structurally coloured dorsal plumage. Female tree swallows also have delayed plumage maturation, displaying predominantly brown dorsal plumage in their first year, and uniformly blue-green dorsal plumage thereafter (Hussell, 1983). However, all adult tree swallows (including brown females) have blue-green feather tips, and there is extensive overlap between the adult sex and age classes in the hue of these feather tips (Fig. 1). Plumage colour is

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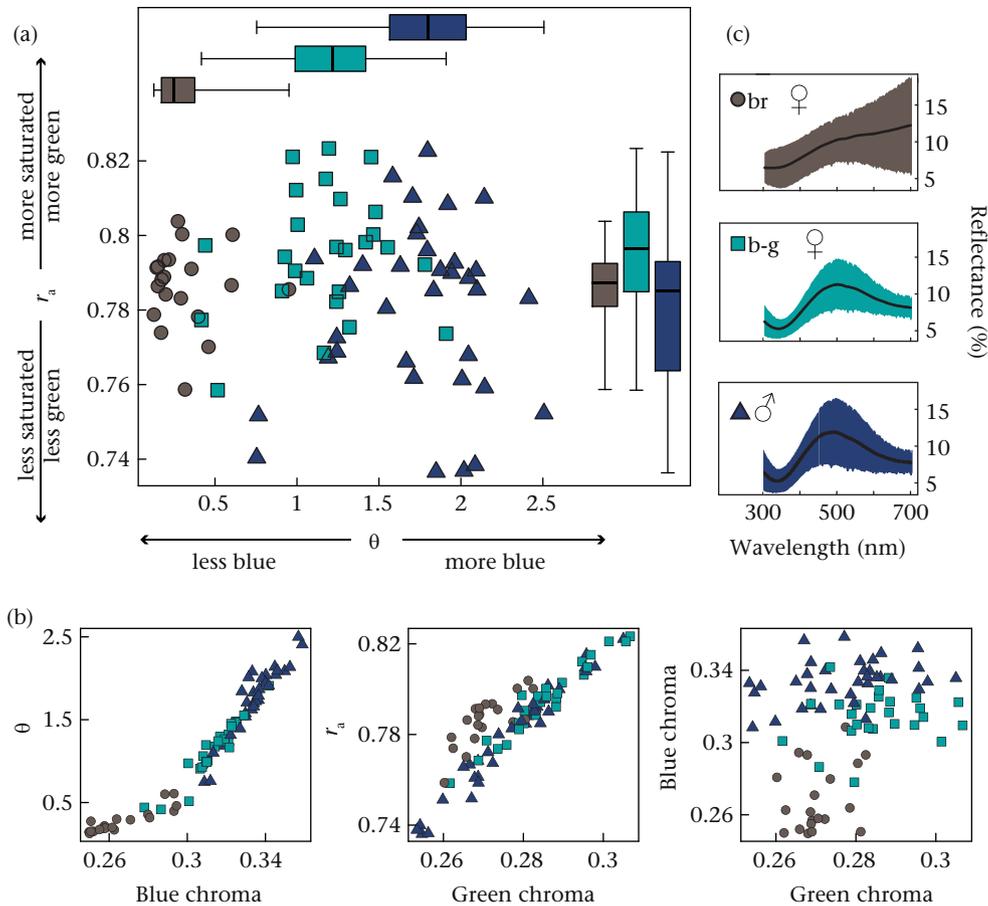
Figure 1. (a) Plumage greenness/saturation (r_a) and blueness (θ) for adult male ($N = 35$) and female ($N = 46$; 20 brown 'br' and 26 blue-green 'b-g') tree swallows. (b) Individuals with higher θ have higher blue chroma; individuals with higher r_a have higher green chroma; and these two dimensions vary independently among tree swallows. Blue chroma is calculated as the reflectance between 400 and 510 nm relative to total reflectance (300–700 nm). Green chroma is calculated as the reflectance between 510 and 605 nm relative to total reflectance. Blue chroma is correlated with derived colour metrics associated with reproductive performance in previous studies of tree swallows (Bentz & Siefferman, 2013; Bitton & Dawson, 2008; Bitton et al., 2008). (c) Average colour spectra of adult tree swallow rump feather tips with shaded 95% confidence intervals. Black lines are smoothed averages. Note this figure shows data from 81 adult individuals that were captured in 2013, including 19 individuals that were not part of the study of parental care.

also related to reproductive performance, life history and physiological traits in this species. Previous studies quantified plumage colour using measures of hue that ranged on a scale from more blue to more green. Among blue-green females in their second year or older, these hue traits covaried with the average mass of eggs laid (bluer females laid heavier eggs than greener females) and fledging success (bluer females fledged more young) (Bentz & Siefferman, 2013; Bitton, Dawson, & Ochs, 2008). Among males, hue covaried with the likelihood that a male would be recaptured the following year (males with bluer plumage were more likely to be recaptured than greener males; Bitton & Dawson, 2008). Together, these results suggest that tree swallows with bluer-hued plumage may have greater reproductive performance and survival than greener-hued individuals as a result of unknown genetic, epigenetic and/or somatic factors. Among females, plumage colour is also correlated with immune activity (bluer females have less change in wing web thickness in response to cell-mediated phytohemagglutinin (PHA), indicating lower immune activity) and blood oxygen-carrying capacity (bluer females have lower haematocrit; Bentz & Siefferman, 2013). These correlations with physiological traits could be interpreted as evidence that bluer females are in worse condition, or alternatively, that bluer females pay a cost to their heavy investment in reproduction. Although the mechanisms underlying covariation in plumage hue and other phenotypic and life history

traits in tree swallows are not yet understood, a previous study of adult male tree swallows found no significant change in dorsal colour from one year to the next, suggesting that age-related changes are likely minimal (Bitton & Dawson, 2008).

In this study, we used tetrahedral colour space models of avian colour vision to quantify tree swallow rump colour variation. These models account for the fact that receivers are not equally sensitive to all wavelengths of light (Goldsmith, 1990; Stoddard & Prum, 2008), providing a powerful tool for evaluating the function of chromatic trait variation (e.g. Baldassarre, Thomassen, Karubian, & Webster, 2013; Dakin & Montgomerie, 2013; Stoddard & Stevens, 2011; Théry, Debut, Gomez, & Casasbery, 2005). We identified two traits that were correlated with measures of blueness and greenness, respectively, and that vary independently (Fig. 1). If plumage hue indicates a bird's own capacity for parental care (parental quality signal hypothesis), we predicted that tree swallows with bluer plumage would feed their offspring at higher rates (consistent with the 'good parent process'; Hoelzer, 1989). If parental behaviour is instead more strongly influenced by partner colour traits (differential allocation hypothesis), we predicted that tree swallows paired to bluer partners would feed their offspring at higher rates. Although we based the directions of our predicted relationships on expected positive relations between plumage blueness, quality and care, note that higher-quality individuals may

sometimes provide less care, for instance if they benefit from engaging in additional mating opportunities (e.g. Burley, 1986; Magrath & Komdeur, 2003; Mitchell, Dunn, Whittingham, & Freeman-Gallant, 2007; Møller & Thornhill, 1998). Furthermore, under differential allocation, individuals paired to low-quality partners may sometimes provide more care to compensate for the low quality of their mates (i.e. reproductive compensation; Gowaty et al., 2007).

Upon finding a relationship between offspring provisioning rate and partner plumage colour traits, we conducted two additional analyses. First, we used structural equation modelling (path analysis) to investigate potential relationships between tree swallow plumage colour, parental care and offspring body mass. Second, given that other studies have reported that tree swallows pair nonrandomly by their plumage colour traits (e.g. Bitton et al., 2008; Dakin, 2006), we also analysed whether the birds in our study population paired nonrandomly by the same traits that were associated with partner provisioning.

METHODS

Field Methods

We studied box-nesting tree swallows at the Queen's University Biological Station (QUBS) in Ontario, Canada (44°34′N, 76°19′W). We determined the date of the first egg to hatch (hatch date) for broods laid in May 2013, and quantified both maternal and paternal provisioning rates at 31 nests where both parents were still present >3 days posthatch. Three days posthatch, we observed nests for 1 h between 0730 and 1300 hours Eastern Daylight Time and counted the number of times each parent entered the nestbox as a measure of provisioning rate (McCarty, 2002; Ouyang et al., 2015). During observations, we differentiated males and females using plumage coloration at 14 nests where the female was in her first year of breeding. Females in their first year of breeding have predominantly brown dorsal plumage and are easily distinguished from their mates (Hussell, 1983; see Supplementary Fig. S1). We classified any females with ≤90% blue-green upperparts as 'brown' females (note that our classification of 'brown' includes both 'brown' and 'intermediate' females in Hussell's (1983) terminology). Females with >90% blue-green upperparts were classified as 'blue-green'. At the remaining 17 nests where the female had uniformly blue-green plumage, parents were differentiated using either leg bands from previous years ($N = 4$ nests), or acrylic paint that was applied during the incubation period ($N = 13$ nests). Paint was applied passively by mounting a small sponge with a dab of paint on the nestbox entrance to mark the incubating bird (males do not incubate; Ardia, Cooper, & Dhondt, 2006).

At 26 nests, we captured males and females the following day (4 days posthatch) to measure body mass (±0.1 g) and skull length (cranium–bill tip, ±0.1 mm), and we removed five to seven rump feathers for colour measurements. At five remaining nests, we captured parents 13 days posthatch instead, because these nests were not part of a separate hormone manipulation experiment (Ouyang et al., 2015). Note that the hormone treatment was applied after the observations of parental care for this study. Birds at the five nests captured 13 days posthatch did not differ significantly from those captured on day 4 in parental visit rate (Gaussian linear regression models: all $F_{1,29} < 0.81$, $P > 0.37$), body condition (see below; all $F_{1,29} < 1.45$, $P > 0.23$) or plumage colour metrics (see below; all $F_{1,29} < 1.60$, $P > 0.21$). Thus, in all following analyses, we present results without controlling for the timing of adult capture. At 25 nests, we measured the body mass of each nestling (±0.01 g) immediately after capturing both parents 4 days posthatch. At the six remaining nests (five controls in a separate experiment plus one

that was missed on day 4 due to error), we weighed nestlings 6 days posthatch. We calculated average nestling mass for each brood, and, as a measure of offspring quality comparable across nests, we took the residual from a linear model of average nestling mass controlling for age when weighed (estimate ± SE = 1.52 ± 0.34, $N = 31$; $F_{1,29} = 20.2$, $P = 0.0001$). Results of analyses involving nestling mass were qualitatively the same when using only the 25 nests measured 4 days posthatch.

Ethical Note

All procedures followed guidelines for animal care outlined by ASAB/ABS and the Canadian Council on Animal Care (CCAC), and were approved by the Virginia Tech's Institutional Animal Care and Use Committee (protocol no. 12-020) and Queen's University Animal Care Committee (2013-019). All birds were banded under Canadian Wildlife Services banding permit number 10771. Adult birds in our study of parental care were held for banding and measurements for 13.2 min on average (range 5–36 min, $N = 62$), with the majority of individuals (84%) held for <20 min. The study year was characterized by unusually cold and rainy weather, which caused very high nest failure (90.5% in 2013, as opposed to an average of 53% failure in this population over the previous 5 years, with similar capture and handling of birds). Note that all parental behaviours observed and analysed in this study occurred prior to capture and prior to a corticosterone hormone experiment conducted as part of a separate study (Ouyang et al., 2015).

Colour Measurements

Feathers were kept in sealed plastic bags in the field and then transferred to opaque paper envelopes for 3 months prior to taking measurements. We stacked and mounted all feathers collected from one bird on a white card (Keyser & Hill, 1999) and used an Ocean Optics USB4000 spectrometer and a PX-2 lamp with a 400 nm UV/VIS bifurcated fibre-optic cable in a cylindrical metal sheath to take reflectance spectra at 90° to the measurement surface. Each spectral measurement was the average of 10 scans at 100 ms integration time, with a boxcar smoothing function of width 10, taken relative to a Spectralon white standard (Spectralon) using OceanView 1.3 software. We took five measurements of the coloured feather tips, moving the measurement probe haphazardly between each measurement, and retaking white and dark standards for each sample (bird). This procedure was repeated twice on each sample (bird), shuffling the order of all samples in between.

We used the package pavo (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013) in R 3.2.1 (R Core Team, 2015) to quantify colours of the rump feather tips in bird-perceived tetrahedral colour space under standard noon daylight conditions (International Commission on Illumination (CIE) D65; see Supplementary Material for details of tetrahedral colour space models). We used spectral sensitivity curves for the blue tit (Hart, Partridge, Cuthill, & Bennett, 2000) in our tetrahedral colour space model, because tree swallow cone sensitivities have not been directly measured. Blue tit cone sensitivities are expected to be representative of those of tree swallows and other members of the family Hirundinidae, as the SWS1 opsin gene sequences are highly conserved in the Passerida suborder (Hart & Hunt, 2007; Ödeen, Håstad, & Alström, 2011).

We focus on two individual colour traits representing bird-perceived colour: theta (θ), a measure of bird-perceived hue in the non-UV range, and achieved saturation (r_a), a measure of the extent to which a colour stimulates the cone photoreceptors given its hue (Fig. 1; Stoddard & Prum, 2008). Interpretation of both of these measures depends on the data set at hand. In our data set, higher values of θ correspond to bluer-hued plumage, and lower

values correspond to less intense blue; thus we refer to θ as 'blueness' (Fig. 1b). Higher values of r_a in our data set correspond to more saturation perceived in the 'green' range for both sexes, and are correlated with measures of plumage greenness (Fig. 1b); thus we refer to r_a as 'greenness/saturation'. These two traits also vary independently (Fig. 1a, b). We interpret individuals that scored highly on both traits as having plumage that is more intensely blue-green. Note, however, that descriptors such as 'blueness' and 'greenness' are based on human vision and are not intended to represent what the birds actually perceive. The advantage of our approach (as opposed to measuring hue as the wavelength of peak reflectance) is that θ and r_a capture spectral variation in a way that accounts for receiver sensitivity. Human-based descriptors ('blue' and 'green') are used for convenience only. We also calculated phi (or ϕ), a measure of UV reflectance that is also based on tetrahedral colour space. We chose to omit phi (ϕ) from our analyses of parental care to reduce the number of variables under consideration, because θ and ϕ were highly correlated in our data set for both males and females, and because r_a and ϕ were also highly correlated for males (see Supplementary Table S1). For each mated pair, we also calculated the difference in colour (Δ_T) between the male and female as the Euclidean distance between their plumage colours in tetrahedral colour space (Endler & Mielke, 2005; Stoddard & Prum, 2008).

Data Analysis

All statistical analyses were performed in R 3.2.1 (R Core Team, 2015). Preliminary data exploration indicated that parental visit rates were positively correlated for paired males and females ($R^2 = 0.33$, $F_{1,29} = 14.5$, $N = 31$ pairs, $P = 0.0007$; see Fig. 2). This correlation could be due to a positive influence of partner investment on visit rate (Hinde & Kilner, 2007), or to shared factors affecting both parents during the observation period, such as offspring state, prey abundance or current weather conditions (Leffelaar & Robertson, 1986; Rose, 2009; Winkler, Luo, & Rakhimberdiev, 2013). To account for this covariance, we used mixed-effects models to examine relationships between parental colour traits and visit rates, including 'nest' as a random effect. Our measure of visit rate did not depart significantly from normality for
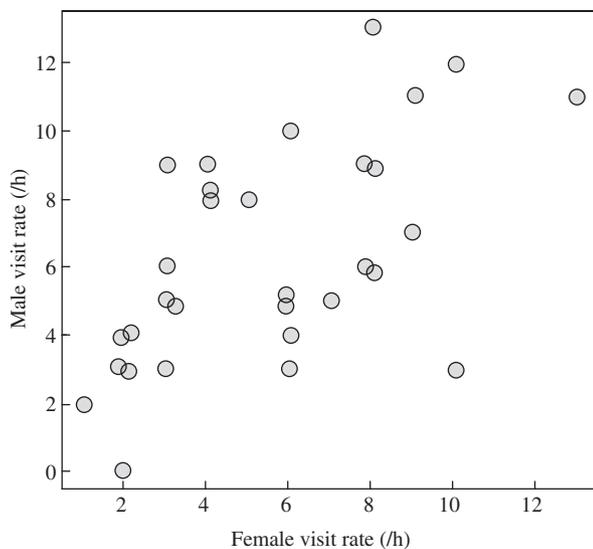
either sex (Shapiro–Wilk tests: all $P > 0.07$). Thus, we used models with Gaussian error distributions and the identity link, and we verified that the residuals for fitted models were normally distributed in every case.

We used an information-theoretic approach (Burnham & Anderson, 2002) to consider the following 10 candidate models of provisioning rate: (1) sex + own plumage r_a + own plumage θ + hatch date; (2) sex*own plumage r_a + sex*own plumage θ + hatch date; (3) sex + partner plumage r_a + partner plumage θ + hatch date; (4) sex*partner plumage r_a + sex*partner plumage θ + hatch date; (5) sex + own plumage r_a + own plumage θ + partner plumage r_a + partner plumage θ + hatch date; (6) sex + pair colour difference (Δ_T) + hatch date; (7) sex*pair colour difference (Δ_T) + hatch date; (8) sex + female age class + hatch date; (9) sex*female age class + hatch date; (10) no fixed effects (intercept only).

All candidate models that included interactions between sex and a given trait (denoted by '*' above) also included all main effects associated with any interaction terms. Candidate models 1 and 2 correspond to the parental quality signalling hypothesis, candidates 3 and 4 to the differential allocation hypothesis, and candidate 5 to the scenario where parents respond to both their own traits and their partner's traits. Candidate models 6 and 7 correspond to the scenario where parental provisioning is associated with the difference in colour between the two members of a pair. Candidate models 8 and 9 correspond to the scenario where female age class best explains variation in parental care (i.e. whether the female is in her first year of breeding with predominantly brown plumage). All models that included fixed effects of colour traits also included hatch date to account for potential associations between colour traits and the date when pairs commenced breeding (see Supplementary Material), as well as between date and parental care.

Although Ardia (2007) showed that manipulating brood size ($\pm50\%$) can influence tree swallow provisioning rates, we did not detect an association between brood size and parental visit rate in our study population (Gaussian mixed models, brood size coefficient (95% confidence interval): all pairs: 0.74 ((−0.45, 1.92)), $t = 1.22$, $P = 0.23$; blue-green female pairs: 0.55 ((−1.28, 2.38)), $t = 0.59$, $P = 0.56$; range 3−7 chicks/brood). For this reason, we did not include brood size as a fixed effect in any of our candidate models. However, when we included additional candidate models with brood size as a fixed effect, our best-supported models remained the same, as the models with brood size added were not supported.

Because blue-green females are older and their colour signals might function differently, we separately analysed two candidate model sets: one model set for all pairs ($N = 62$ birds) and a separate model set for the subset of pairs where the female had uniform blue-green dorsal plumage ($N = 34$ birds; note that this model set omits candidate models 8−9). We report standardized regression coefficients and their confidence intervals to evaluate effect sizes for predictors, and, as a measure of the total variance explained, we also report $R^2_{GLMM(m)}$ and $R^2_{GLMM(c)}$ (Nakagawa & Schielzeth, 2013). The R^2_{GLMM} statistics estimate the amount of variance explained by the fixed effects ($R^2_{GLMM(m)}$) and the whole model ($R^2_{GLMM(c)}$; fixed + random effects), respectively. We report these results for the average of all models within 2 AICc units of the best-fit model, as these models are considered equally well supported (Burnham & Anderson, 2002). If there were no other candidate models with AICc values within 2 units of the best-fit model, we report results for the best-fit model instead. Details of all candidate models are provided in the Supplementary Material.

All regression models in this study met the assumptions of homoscedastic, normally distributed residuals (Shapiro–Wilk

Figure 2. Relation between parental visit rates of paired male and female tree swallows. Points are jittered to eliminate overlap in cases where pairs had identical visit rates.

tests: all $P > 0.05$), with no outliers. We also checked variance inflation factors as a measure of the severity of multicollinearity for best-fit models of parental visit rate, and confirmed that all variance inflation factors were between 1.00 and 2.00, indicating that results of these analyses were not unduly influenced by multicollinearity.

Path Analysis

To determine how individual parent colour traits and provisioning behaviour are related to offspring mass, we performed a path analysis on individual colour traits r_a and θ, parental visit rates and residual average nestling mass (i.e. average nestling mass controlling for age in days when weighed; see Field Methods above) using the R package sem 3.1-3 (Fox, Kramer, & Friendly, 2013). The path model included covariance structures for male and female provisioning rates (Fig. 2), as well as directional paths for each sex between r_a and θ and partner provisioning rate, between r_a and θ and own provisioning rate, between provisioning rate and residual average nestling mass and between r_a and θ and residual average nestling mass. We performed this analysis on all pairs to maintain a large sample, and because blue-green saturation (r_a), the individual trait most strongly related to partner provisioning in our other analyses, is continuously distributed with overlap between brown and blue-green females and males (Fig. 1). To test model fit, we used a chi-square test with a root mean square error approximation (RMSEA) to correct for small sample size and parsimony. An RMSEA value close to zero with a nonsignificant P value indicates a good model fit. The fitted model had an RMSEA index of <0.01 (95% CI ((0, 0.15)), $P = 0.90$). All variables entered into the path analysis were standardized to have a mean of 0 and SD of 1, and we report standardized path coefficients (i.e. partial regression parameters) to describe relationships between variables.

Nonrandom Pairing

Upon finding an association between plumage hue and parental provisioning, we tested for nonrandom pairing by hue- and saturation-based colour traits in our study population using two methods. First, we examined correlations between UV reflectance (ϕ), blueness (θ) and greenness/saturation (r_a) of colour traits of paired males and females. Following this, we also compared the population average pair colour difference (Δ_T) with that obtained when pairs were randomized in a permutation randomization test (10 000 replicates). We present raw P values (uncorrected for multiple testing), because all results for nonrandom pairing were nonsignificant, so correcting for false discovery rate would not change the interpretation of these results.

RESULTS

Sex and Age Class Differences in Colour

Male plumage was bluer (higher θ), less saturated (lower r_a) and less UV reflectant (lower ϕ) than that of females. Older females (as defined by their uniform blue-green dorsal plumage; Hussell, 1983) had plumage that was bluer (higher θ), more saturated (higher r_a) and less UV reflectant (lower ϕ) than that of younger brown-plumaged females (Fig. 1, Table 1).

Colour and Offspring Provisioning

In our analysis of all pairs, two models were equally well supported: candidate model 6, in which provisioning rate was associated with the difference in male and female coloration (Δ_T), and candidate model 8, in which provisioning rate was associated with female age class (see Supplementary Table S5 for details). Pairs with a greater difference in coloration (Δ_T) and pairs with 1-year-old brown-plumaged females provisioned their offspring at a lower rate than pairs that were more similarly coloured (Table 2, Fig. 3a). As both models were equally well supported, we cannot distinguish between the predictive power of continuous colour trait variation (Fig. 1) and the categorical determination of female age class.

Examining the subset of pairs where the female had uniform blue-green plumage, two models received equal support: candidate model 3, in which provisioning rate was associated with partner colour traits, and candidate model 5, in which provisioning rate was associated a bird's own colour traits and partner colour traits (Supplementary Table S5). Males and females paired to partners with greener, more saturated plumage (higher partner r_a) provisioned their offspring at a higher rate (Fig. 3b, Table 2). Males and females with greener, more saturated plumage (higher own r_a) also tended to provision their offspring at a higher rate, independent of their partner's coloration (Table 2).

We did not find evidence that males and females respond to colour traits differently, as models that included interactions between sex and colour traits were not supported in either model set (Akaike weights ≤0.12; Supplementary Table S5). In addition, there was no support for candidate models containing only a bird's own colour traits (candidate models 1 and 2, Akaike weights ≤0.03; Supplementary Table S5).

Offspring Mass, Parental Provisioning and Colour

Path analysis results indicated that males paired to females with greener, more saturated plumage and bluer coloured plumage (higher r_a and higher θ) provisioned their offspring more often ($P = 0.006$ and 0.02 for r_a and θ, respectively; Table 3, Fig. 4). Thus, males provisioned more when paired to more intensely blue-green

Table 1
Plumage colour metrics (blueness (θ), greenness/saturation (r_a) and UV reflectance (ϕ)) in relation to sex and female age class for all tree swallows captured in 2013

	N	Predictor	Response	Estimate (95% CI)	F	P
Males vs females (all)	35 males	Sex	Blueness θ	0.94 (0.73, 1.16)	77.0	<0.0001
	46 females		Greenness/saturation r_a	−0.01 (−0.02, −0.003)	7.4	0.008
			UV reflectance ϕ	−0.10 (−0.13, −0.06)	30.8	<0.0001
Males vs blue-green females	35 males	Sex	Blueness θ	0.57 (0.37, 0.77)	31.8	<0.0001
	26 females		Greenness/saturation r_a	−0.02 (−0.03, −0.005)	8.1	0.006
			UV reflectance ϕ	−0.03 (−0.05, −0.01)	10.0	0.002
Blue-green females vs brown females	26 blue-green	Age class	Blueness θ	0.86 (0.67, 1.04)	89.8	<0.0001
	20 brown		Greenness/saturation r_a	0.01 (−0.0009, 0.02)	4.0	0.05
			UV reflectance ϕ	−0.15 (−0.19, −0.11)	61.9	<0.0001

Coefficient estimates are given for the italicized group. Note that these analyses include 19 individuals that were not part of our study of parental care.

Table 2
Parental visit rate in relation to plumage colour traits in tree swallows

Response	Model set	Candidate models supported	Predictor	ß	95% CI	$R^2_{GLMM(m)}$ fixed effects	$R^2_{GLMM(c)}$ whole model
Visit rate *Gaussian*, *random=nest*	All pairs $N=62$ birds, 31 pairs	6, 8	Sex (*male*)	0.81	−0.27, 1.88	0.18	0.60
			Hatch date	−0.67	−1.62, 0.29		
			Pair difference Δ_T	−1.07	−1.99, −0.15		
			Female age class (*blue*)	1.96	0.01, 3.91		
	Blue-green female pairs $N=34$ birds, 17 pairs	3, 5	Sex (*male*)	0.75	−1.23, 2.73	0.43	0.72
			Hatch date	−1.00	−2.45, 0.46		
			Partner greenness/saturation r_a	1.34	0.02, 2.67		
			Partner blueness θ	−0.13	−1.24, 0.99		
			Own greenness/saturation r_a	1.23	0.11, 2.35		
			Own blueness θ	0.19	−0.93, 1.31		

Standardized coefficient estimates and R^2_{GLMM} values are given for the average of supported models within 2 AICc units of the best-fit model. See Supplementary Table S5 for details on other candidate models.

coloured females. In addition, males with higher provisioning rates had heavier nestlings, independent of parental coloration ($P = 0.04$). Females paired to males with greener, more saturated (higher r_a) plumage also tended to provision their offspring more often (ß $= 0.25$), although this relationship was not statistically significant ($P = 0.07$). Nestling mass was not significantly associated with variation in female provisioning rate ($P = 0.25$). Males and females with greener, more saturated plumage colour tended to have heavier offspring, independent of parental provisioning rates (ß $= 0.39$ and 0.22 for males and females, respectively); the path from plumage r_a to nestling mass was statistically significant for males ($P = 0.009$) but not for females ($P = 0.17$).

Nonrandom Pairing

There was no significant correlation between paired male and female blueness (θ), greenness/saturation (r_a) or UV reflectance (ϕ) (Pearson correlations: all $r < 0.11$, $N = 31$ pairs, all $P > 0.56$). Results were similar when examining only the subset of pairs where the female had uniform blue-green dorsal plumage (all $r < 0.24$, $N = 17$ pairs, all $P > 0.35$). In addition, there were no significant differences in the colour traits of males paired to brown versus blue-green females (all $F_{1,29} < 2.64$, $N = 31$ pairs, all $P > 0.11$). The average pair colour difference (Δ_T) in our study population (0.050 ((95% CI $= 0.039$, 0.061)), $N = 31$ pairs) was not significantly different from that obtained under random pairing in a permutation randomization test (0.050 ((0.049, 0.053)), two-tailed $P > 0.45$). Results were similar when examining only pairs with blue-green females (observed: $\Delta_T = 0.030$ ((0.024, 0.036)), random pairing: $\Delta_T = 0.032$ ((0.028, 0.034)), $N = 17$ pairs, $P > 0.40$). Thus, we found no evidence that the birds in our study population paired non-randomly by plumage hue, saturation or colour disparity.

DISCUSSION

In support of mutual differential allocation, we found that both male and female parents provisioned their offspring more often when paired to partners that had greener, more saturated (higher r_a) plumage colour (Fig. 3b). Furthermore, our path analysis suggests that increased provisioning by males may translate into increased offspring mass. This is consistent with previous studies showing that males that provision more often tend to have heavier offspring (Ardia, 2007; Leffelaar & Robertson, 1986). Females that display plumage with a more intense blue-green coloration (i.e. higher r_a and higher θ) may achieve greater reproductive success than they would otherwise, as a result of additional care allocation by their partners (Fig. 4; Schwagmeyer & Mock, 2008).

Why invest more when paired to a partner with greener plumage colour (Fig. 3b)? Previous studies indicate that tree swallows with greener-hued coloration may have reduced reproductive performance relative to bluer-hued individuals (Bentz & Siefferman, 2013; Bitton & Dawson, 2008; Bitton et al., 2008). It is difficult to compare our results to those of previous studies because our results focus on two independent axes of colour trait variation (Fig. 1), whereas the previous studies evaluated a single dimension of hue (ranging from more blue to more green). Nevertheless, we
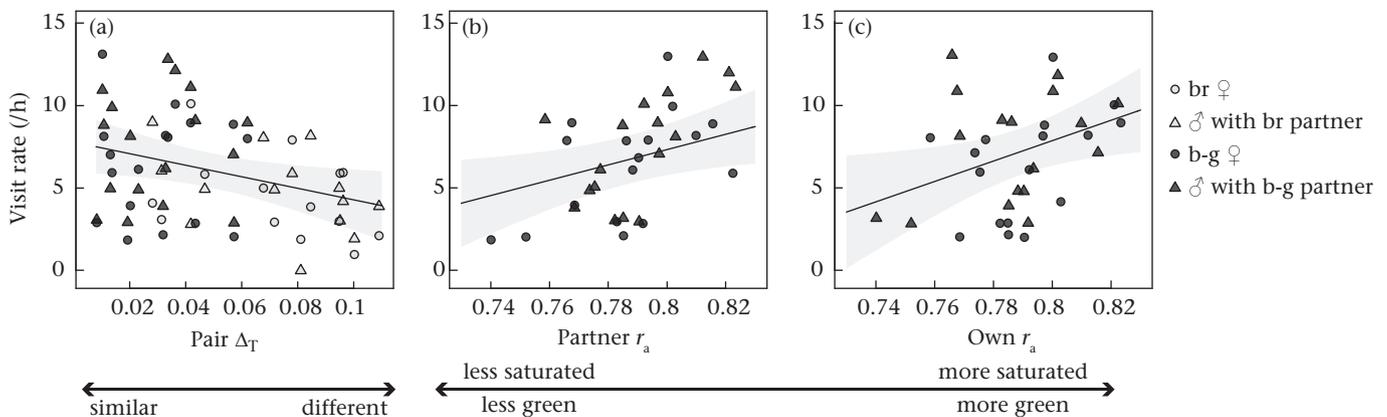
Figure 3. Relation between parental nest visit rate and (a) pair colour difference (Δ_T) among all tree swallow pairs ($N = 62$ birds), and (b) partner greenness/saturation (r_a) and (c) own greenness/saturation (r_a) among pairs where the female had uniform blue-green coloration ($N = 34$ birds). Partial regression slopes ±95% CI for predicted values are shown for the best-supported models (assuming the median value for other predictors, and averaging predictions across the sexes). br: brown; b-g: blue-green.

Table 3
Path analysis of parent plumage coloration, provisioning rates and residual average nestling mass in tree swallows

Path	ß	95% CI	Z	P
Male visit→resid. avg. nestling mass	0.41	0.02, 0.80	2.05	0.04
Female r_a→male visit	0.41	0.12, 0.70	2.73	0.006
Male r_a→resid. avg. nestling mass	0.39	0.10, 0.68	2.61	0.009
Female visit←→male visit	0.36	0.07, 0.65	2.42	0.02
Female θ→male visit	0.35	0.05, 0.64	2.31	0.02
Male r_a→female visit	0.30	−0.02, 0.62	1.85	0.07
Female θ→female visit	0.22	−0.10, 0.54	1.34	0.18
Female r_a→resid. avg. nestling mass	0.22	−0.10, 0.53	1.36	0.17
Female visit→resid. avg. nestling mass	−0.21	−0.57, 0.15	−1.16	0.25
Female r_a→female visit	0.19	−0.13, 0.51	1.16	0.24
Male θ→female visit	−0.16	−0.48, 0.16	−0.97	0.33
Male r_a→male visit	0.11	−0.18, 0.41	0.76	0.45
Male θ→resid. avg. nestling mass	−0.10	−0.38, 0.18	−0.71	0.48
Female θ→resid. avg. nestling mass	0.08	−0.22, 0.38	0.53	0.60
Male θ→male visit	−0.06	−0.35, 0.23	−0.39	0.69

Paths are ordered by the magnitude of the standardized path coefficient ß.

hypothesize based on these previous studies that tree swallows with greener, more saturated plumage may be poorer-quality individuals, and that their partners may benefit by compensating for poor genetic or phenotypic quality of their mates (Gowaty et al., 2007; Ratikainen & Kokko, 2010). We also found that male tree swallows with greener, more saturated coloration tended to have heavier offspring (Fig. 4), independent of the provisioning rate of both parents. Given the evidence from previous studies that male tree swallows with greener coloration tend to be lower quality (Bitton & Dawson, 2008; Bitton et al., 2008), we hypothesize that this association may also result from compensatory investment on the part of females (e.g. reproductive compensation via investment in eggs or in the quality of food delivered independent of provisioning rate). There is some evidence for compensatory reproductive investment in other species. For instance, several studies have shown that female birds paired to unattractive males increase the amount of carotenoid antioxidants they deposit into their eggs. Female European barn swallows, *Hirundo rustica*, paired to males that were made less attractive by shortening their tails deposited more carotenoids into their egg yolks than females paired to control and tail-elongated males (Saino et al., 2002). Female house finches, *Haemorhous mexicanus*, and zebra finches, *Taeniopygia guttata*, similarly deposited more antioxidants, and, in the case of zebra finches, more total volume, into their eggs when paired to less attractive males (Bolund, Schielzeth, & Forstmeier, 2009;
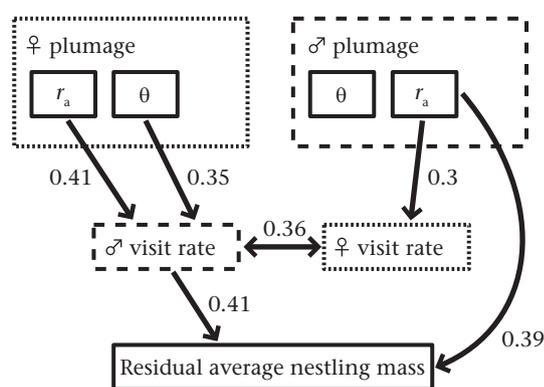
Navara, Badyaev, Mendonça, & Hill, 2006). In addition, female pronghorn antelope, *Antilocapra americana*, that mated with less attractive sires spent more time suckling their fawns (Byers & Waits, 2006).

Across all tree swallow pairs (blue-green and brown-plumaged females pooled), we also found evidence that both parents tended to provision offspring more often when the female had uniform blue-green dorsal plumage (as opposed to 1-year-old brown-plumaged females; Table 2, Fig. 3a). A possible explanation for this difference is that older females with uniform blue-green dorsal plumage may have acquired increased parenting skill or capacity with age (Robertson & Rendell, 2001). Alternatively, these older females may obtain higher-quality male partners, or males may invest more when paired with these older females. Although previous studies have reported that tree swallows mate assortatively by achromatic (Bitton et al., 2008) and chromatic (Dakin, 2006) colour trait variation, we found no evidence of nonrandom pairing by chromatic colour variation in our study population and year. Either tree swallows do not pair nonrandomly by the colour traits that were associated with partner provisioning in this study, or we may have failed to detect an association, perhaps because patterns of nonrandom pairing vary geographically and/or across years.

An alternative explanation for the positive relationship between provisioning rate and partner greenness/saturation (Fig. 3b) is that tree swallows with greener, more saturated plumage colour may actually be better parents, or they may provide some other direct benefit to their mates (Hoelzer, 1989). Indeed, our results also suggest that birds with greener, more saturated plumage may have provided more care (Fig. 3c), although we did not find support for this in our path analysis of all pairs (Table 3). In some bird species, males with less exaggerated display traits have been shown to provide more care, possibly because they lack additional mating opportunities (unlike more attractive males; Møller & Thornhill, 1998). These individuals may have provided other direct benefits that we did not measure, such as a higher quality of food delivered. Another possibility is that birds with greener, more saturated plumage colour may be less likely to abandon their broods. We were not able to evaluate the effect of plumage colour on abandonment due to a hormone manipulation applied after our behavioural observations (Ouyang et al., 2015). If birds with greener, more saturated plumage colour provide more or better care, it could increase the reproductive value of the brood, providing a benefit to partners that invest additional care.

Yet another possibility is that females (and males) with greener, more saturated plumage colour tended to pair with birds that are better parents. Because this study was observational, we cannot rule out any of these explanations. Experiments are needed to disentangle the relationships between quality, plumage colour traits and parental effort, and to determine whether our results are truly due to tree swallows dynamically adjusting investment in response to partner traits, as we suggest (Burley, 1988; Limbourg, Mateman, Andersson, & Lessells, 2004; Limbourg et al., 2013). Regardless of the underlying mechanisms (dynamic adjustment versus nonrandom pairing with respect to colour and parental care; and in the case of dynamic adjustment, differential allocation versus reproductive compensation), our results suggest that increased provisioning by males paired to partners with more intensely blue-green plumage may translate into increased offspring mass (Fig. 4), and potentially greater reproductive success for more intensely blue-green females (Ardia, 2007; Leffelaar & Robertson, 1986; Schwagmeyer & Mock, 2008). Our findings therefore emphasize the role of partner parental care in selection on female ornamentation in this species (Gowaty et al., 2007; Qvarnström & Price, 2001; Ratikainen & Kokko, 2010).

Figure 4. Path diagram illustrating relationships between parent coloration, provisioning rates and residual average nestling mass for all tree swallow pairs ($N = 31$ pairs). Only paths with $P < 0.10$ are illustrated, with standardized path coefficients shown. See Table 3 for detailed path analysis results.

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.10.006.

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