



Experimentally altered plumage brightness of female tree swallows: a test of the differential allocation hypothesis

Lisha L. Berzins* and Russell D. Dawson

Ecosystem Science and Management, University of Northern British Columbia,
3333 University Way, Prince George, BC, Canada V2N 4Z9

*Corresponding author's e-mail address: berzins@unbc.ca

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Abstract

The differential allocation hypothesis posits that individuals should invest in the current reproductive attempt according to the attractiveness of their mate, but studies of allocation by males when female traits are manipulated to be more attractive are lacking. In the current study, we experimentally enhanced and reduced the plumage brightness of female tree swallows (*Tachycineta bicolor*) relative to controls to examine whether males adjust investment in parental care according to female attractiveness, while simultaneously performing a brood size manipulation. Contrary to our predictions, we found no evidence that males provisioned nestlings according to the plumage brightness of females. However, we found that nestling quality and fledging success were lowest when female plumage brightness was reduced and brood size was enlarged. This may be due to the plumage brightness treatment influencing agonistic interactions with other females, and may suggest that plumage brightness is a signal assessed by females.

Keywords

attractiveness, brood size manipulation, differential allocation, female ornamentation, parental care, provisioning rate, sexual selection, social feedback.

1. Introduction

It is widely recognized in a variety of taxa that females display elaborate ornaments, such as brightly coloured plumage. Two mechanisms often used to explain the presence of ornamental traits in females are a genetic linkage with selection on male traits or direct selection on female traits (Lande, 1980; Amundsen, 2000). Direct selection on female traits can arise by male mate

choice or female–female competition for mates or resources, and so may be driven by sexual and/or social selection (LeBas, 2006; Clutton-Brock, 2009; Edward & Chapman, 2011; Tobias et al., 2012). Ornamental traits may provide honest information about the quality of their bearer (Zahavi, 1975; Kodric-Brown & Brown, 1984; Grafen, 1990), and an accumulating number of studies have demonstrated that ornamental traits reflect aspects of female quality (see Doutrelant et al., 2008; Gladbach et al., 2010; Martinez-Padilla et al., 2011; Henderson et al., 2013). For example, some studies suggest that elaborately ornamented females transmit more resources to eggs (Midamegbe et al., 2013), have higher fecundity (Jawor et al., 2004; Cornwallis & Birkhead, 2007), provide more parental care to offspring (Linville et al., 1998; Weiss, 2006; Silva et al., 2008; García-Navas et al., 2012), or produce offspring of higher genetic quality (e.g., offspring with greater immune defenses; Roulin et al., 2000; Remeš & Matysioková, 2013). As such, males may benefit from assessing the attractiveness of female ornamentation when deciding how much parental care to investment in offspring.

Investing in the current reproductive attempt according to mate attractiveness is known as differential allocation (Burley, 1986; Sheldon, 2000), and is expected to occur when there is a trade-off between current and future reproduction, and when the attractiveness of one's mate signals the reproductive value of the brood, thereby influencing this trade-off (Sheldon, 2000). Positive differential allocation occurs when mates of attractive individuals invest more in offspring, whereas negative differential allocation occurs when mates of unattractive individuals invest more in offspring (Ratikainen & Kokko, 2010). Providing greater investment in parental care when mated to an unattractive individual is a form of reproductive compensation (reviewed in Harris & Uller, 2009), but compensation is not restricted to negative differential allocation; mates may also increase investment as a compensatory mechanism when paired to an attractive individual to improve a poor situation, such as a lack of parental care from an attractive mate (Ratikainen & Kokko, 2010) or when paired to partners that are not preferred (Gowaty, 2008).

Overall, the differential allocation hypothesis has received empirical support in a variety of taxa (Sheldon, 2000), including birds (Horváthová et al., 2012); however, the majority of studies have focused on differential allocation by females, whereas studies assessing how female attractiveness influences male reproductive decisions are comparatively less common

(Ratikainen & Kokko, 2010; Edward & Chapman, 2011). Since the first experimental demonstration of differential allocation by male birds in relation to female attractiveness (Burley, 1988), general support for positive differential allocation has come from studies experimentally altering female ornamental traits to be less attractive. These studies have generally found that males provide lower parental investment in the form of brood defense or provisioning nestlings when paired to unattractive females (Roulin, 1999; Pilastro et al., 2003; Matessi et al., 2009; Mahr et al., 2012). One study found the opposite, where male provisioning increased in response to experimentally reduced ultraviolet (UV) crown reflectance of female blue tits (*Cyanistes caeruleus*; Limbourg et al., 2013). In contrast, the only study that we are aware of that experimentally altered the phenotypic appearance of females to be more attractive found no support for the differential allocation hypothesis; males paired to female rock sparrows (*Petronia petronia*) with increased breast patch size showed no difference in brood defence or nestling provisioning compared to controls (Pilastro et al., 2003). Therefore, support for positive differential allocation by males when paired to females whose phenotypic traits have been manipulated to be more attractive, as demonstrated by Burley (1988), is lacking.

In the current study, our aim was to test how variation in female attractiveness influences male investment in parental care, and how investment decisions affect offspring quality and fledging success in tree swallows (*Tachycineta bicolor*). Tree swallows are an appropriate species to test male differential allocation because females that are in at least their second breeding season (after-second-year; ASY) display ornamented dorsal plumage that is similar to males (i.e., iridescent blue-green), and males contribute to parental care by defending territories, feeding nestlings, and performing nest sanitation (Winkler et al., 2011). Previous studies examining plumage color in females have found that females displaying brighter plumage with greater UV and blue chroma, and bluer hues are older, make greater investments in reproduction and fledge more offspring (Bitton et al., 2008; Bentz & Siefferman, 2013).

We tested whether the perceived attractiveness of females influences male investment in parental care by experimentally enhancing and reducing the plumage brightness of females relative to controls. We chose to manipulate plumage brightness because previous studies have shown brighter female tree swallows lay heavier eggs, thereby suggesting that brightness may signal

female quality (Bitton et al., 2008), and positive assortative pairing occurs for plumage brightness where bright females pair with bright males, which may result from mutual mate choice or competition among females for nest sites (Bitton et al., 2008). Given that competition among females is intense (Lef-felaar & Robertson, 1985; Rosvall, 2008), and can lead to injury or death (Lef-felaar & Robertson, 1985; Robertson et al., 1986), it may be more likely that bright plumage of females is related to competitive ability. Nevertheless, ornamental traits that evolve by social or intra-sexual competition, may still be exploited by males when choosing mates (LeBas, 2006) or deciding how much effort to invest in parental care. Therefore, if males invest in parental care according to female attractiveness, we predicted that males paired to females with enhanced plumage brightness would provision at a higher rate and produce offspring that grew faster and were larger at fledging than males paired to females with control or reduced plumage brightness. To explore whether adjustments in feeding rates of males in response to varying in plumage brightness of females was contingent on demands of the brood, we also simultaneously performed a brood size manipulation. We expected to see the greatest increase in feeding rates for males rearing enlarged broods where female plumage brightness was enhanced, whereas the greatest decrease in feeding rates was expected to occur for males rearing enlarged broods where female plumage brightness had been reduced.

2. Material and methods

2.1. Study site and general field methods

We studied tree swallows breeding in nest boxes at three study areas within 30 km of each other near Prince George, BC, Canada (53°N, 123°W) from May to August in 2010 and 2011. These sites are located in areas consisting of open agricultural fields and small wetlands mixed with patches of both coniferous and deciduous trees (see Bitton et al., 2007; Dawson, 2008 for more details). In early May we visited nest boxes every 1–2 days to document the start of egg-laying, at which time we began to check boxes daily until clutches were complete. Beginning 12 days after clutch completion, we checked nests daily to determine hatching date (where January 1 = 1), which was defined as the date the first egg in each nest hatched (designated day 0 of the nestling period).

On day 2 of the nestling period, we captured adults in nest boxes while they were feeding nestlings. All individuals received an individually numbered aluminium leg band, and five feathers were collected from the rump, and stored in opaque envelopes at room temperature until spectral analysis (details below). Males were marked with a small white dot on their back using non-toxic acrylic paint for identification during provisioning trials (see below). We determined the age of females using dorsal plumage colour (Husell, 1983), and ASY females were allocated to treatment groups (enhanced, reduced or control plumage brightness) sequentially upon capture after determining the order of treatment randomly. Prior to manipulation, females in each treatment did not differ in their plumage characteristics (all p values > 0.88; see below for description of plumage characteristics) or hatching date ($p > 0.76$).

We altered female plumage brightness by applying evenly to the head, nape, mantle, and rump feathers, a non-toxic permanent blue marker (Prismacolor® PM-39: True blue) to enhance brightness, or silicon paste (Mucilin®) to reduce brightness (Figure 1); control females were treated in the same manner, but the marker used contained water. We were confident that our treatment would produce the desired effect throughout the study since these permanent markers and silicone paste have been used previously (Ballentine & Hill, 2003; Johnsen et al., 2005; Safran et al., 2005; Liu et al., 2007), and the effects can still be detected on average 15 days after manipulation (Johnsen et al., 2005). We tested the effectiveness of our treatment in the laboratory by measuring plumage characteristics (see below for more details) before and after the application of permanent marker or silicon paste to rump and back feathers collected from females that were not part of the present study. Treatment of feathers with the blue permanent marker significantly increased the average brightness of feathers (paired $t_{13} = -8.10$, $p < 0.001$) without altering hue (paired $t_{13} = -1.50$, $p = 0.16$), while the application of silicon paste reduced the average feather brightness (paired $t_{13} = 7.97$, $p < 0.001$) and slightly shifted hue 9.07 ± 1.79 standard error (SE) nm toward longer wavelengths (i.e., made females slightly greener; paired $t_{13} = -5.08$, $p < 0.001$). The phenotypes produced by our experimental manipulation fell within the natural range of plumage brightness for female tree swallows (Berzins, unpublished data). To test whether enhanced plumage remained bright throughout the study period, we exposed a subset of feather samples treated with blue marker to sunlight for 15 days,

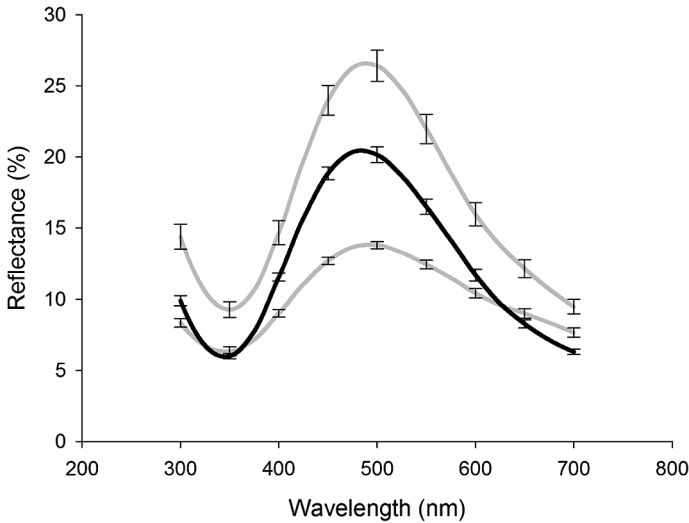


Figure 1. Reflectance spectra from the back and rump feathers of female tree swallows measured before (solid black line) and after treatment with blue permanent marker to enhanced plumage brightness (top grey line; $N = 14$) and silicone paste to reduce plumage brightness (bottom grey line; $N = 14$). Presented are the means (\pm SE) at every 50 nm interval from 300 to 700 nm. See Methods for specific details regarding plumage manipulations.

and although plumage brightness had faded somewhat, feathers were still significantly brighter than they were prior to treatment (paired $t_8 = -3.94$, $p < 0.01$). In total, we manipulated the plumage brightness of females from 46 nests (enhanced = 22, reduced = 24) while 24 females served as controls.

Two days after hatching, we performed a brood size manipulation to determine whether male investment in parental care when paired females that differ in attractiveness is contingent on the demand of the brood. Nests were matched for hatching date (± 1 day), and randomly assigned to a brood-size treatment (enlarged, reduced, or control) independent of the plumage treatment of the female. Each nestling was uniquely marked with non-toxic markers, and two nestlings were removed from reduced broods and added to the enlarged brood size group. In addition, we also cross-fostered 1–4 nestlings among nests when possible to ensure nests contained original and cross-fostered offspring, thereby controlling for the potential genetic effects on offspring quality. For these manipulations, we weighed all nestlings using a spring balance (nearest 0.125 g) and selected only intermediate-sized nestlings that were similar in mass to transfer between nests to ensure that overall size hierarchies within nests were not altered (Dawson & Bor-

tolotti, 2003). Following our experimental manipulation of brood size, average nestling mass of the brood on day 2 did not differ by plumage treatment ($F_{2,60} = 2.60$, $p = 0.08$) or brood size treatment ($F_{2,60} = 1.87$, $p = 0.16$) after controlling for hatching date ($F_{1,60} = 3.21$, $p = 0.08$). The suggestion of a trend for the average mass of nestlings to differ by plumage treatment on day 2 was due to nestlings in control nests tending to be lighter (mean \pm SE = 3.25 ± 0.15) than nestlings in reduced (3.66 ± 0.15) and enhanced broods (3.65 ± 0.16). Mass of nestlings was subsequently measured with a spring balance (nearest 0.125 g) from day 4 to 16 and the length of the ninth primary flight feather with a ruler (nearest 0.5 mm) from day 8 to 16. We visited nests on day 22 to determine the number of young that successfully fledged.

2.2. Parental provisioning

Investment in parental care was estimated by quantifying provisioning rates of parent birds during 40 min sessions on days 6, 8 and 10 of the nestling period. Males were distinguished from females in provisioning observations by the white dot applied to the back of males following capture earlier in the nestling period. Observations were performed between 0830 and 1900 h PST. For each session, the observer was situated approximately 50 m from the nest and used binoculars to document every visit each parent made to the nest box. Since parent tree swallows rarely visit the nest box without bringing food, the number of visits to the nest provides an accurate measure of food delivery (McCarty, 2002). Moreover, the load sizes of food delivered to the nests is similar between the sexes and consistent throughout the feeding period (McCarty, 2002). Observations were performed at 25 boxes in 2010 and 17 boxes in 2011.

2.3. Spectral analysis

To quantify plumage characteristics of females prior to our experimental manipulation (hereafter referred to as original plumage colour in analysis), four rump feathers were taped to a piece of cardboard in an overlapping fashion that mimicked the natural arrangement of rump feathers on the bird, following Bitton et al. (2007). Samples were then placed on a black non-reflective background and reflectance spectra were measured using a JAZ-PX spectrometer with a xenon light source (Ocean Optics, Dunedin, FL, USA) and a bifurcated probe enclosed in a black holder that excluded ambient light.

The probe was held 90° to the surface of the feather and three measurements were taken, removing the probe between each measurement. Spectral data were recorded using SpectraSuite software (Ocean Optics) and reflectance was calculated as the proportion of light reflected in 1-nm intervals between 300–700 nm relative to the reflectance of a WS-1 diffuse white standard (Ocean Optics).

We used the PAVO package (Maia et al., 2013) for R (R Development Core Team, 2013) to smooth the spectral curves and quantify plumage characteristics that summarized the spectral curve for each individual. Specifically, we quantified measures of hue, UV chroma, blue chroma and average brightness because these plumage characteristics have been shown previously to be biologically relevant measures of quality in tree swallows (Bitton et al., 2007, 2008; Bitton & Dawson, 2008; Bentz & Siefferman, 2013). Hue was calculated as the wavelength of maximum reflectance, UV and blue chroma were each calculated as the relative proportion of light reflected in the UV (300–400 nm) and blue (400–512 nm) range relative to the entire spectrum (300–700 nm), and average brightness was calculated as the average amount of light reflected by the feather over the entire spectrum (300–700 nm; see Montgomerie, 2006). To reduce these plumage characteristics to individual colour scores that reflect variation in plumage colour among individuals we used a principle components analysis (Montgomerie, 2006) using all ASY females from which we collected feather samples over a 4-year period (2010–2013). The first principle component (PC1) explained 55.8% of the total variation and the factor loadings (hue: -0.98 ; UV chroma: 0.88 ; blue chroma: 0.70 ; brightness: -0.07) suggest females with larger positive PC1 scores had greater UV and blue chroma, and reflected at shorter wavelengths, i.e. were bluer. PC2 explained 26.2% of the total variation and was heavily weighted by brightness (factor loadings = 0.12 , -0.18 , 0.30 and 0.95 , respectively), so large positive PC2 scores represent females with brighter plumage. Overall, females displaying brighter plumage with greater UV and blue chroma, and bluer hues (larger, positive PC scores) are considered more ornamented because such females have been shown to make greater investments in reproduction and/or have greater reproductive success (Bitton et al., 2008; Bentz & Siefferman, 2013).

2.4. Statistical analysis

To determine whether the experimental manipulation of female plumage brightness influenced male investment in parental care, we analysed the rate

of food delivered to the nest by male tree swallows using linear mixed models (LMM). Brood identity was the subject grouping variable and chick age defined the repeated effect to account for the feeding observations that occurred on day 6, 8 and 10. We were interested both in assessing how much males invested into each individual nestling and in the brood as a whole, so we ran models using the number of feeding trips per hour per nestling and number of feeding trips per hour as the dependent variables. Plumage brightness treatment and brood size treatment, as well as study area were included as fixed factors, and we tested for an interaction between plumage brightness and brood size treatments. We did not include year as a factor because it was confounded with study area. As covariates, we included the feeding rate and original plumage colour (PC1 and PC2) of the female, and the start time of the observation. Since climatic variation can influence parental feeding rates in tree swallows (Rose, 2009), we also included rain as a categorical variable to indicate whether the trial ended because it had started to rain, as well as the average temperature and wind speed for the 3 hour period prior to each feeding observation; these data were obtained from weather stations located at each study area.

To test for effects of female plumage brightness and brood size treatments on offspring quality, we used LMM to examine length of the ninth primary feather and mass at day 16 (just prior to fledging), as well as growth rates of nestlings. Growth rate constants of individual nestlings were calculated using a linear model for ninth primary and a logistic model for mass following Dawson et al. (2005). Growth rate constants were only calculated for nestlings that had complete growth measures, i.e., day 8–16 for ninth primary feather and day 4–16 for mass. In models, the size or growth rate of nestlings was the dependent variable, and study area, plumage brightness treatment and brood size treatment were included as fixed factors, as well as the interaction between plumage brightness and brood size treatments. Original brood size was included as a covariate for models testing size and growth, and as an additional covariate for offspring size we included the time of day when nestlings were measured; this covariate was not included in models testing nestling growth since we corrected for time when calculating growth rate constants. Hatching date was not included as a covariate in these models because it was negatively related to the time of day that nestlings were measured ($r = -0.34$, $p = 0.01$). Brood of rearing was included as random factor to account for the lack of independence among nestlings reared within

the same environment, and brood of origin to account for any potential genetic or maternal effects on nestling quality. Due to the lack of independence among nestlings reared together, brood of rearing was always retained in the model, and we used the Wald Z statistic to assess the inclusion of brood of origin in each model (Garson, 2012).

Fledging success was calculated as the proportion of nestlings that successfully fledged relative to the total number of offspring in the nest following the brood size manipulation on day 2. We tested whether fledging success differed by treatment using analysis of covariance, with proportion of offspring that fledged successfully as the dependent variable. As fixed factors, we included plumage brightness and brood size treatments, as well as study area, and tested for an interaction between plumage brightness and brood size treatments. Hatching date, standardized to a mean of 0 and standard deviation of 1 for experimental nests within each study area was included as a covariate.

For all analyses, we removed interactions, covariates and main effects that did not approach significance ($p \geq 0.10$) in a backwards, stepwise fashion, but always retained plumage brightness and brood size treatments in models. Residuals of models were checked for normality and heteroscedasticity (Cleasby & Nakagawa, 2011). Results were considered significant at $p \leq 0.05$, and we report least squares means ± 1 SE. The overall significance of omnibus tests was examined using post-hoc tests with a Bonferroni adjustment for multiple comparisons. Effects sizes were calculated as partial eta squared (η_p^2) for omnibus statistical tests (Lakens, 2013) and as the correlation coefficient (r) for post-hoc comparisons (Field et al., 2012). All statistical analyses were performed using SPSS v20 statistical software (IBM, 2011).

3. Results

3.1. Parental care

Feeding rates (trips/hour/nestling) of male tree swallows did not vary among plumage brightness treatments ($F_{2,95.67} = 1.61$, $p = 0.21$; Figure 2a) or brood size treatments ($F_{2,94.37} = 2.11$, $p = 0.13$; Figure 3a), but increased with higher feeding rates by females (estimate = 0.16 ± 0.07 , $F_{1,104.70} = 4.61$, $p = 0.03$) and decreased as original brood size increased (estimate = -0.11 ± 0.05 , $F_{1,87.81} = 4.52$, $p = 0.04$). When wind speeds were higher

prior to the observation period, males fed nestlings at a greater rate (estimate = 0.19 ± 0.09 , $F_{1,85.96} = 4.07$, $p = 0.047$). Original plumage colour of the female (PC1 and PC2), start time, temperature and rain had no effect on male feeding rates (p values > 0.22). Performing the analysis using trips per hour showed the same overall conclusions, but feeding rates differed by brood size treatment ($F_{2,102.00} = 3.99$, $p = 0.02$; Figure 3b). Post-hoc tests showed that the number of feeding trips per hour by males was greater for enlarged versus both reduced ($t_{97.80} = 2.56$, $p = 0.04$, $r = 0.25$) and control broods ($t_{105.13} = 2.28$, $p = 0.07$, $r = 0.22$), but no difference was detected between control and reduced broods ($t_{102.66} = 0.38$, $p = 1.00$, $r = 0.04$).

Although our results showed no effects of plumage treatments on provisioning by males (Figure 2a), we further investigated whether male behaviour was influenced simply by their mates having altered plumage brightness, regardless of whether it was reduced or enhanced. Results that compared males paired to control females with those where data from both experimental treatments were combined showed a trend for feeding rates of males to be higher in experimental than control treatments ($F_{1,95.00} = 3.38$, $p = 0.069$; Figure 2b). Manipulated brood size, female feeding rate and wind were still significant predictors of male feeding rates (all p values < 0.046). To clarify whether the increase in male feeding rates when paired to experimental females was due to differential allocation or compensation by males, we additionally analysed the feeding rates of females. Feeding trips per hour per nestling did not differ by plumage brightness treatment ($F_{2,110.18} = 0.51$, $p = 0.60$), but varied by brood size treatment ($F_{2,109.76} = 13.82$, $p < 0.001$). Post-hoc tests showed that females fed nestlings in the enlarged treatment at a lower rate than nestlings in the reduced ($t_{109.77} = 4.94$, $p < 0.0001$, $r = 0.43$) and control brood sizes ($t_{108.80} = 4.07$, $p < 0.0001$, $r = 0.36$). Female feeding rates also differed by the age of nestlings ($F_{2,64.57} = 5.41$, $p = 0.007$) and study area ($F_{1,109.87} = 4.47$, $p = 0.04$), and were related to the original size of the brood (estimate = -0.28 ± 0.06 , $F_{1,109.82} = 20.31$, $p < 0.0001$). When we analysed how many times females provisioned per hour, we similarly found that female feeding rate did not differ by plumage brightness treatment ($F_{2,113.40} = 0.001$, $p > 0.99$) and the number of feeding trips per hour also did not differ according to brood size treatment ($F_{2,113.17} = 1.28$, $p = 0.28$). Nestling age and original brood size were still significant predictors of female feeding rates (both p values < 0.004).

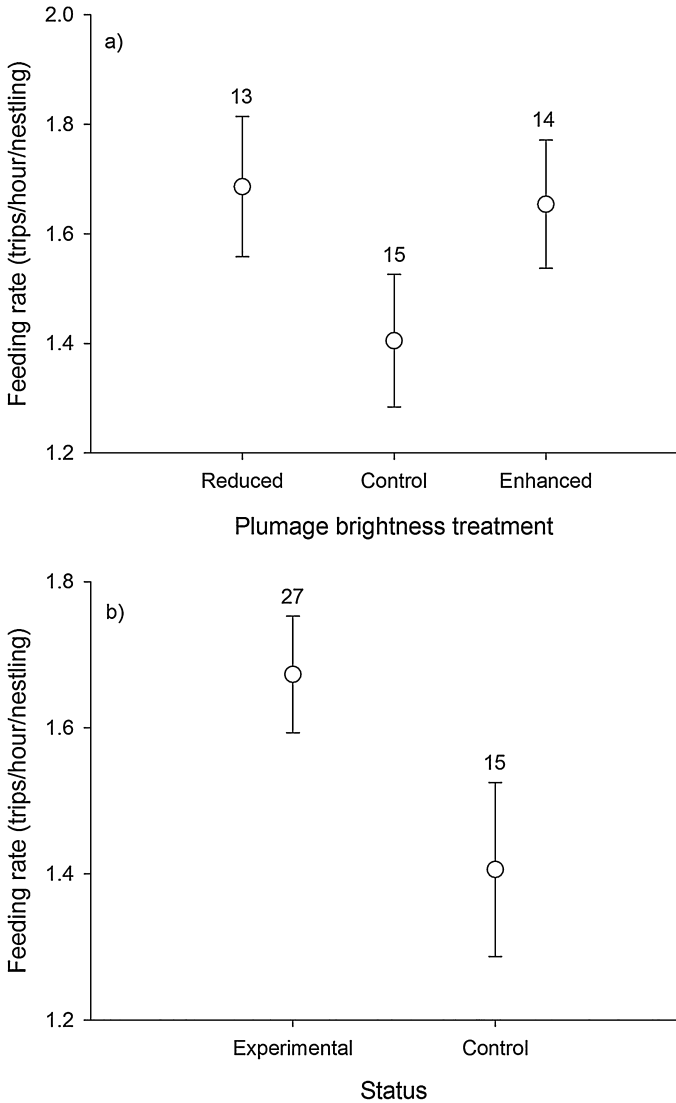


Figure 2. Mean (\pm SE) feeding rates (trips/hour/nestling) of male tree swallows rearing broods where (a) female plumage brightness was experimentally reduced or enhanced, or remained unchanged (controls) and (b) female plumage was experimentally altered (enhanced and reduced treatments combined) or remained unchanged (control). Sample sizes indicate the number of broods within each treatment group and are given above error bars.

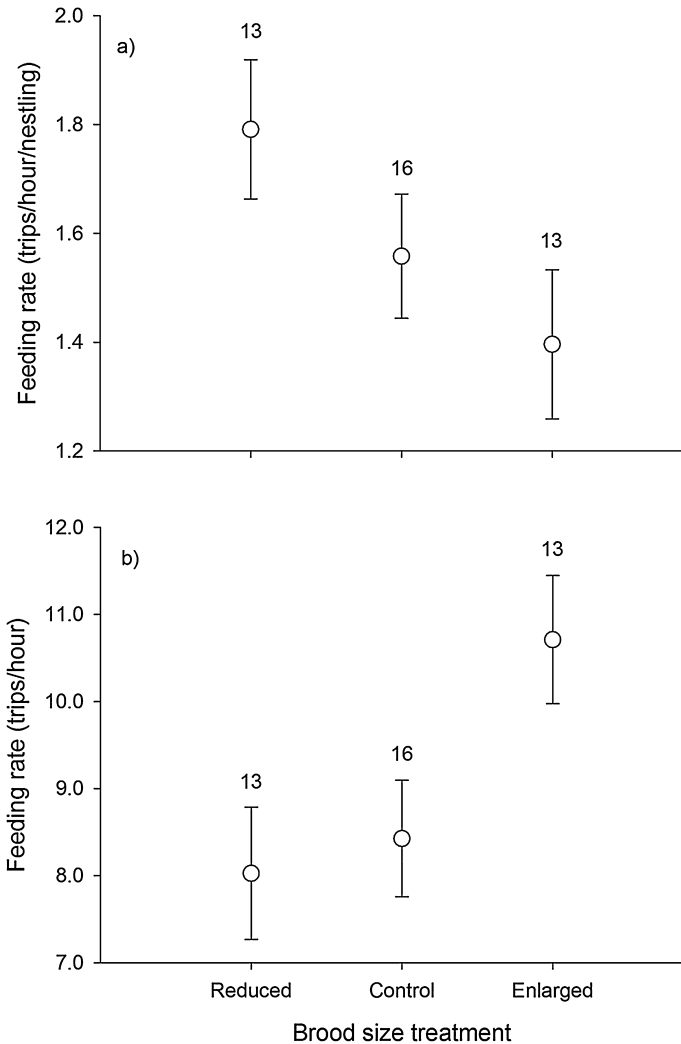


Figure 3. Mean (\pm SE) feeding rates expressed as (a) trips/hour/nestling and (b) trips/hour of male tree swallows rearing broods where brood size was reduced by removing two nestlings, enlarged by adding two nestlings, or remained unchanged (controls). Sample sizes indicate the number of broods within each treatment group and are given above error bars.

3.2. Nestling quality

Analysis of length of ninth primary feathers of nestlings revealed a significant interaction between female plumage brightness and brood size treatments (Table 1). Analysing data by plumage brightness treatment showed

Table 1.

Results of random intercept linear mixed models testing whether nestling size or growth differed among broods where the plumage brightness of females was experimentally reduced or enhanced, or remained unchanged (controls), and where brood size was reduced by removing two nestlings or enlarged by adding two nestlings, compared to control broods (see text for more details).

	<i>F</i>	df	<i>p</i>
Nestling size			
Ninth primary feather (mm)			
Plumage brightness treatment	1.39	2, 39.49	0.26
Brood size treatment	1.22	2, 39.88	0.31
Time of measurement	4.65	1, 39.31	0.04*
Plumage brightness × brood size	3.39	4, 39.71	0.02*
Mass (g)			
Plumage brightness treatment	0.03	2, 46.89	0.97
Brood size treatment	9.99	2, 45.65	<0.0001*
Time of measurement	6.53	1, 49.25	0.01*
Nestling growth			
Ninth primary			
Plumage brightness treatment	2.14	2, 41.52	0.13
Brood size treatment	3.58	2, 40.87	0.04*
Study area	2.96	2, 41.83	0.06
Mass			
Plumage brightness treatment	0.42	2, 43.65	0.66
Brood size treatment	1.25	2, 43.03	0.30
Study area	9.49	2, 43.96	<0.0001*

*Significant value ($p \leq 0.05$).

that in the reduced plumage brightness treatment the length of ninth primaries at day 16 differed by brood size treatment ($F_{2,13.43} = 23.59$, $p < 0.0001$; Figure 4a). Post-hoc tests showed that nestlings reared in enlarged broods had shorter primary feathers compared to nestlings reared in control ($t_{11.30} = 5.90$, $p < 0.0001$, $r = 0.87$) and reduced broods ($t_{13.38} = 6.53$, $p < 0.0001$, $r = 0.87$; Figure 4a), but there were no differences between control and reduced broods ($t_{16.20} = 1.36$, $p = 0.58$, $r = 0.32$). Nestlings reared in nests where female plumage brightness treatment was control or experimentally enhanced had similar sized ninth primary feathers prior to fledging regardless of brood size treatment (p values > 0.51).

Nestling body mass at 16 days of age was similar among plumage brightness treatments, but increased with time of day nestlings were measured

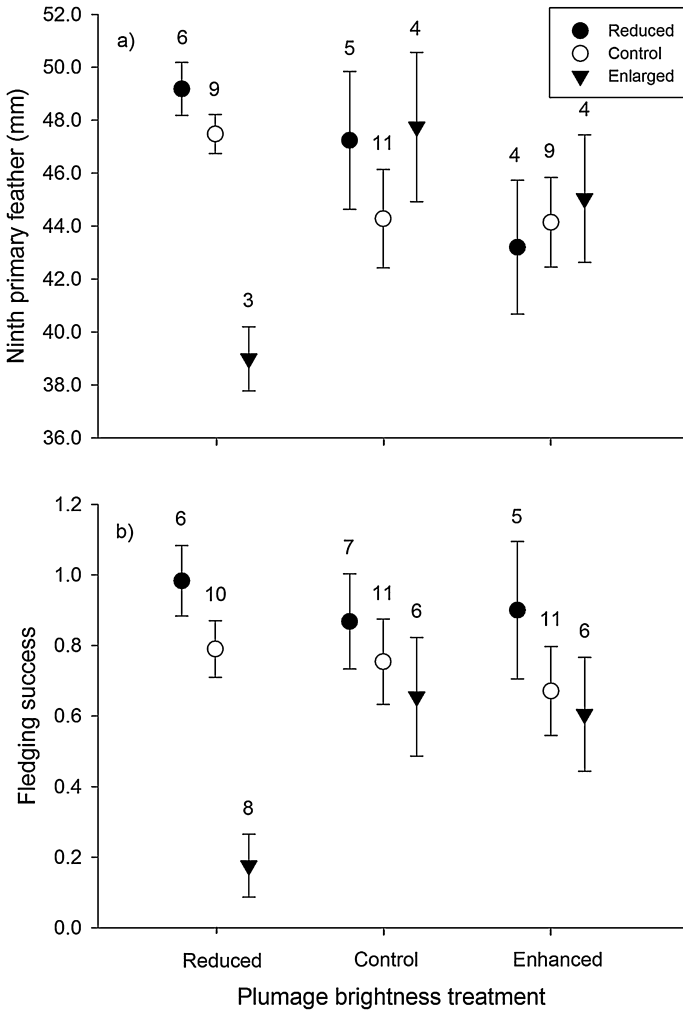


Figure 4. Mean (\pm SE) (a) length of ninth primary flight feathers (mm) at day 16 and (b) fledging success (proportion of nestlings fledged per brood) for nestling tree swallows according to brood size treatment (reduced by two nestlings, controls) and female plumage brightness treatment (experimentally reduced and enhanced compared to controls). Sample sizes indicate the number of broods within each treatment group and are given above error bars.

(estimate = 0.23 ± 0.09) and varied by brood size treatment (Table 1). Post-hoc tests indicated that nestlings raised in broods that were experimentally reduced in size were heavier than nestlings reared in control ($t_{51.00} = 2.75$,

$p = 0.02$, $r = 0.36$) and enlarged ($t_{40.80} = 4.44$, $p < 0.0001$, $r = 0.57$) broods. Nestlings raised in control broods also tended to be heavier than nestlings raised in enlarged broods ($t_{45.38} = 2.28$, $p = 0.08$, $r = 0.32$). Random intercepts brood of rearing and brood of origin also predicted nestling mass among broods (estimate = 1.74 ± 0.50 , Wald $Z = 3.48$, $p = 0.001$ and estimate = 0.42 ± 0.24 , Wald $Z = 1.78$, $p = 0.08$, respectively).

Growth of nestling ninth primary feathers was not influenced by the plumage brightness treatment of the female, but differed by brood size treatment (Table 1). Post-hoc tests indicated that nestlings raised in enlarged broods grew ninth primary feathers slower than nestlings in reduced broods ($t_{40.28} = -2.65$, $p = 0.03$, $r = 0.39$). No differences between enlarged and control broods ($t_{40.04} = -1.50$, $p = 0.42$, $r = 0.23$) or reduced and control broods ($t_{42.00} = 1.61$, $p = 0.34$, $r = 0.28$) were detected. Nestlings gained mass at a similar rate regardless of the plumage brightness treatment of the female or brood size treatment; however, the study area influenced how fast nestlings gain body mass (Table 1).

3.3. *Fledging success*

The proportion of nestlings that fledged per brood was similar among plumage brightness treatments ($F_{2,58} = 0.07$, $p = 0.93$, $\eta_p^2 = 0.002$), but differed among brood size treatments ($F_{2,58} = 8.14$, $p = 0.001$, $\eta_p^2 = 0.22$) and study areas ($F_{2,58} = 3.62$, $p = 0.03$, $\eta_p^2 = 0.11$), and decreased with hatching date ($B = -0.09 \pm 0.04$, $F_{1,58} = 4.95$, $p = 0.03$, $\eta_p^2 = 0.08$); however, there was also some suggestion of an interaction between plumage brightness treatment and brood size treatment ($F_{4,58} = 2.29$, $p = 0.07$, $\eta_p^2 = 0.14$). Analyzing the data by plumage treatment showed that within the reduced plumage brightness treatment fledging success differed by brood size treatment ($F_{2,18} = 21.58$, $p < 0.0001$, $\eta_p^2 = 0.71$; Figure 4b), but no effects of hatching date ($F_{1,18} = 2.79$, $p = 0.11$, $\eta_p^2 = 0.13$) or study area ($F_{2,18} = 0.32$, $p = 0.73$, $\eta_p^2 = 0.03$) were detected. Post-hoc tests showed that fewer nestlings fledged from enlarged broods compared to control ($t_{18} = 5.20$, $p < 0.0001$, $r = 0.77$) and reduced broods ($t_{18} = 6.02$, $p < 0.0001$, $r = 0.82$; Figure 4b), but no differences in fledging success were detected between control and reduced broods ($t_{18} = 1.50$, $p = 0.46$, $r = 0.33$). The low proportion of fledging success for the enlarged treatment group was because 5 of 8 nests failed prior to fledging, presumably because parents abandoned their nesting attempts. In contrast, fledging success did not differ by brood size treatment

in the control or enhanced plumage brightness treatments (all p values > 0.35 ; Figure 4b). Fledging success differed by study area ($F_{2,18} = 3.82$, $p = 0.04$, $\eta_p^2 = 0.30$) and was negatively related to hatching date in control broods ($B = -0.15 \pm 0.07$, $F_{1,16} = 4.72$, $p = 0.04$, $\eta_p^2 = 0.21$); these effects were not detected in broods where female plumage was experimentally enhanced (study area: $F_{2,16} = 1.28$, $p = 0.31$, $\eta_p^2 = 0.14$; hatching date: $B = -0.04 \pm 0.09$, $F_{1,16} = 0.20$, $p = 0.66$, $\eta_p^2 = 0.01$).

4. Discussion

Our aim was to test whether female attractiveness influenced male investment in parental care by experimentally altering the plumage brightness of female tree swallows. We also simultaneously manipulated brood size to determine whether male investment in parental care when mated to females that differed in attractiveness is contingent on the demand of the brood. Contrary to our predictions, we found no evidence that males adjust their feeding rates when paired to females that differed in plumage brightness (Figure 2a); therefore, our experiment provides no support that differential allocation occurs in tree swallows in response to variation in plumage brightness of females, although we recognize our sample sizes were small and may have limited our ability to detect differences in male feeding rates. However, when we compared feeding rates of males between all experimental broods (i.e., reduced and enhanced treatments combined) and control broods, our results showed that males tended to feed experimental broods at a higher rate than control broods (Figure 2b).

Higher feeding rates by males rearing experimental broods may be due to males in each treatment group responding differently to the change in plumage brightness of their mate. For example, males in the enhanced plumage brightness treatment may have increased their investment in parental care when mated to an attractive mate (positive differential allocation), as previously demonstrated by Burley (1988), whereas males rearing broods where female plumage brightness was reduced may have increased their feeding rate to compensate for the perceived poor quality of their mate (Harris & Uller, 2009). This pattern of negative differential allocation has been previously demonstrated in blue tits, where males increased their provisioning rates in response to an experimental reduction of their mates UV crown colour (Limbourg et al., 2013). Negative differential allocation was

also recently suggested to occur in tree swallows by a study showing that both sexes provisioned at higher rates when mated to partner with greener plumage (Dakin et al., 2016). However, it seems unlikely that our results are the response of males adjusting their level of care according to the attractiveness of female plumage brightness. Since our experiments were performed when nestlings were two days old, a more likely explanation for this trend is that males perceived the sudden change in their mates' phenotype as an indication that something was amiss, and increased provisioning to compensate. That female feeding rates did not differ in relation to the plumage brightness treatment is consistent with the idea that males increased provisioning to compensate for the changed appearance of females and not because of lower parental investment by females with manipulated plumage brightness.

Previous studies testing male differential allocation have generally found that males adjust investment in parental care according to mate attractiveness as predicted by positive differential allocation (e.g., Burley, 1988; Roulin, 1999; Pilastro et al., 2003; Matessi et al., 2009; Mahr et al., 2012, but see Limbourg et al., 2013). For example, in response to reduced plumage spottness in female barn owls (*Tyto alba*) and reduced UV crown reflectance in female blue tits, males provisioned nestlings less than males paired to control females (Roulin, 1999; Mahr et al., 2012). While provisioning rate of male rock sparrows was not influenced by the reduced breast patch size of females, males did reduce their level of nest defence when paired to females displaying the less attractive phenotype compared to control females (Pilastro et al., 2003; Matessi et al., 2009). That male tree swallows did not provision in relation to female attractiveness suggests that plumage brightness is not a signal assessed by males, at least when making decisions on how much to invest in parental care. Given that less ornamented female tree swallows receive less aggression from older conspecific females (Coady & Dawson, 2013), it is possible that plumage brightness of females is instead a signal assessed by conspecific females.

Since males did not provision nestlings less when paired to females whose plumage brightness had been reduced and females fed at a similar rate regardless of their plumage brightness treatment, it is difficult to reconcile why nestlings reared in the treatment where female plumage brightness was reduced and brood size was enlarged grew shorter ninth primary flight feathers and were less likely to fledge (Figure 4a, b). Because we performed our observations during early to mid-brood rearing to ensure females retained

their manipulated plumage brightness during the feeding observations, we may not have detected an effect of treatment if males or females adjusted their feeding rates later in the season. This would be reflected in the size of nestlings at day 16 and fledging success, but not provisioning rate. Alternatively, nestlings in this treatment may have performed poorly if the plumage brightness treatment affected the behaviour of manipulated females. While it is unlikely that the plumage treatment directly affected female behaviour since the application of these markers and silicone paste have been used previously with no reported adverse effects on behaviour or feather quality (Ballentine & Hill, 2003; Johnsen et al., 2005; Liu et al., 2007), it is possible that the altered plumage brightness influenced social interactions among females, and the feedback females received from these interactions influenced their behaviour or physiology (reviewed in Vitousek et al., 2014b). This social mechanism has been proposed to explain the increased and decreased levels of androgens in male and female barn swallows (*Hirundo rustica erythrogaster*), respectively, the week following an experimental darkening the ventral plumage (Safran et al., 2008; Vitousek et al., 2013). In this study, agonistic interactions with other females may have increased levels of the stress hormone corticosterone in females with reduced plumage brightness, a response similar to the increase in corticosterone of female rats experiencing social instability (Haller et al., 1999), which when combined with the demands of rearing an enlarged brood may have caused females to abandon their nesting attempt. Although we have no behavioural or hormonal data to support this mechanism, previous studies have demonstrated that female barn swallows with greater baseline and stress-induced corticosterone levels were more likely to abandon their clutch prior to incubation (Vitousek et al., 2014a) and broods of tree swallows are less likely to survive when corticosterone levels of females were elevated experimentally (Ouyang et al., 2015).

When faced with changes in brood size, total provisioning rates of males rearing reduced broods were similar to males rearing control broods; however, males rearing enlarged broods provisioned nestlings at a higher rate than males rearing control and reduced broods (Figure 3b). Since total provisioning rate was greater in the enlarged brood size treatment, individual nestlings received similar amounts of food in enlarged and control broods (Figure 3a). That per-capita feeding rates did not decline with increased brood size is inconsistent with previous studies in this species (e.g., Lefelaar & Robertson, 1986; Leonard et al., 2000; Murphy et al., 2000; Shutler

et al., 2006; Hainstock et al., 2010). Food abundance at our study area may be low in comparison to other populations of tree swallows (e.g., Bortolotti et al., 2011; Harriman et al., 2013), and so our results may differ from previous studies if males need to invest heavily in offspring when rearing an enlarged brood to maintain their quality. This may also explain why total provisioning rates of males rearing reduced broods were not lower compared to controls. Despite per-capita feeding rates being similar among males (Figure 3a), nestlings reared in enlarged broods were lighter than controls prior to fledging, which suggests that while male tree swallows were willing to increase parental investment they were unable to fully compensate for the lower per capita feeding rates of females rearing enlarged broods.

Overall we found that investment in parental care by male tree swallows was influenced by factors other than female attractiveness, such as brood size (Ardia, 2007; Bortolotti et al., 2011) and weather (Rose, 2009). Our results also showed that male feeding rates were positively related to female feeding rates (also see Dakin et al., 2016). This relationship may exist if males and females similarly adjust their feeding rates to the perceived needs or cues of nestlings, such as age or the number of nestlings (Leffelaar & Robertson, 1986; Ardia, 2007), or the begging intensity of hungry nestlings (Leonard & Horn, 1998; Leonard & Horn, 2001), which increases with brood size (Leonard et al., 2000; Thomas & Shutler, 2001). In addition, each member of the pair may respond directly to the level of provisioning effort exerted by their mate (Hinde, 2006). Experiments that carefully tease apart the relative contributions of brood size, nestling cues and partner behaviour (e.g., Hinde & Kilner, 2007) will improve our understanding of how parental investment decisions in tree swallows are determined.

In conclusion, we found that males did not adjust their investment in parental care in relation to the experimentally altered plumage brightness of female tree swallows. Our results also showed that offspring quality and fledging success were lowest when female plumage brightness was reduced and brood size was enlarged. This may be due to social feedback females with reduced plumage brightness received following agonistic interactions with other females combined with the increased demands of rearing an enlarged brood. Collectively, the findings of our study suggest that plumage brightness of females is not assessed by males, but may instead be assessed by females. As such, selection on female plumage brightness may arise if brightness signals competitive ability, thereby influencing female–female

competition for access to nest boxes (Bitton et al., 2008). Future work that experimentally manipulates ornamental traits in females prior to breeding would greatly improve our understanding of how sexual or social selection acts to promote or maintain elaborate phenotypic displays in females.

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