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Experimentally altered plumage brightness of female Tree Swallows (*Tachycineta bicolor*) influences nest site retention and reproductive success

Lisha L. Berzins and Russell D. Dawson

Abstract: That ornamental traits of females can act as signals of quality has gained empirical support, but whether and how such ornaments of females mediate social interactions with conspecifics remains less clear. Female Tree Swallows (*Tachycineta bicolor* (Vieillot, 1808)) aggressively compete for and defend nest sites, and as such, nest site intrusions by conspecific females challenging ownership of a nest may prevent territory-owning females from dishonestly displaying ornamented plumage. We tested whether plumage brightness of female Tree Swallows influences nest site retention and reproductive success by experimentally enhancing or reducing their plumage brightness relative to controls prior to breeding. Females with reduced brightness were more likely to retain their nests sites and breed relative to control females and females with experimentally enhanced brightness. Females displaying enhanced brightness also tended to initiate clutches later than females with control and reduced brightness. Overall, lower nest site retention and reproductive success for females with enhanced brightness is consistent with social costs imposed on individuals dishonestly signalling high quality. Future studies in female birds should consider whether costs of losing a nest site to intruding conspecific females, especially in species where nest sites are limited, is a mechanism that maintains the honesty of signals of quality.

Key words: competition, ornamentation, nest site quality, plumage manipulation, signal honesty, social interactions, *Tachycineta bicolor*, Tree Swallow, usurpation.

Résumé : De plus en plus d'observations empiriques appuient l'idée que les caractères ornementaux des femelles puissent agir comme signaux de la qualité, mais il n'est pas encore bien établi si de tels caractères modulent les interactions sociales entre individus d'une même espèce. Les hirondelles bicolores (*Tachycineta bicolor* (Vieillot, 1808)) femelles se disputent et défendent de manière agressive les sites de nidification, de sorte que l'intrusion dans des sites de femelles conspécifiques tentant de s'emparer d'un nid pourrait empêcher les femelles qui détiennent les territoires d'afficher un plumage ornementé de manière trompeuse. Nous avons vérifié si l'éclat du plumage d'hirondelles bicolores femelles influence la rétention des sites de nidification et le succès de reproduction en rehaussant ou en réduisant expérimentalement l'éclat de leur plumage par rapport à celui de témoins avant la reproduction. Les femelles dont l'éclat du plumage était réduit étaient plus susceptibles de retenir leurs sites de nidification et de se reproduire que les femelles témoins et les femelles dont l'éclat avait été rehaussé expérimentalement. Les femelles à l'éclat rehaussé tendaient également à initier leur ponte plus tard que les femelles témoins ou à éclat réduit. Globalement, une rétention des sites de nidification et un succès de reproduction plus faibles pour les femelles au plumage à l'éclat rehaussé concordent avec les coûts sociaux imposés aux individus qui signalent une bonne qualité de manière trompeuse. Des études futures sur des oiseaux femelles devraient vérifier si les coûts de la perte des sites de nidification à des femelles intrusives de la même espèce, particulièrement chez des espèces dont le nombre de sites de nidification est limité, constituent un mécanisme qui maintient l'honnêteté des signaux de la qualité. [Traduit par la Rédaction]

Mots-clés : concurrence, ornementation, qualité du site de nidification, manipulation du plumage, honnêteté des signaux, interactions sociales, *Tachycineta bicolor*, hirondelle bicolore, usurpation.

Introduction

Females from a wide variety of taxa possess ornamental traits, such as elaborate coloration, vocalizations, or aggressive behaviours, that are hypothesized to have evolved either by a correlated response to selection acting directly on traits in males (Lande 1980) or by sexual and (or) social selection (Clutton-Brock 2009; Rosvall 2011; Tobias et al. 2012). Although male mate choice for female ornamental traits has been the focus of many studies (Tarvin and Murphy 2012), competition among females for access to mates or resources is often intense (e.g., Dale and Slagsvold 1995; Rosvall 2008). Females displaying ornamental traits may be more successful at competing for mates or resources if their ornaments signal competitive ability and (or) status to conspecific females (Pryke 2007). Those females that successfully acquire resources, such as nest sites, often are challenged by other conspecific females (e.g., Leffelaar and Robertson 1985; Moreno et al. 2013); however, our understanding of how ornamentation of the territory-owning female and that of the intruding female mediate agonistic interactions is less clear. Most studies to date on the role

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of female ornamentation in social interactions have focused on how the degree of ornamentation displayed by the intruding female influences the response of the territory-owning female. For instance, in both Pied Flycatchers (*Ficedula hypoleuca* (Pallas, 1764)) and Common Kestrels (*Falco tinnunculus* Linnaeus, 1758), the intensity of response by females holding territories to a decoy of an intruding female decreased as ornamentation of the decoy increased (Morales et al. 2014; López-Idiáquez et al. 2016). In contrast, female Collared Flycatchers (*Ficedula albicollis* (Temminck, 1815)) and Streak-backed Orioles (*Icterus pustulatus pustulatus* (Wagler, 1829)) responded with greater intensity to more ornamented decoys of intruding females (Hegyi et al. 2008; Murphy et al. 2009*a*). While these studies demonstrate that the degree of ornamentation displayed by conspecific females influences the response they receive when intruding on the territories of other females, less is known about how the ornamentation displayed by territory-owning females influences whether or not they receive nest site intrusions from conspecific females.

When in possession of a resource, ornamental traits that signal high quality may deter conspecifics from challenging resource ownership so that costly agonistic interactions are avoided. For example, in both American Goldfinches (*Spinus tristis* (Linnaeus, 1758)) and paper wasps (*Polistes dominulus* = *Polistes dominula* (Christ, 1791)), conspecific females avoided food resources guarded by females manipulated to display high-quality signals (Tibbetts and Lindsay 2008; Murphy et al. 2009*b*). Conversely, conspecifics may challenge resource owners displaying high-quality ornaments to test that the quality signalled by their ornamentation reflects their true quality, especially when defended resources are valuable (Tibbetts 2008). It is the cost of engaging in agonistic interactions that enforces the honesty of ornaments that signal quality (see reviews in Senar 2006; Tibbetts 2014). For instance, individuals dishonestly displaying high-quality ornaments may either be attacked when conspecifics detect that an individual's behaviour and ornament do not match (i.e., incongruence hypothesis: Rohwer and Rohwer 1978; Tibbetts and Izzo 2010) or be frequently and aggressively challenged by individuals that are truly of high quality (i.e., like-versus-like aggression: Rohwer 1977; Møller 1987). Indeed, studies that have enhanced the quality of ornaments displayed by individuals have reported that those with enhanced signals receive a greater number of attacks or increased aggression from conspecifics (reviewed in Vitousek et al. 2014). Moreover, studies of male animals have demonstrated that individuals manipulated to dishonestly display high-quality ornaments incur social costs, such as altered physiology (Safran et al. 2008) and a reduced ability to acquire a breeding territory (Qvarnström 1997). While there are fewer examples of ornamentation mediating social interactions in female birds, Moreno et al. (2013) demonstrated that female Pied Flycatchers manipulated during incubation to dishonestly signal high-quality ornamentation incurred social costs, having higher oxidative damage during nestling provisioning compared to control females. Although the behaviour of these manipulated females was not observed, Moreno et al. (2013) hypothesized that intrusions by conspecific females competing for limited nest sites may provide a mechanism to enforce the honesty of female ornamentation, but to our knowledge, this has never been experimentally tested in free-living birds.

In the current study, our aim was to test whether the brightness of plumage displayed by female Tree Swallows (*Tachycineta bicolor* (Vieillot, 1808)) is a signal that is assessed by conspecific females as well as its influence on nest site retention and reproductive success. Female Tree Swallows aggressively compete with conspecifics for access to a male with a nest site (Leffelaar and Robertson 1985), and because some females are competitively excluded from breeding, there often is a large population of nonbreeding floater females (Stutchbury and Robertson 1985). Females successful at acquiring a nest site frequently experience territory intrusions from other conspecific females throughout the breeding season

and must aggressively defend their nest to avoid being usurped (Leffelaar and Robertson 1985). Overall, competition among female Tree Swallows for nest sites is often so intense that it can lead to injury or death (Leffelaar and Robertson 1985).

Dorsal plumage colour of female Tree Swallows is variable, ranging from dull brown to bright iridescent blue-green, the latter being similar to plumage displayed by males. Females displaying dull brown plumage are generally in their first breeding season (second year of life (SY): Hussell 1983), and this delay in maturation of their plumage is hypothesized to signal their low competitive threat; SY females receive less intrasexual aggression when intruding on the territory of conspecific females and also receive fewer nest site intrusions themselves as territory owners from ornamented after-second-year (ASY) females (Coady and Dawson 2013). Among ASY females, those that are more ornamented display plumage that is brighter, with greater ultraviolet (UV) and blue chroma, and reflects light maximally at shorter wavelengths (i.e., bluer hue: Bitton et al. 2008; Bentz and Siefferman 2013). Females displaying brighter plumage lay heavier eggs, suggesting that plumage brightness of females may signal quality (Bitton et al. 2008; Bentz and Siefferman 2013). Moreover, brighter females have been shown to assortatively mate with males displaying bright plumage (Bitton et al. 2008) and this pairing pattern is unlikely to result from male preference for females displaying bright plumage, since experimentally altering the plumage brightness of female Tree Swallows does not influence male investment in parental care or their mating strategies (Berzins 2016; Berzins and Dawson 2016). Instead, assortative mating in this species likely occurs because females with bright plumage have greater competitive ability and outcompete other female conspecifics for access to nest sites.

We manipulated plumage brightness of ASY female Tree Swallows by experimentally enhancing and reducing brightness relative to controls (see Berzins and Dawson 2016). We performed our manipulation once females had acquired a nest site, but prior to having laid any eggs, to determine whether plumage brightness influenced a female's ability to retain her nest site. While female Tree Swallows can be usurped from their nest site at any stage of the breeding season (L.L. Berzins and R.D. Dawson, personal observation), most nest site intrusions occur prior to and during egg laying (Whittingham and Schwabl 2002) and so our manipulation of female plumage brightness occurred while females were competing for nest sites. We hypothesized that if plumage brightness is a signal assessed by conspecific females, then experimentally altering plumage brightness would influence nest site retention by females and consequently their reproductive success. We predicted that females manipulated to display enhanced plumage brightness would be less likely to retain their nest site and have lower reproductive success as a result of defending their nest site from conspecific females challenging their signal quality. In contrast, if dull plumage signals low competitive threat, as similarly demonstrated for less-ornamented SY females (Coady and Dawson 2013), we predicted that females manipulated to display reduced plumage brightness would be more likely to retain their nest site and have higher reproductive success if they were involved in fewer agonistic interactions with conspecific females.

Materials and methods

Study area and general field methods

We studied Tree Swallows breeding in nest boxes near Prince George, British Columbia, Canada (53°N, 123°W) from May to August in 2010 and 2011. The study area consisted of open agricultural areas intermixed with small wetlands and patches of coniferous and deciduous trees (see Dawson et al. 2005 for more details). Shortly after Tree Swallows arrived in our study area in early May, we began to check nest boxes daily to document nest building. Once a nest box contained a nest with a fully formed

cup, but before any eggs had been laid, we captured the resident female. Each female was banded with an individually numbered aluminum leg band and weighed using a spring balance (nearest 0.25 g). We determined the age of females using dorsal plumage colour (Hussell 1983), and ASY females were sequentially allocated to the enhanced, reduced, or control plumage brightness treatments by capture order, after determining a treatment order randomly. Full details of our experimental procedure for manipulating the plumage brightness of female Tree Swallows are described in Berzins and Dawson (2016). Briefly, we collected five rump feathers from each female for spectral analysis (details below) and then plumage brightness of females was either enhanced by applying nontoxic permanent blue marker or reduced by applying silicon paste evenly to the dorsal feathers or remained unchanged by treating females with a marker containing water. While we did not collect additional feathers from females following manipulation of plumage brightness, we have shown previously that treatment of plumage with permanent maker or silicone paste significantly increased and decreased plumage brightness, respectively, of females within the natural range of variation (Berzins and Dawson 2016). The general appearance or quality of feathers did not appear to be negatively altered by our treatment, as similarly reported by previous studies using permanent markers and silicone paste to alter plumage colour (e.g., Ballentine and Hill 2003; Johnsen et al. 2005; Safran et al. 2008). Moreover, Berzins and Dawson (2016) (see also Johnsen et al. 2005) showed that feathers of female Tree Swallows manipulated with marker were still significantly brighter after being exposed to sunlight for 15 days than they were prior to be treated; therefore, we were confident that our treatment produced the desired effect throughout the experimental period. Females in each treatment did not differ by age, body mass, plumage characteristics (see below) prior to experimental manipulation, or capture date (all $P > 0.29$). In total, we enhanced the plumage brightness of 30 females, reduced the plumage brightness of 31 females, and 28 females were in the control group.

To examine whether experimentally altering plumage brightness of females prior to breeding influenced reproductive success, we monitored all nests at our study area daily to record the date of clutch initiation (where January 1 = 1) and clutch size. Freshly laid eggs were numbered with a nontoxic marker for identification and weighed with a digital scale (nearest 0.01 g). We captured all females in our study area after their eggs had hatched and recorded the box and band number to determine whether females retained, left, and (or) switched nest sites after being manipulated. This experimental protocol was approved by the University of Northern British Columbia Animal Care and Use Committee (protocol No. A2010.0412.010(1)n) and was in accordance with the Canadian Council on Animal Care.

Spectral analysis

We quantified plumage characteristics of female Tree Swallows by measuring the reflectance of feathers using a JAZ-PX spectrometer with a xenon light source (Ocean Optics, Dunedin, Florida, USA), as described in Berzins and Dawson (2016). The calamus of four rump feathers were taped to a piece of cardboard so that they resembled the natural arrangement of rump feathers on a bird (see Bitton et al. 2008). Feather samples were placed on a black, spectrally flat surface and spectral data were recorded using SpectraSuite software (Ocean Optics). Three measurements for each bird were taken, moving the probe between each measurement.

The R package pavo (Maia et al. 2013) was used to smooth spectral curves and quantify plumage characteristics, specifically hue, UV and blue chroma, and average brightness, as these variables have been shown previously to reflect aspects of quality in female Tree Swallows (Bitton et al. 2008; Bentz and Siefferman 2013). The three measures of each plumage characteristic were averaged and

then a principal components (PC) analysis was used to reduce each bird's plumage characteristics to a single colour score (Cuthill et al. 1999). Principal components analysis was performed using all ASY females from which we collected feather samples over a 4 year period (2010–2013) at our study area. The first component (PC1) explained 55.8% of the total variation and was heavily weighted by hue, UV chroma, and blue chroma but not by brightness (unrotated factor loadings = −0.98, 0.88, 0.70, and −0.07, respectively) and so females with larger positive values had plumage with greater UV and blue chroma and reflected light at shorter wavelengths (Berzins and Dawson 2016). The second component (PC2) explained 26.2% of the total variation and was heavily weighted by brightness (0.95), but hue, UV chroma, and blue chroma contributed little to PC2 (unrotated factor loadings = 0.12, −0.18, and 0.30, respectively) and so females with larger positive values had brighter plumage (Berzins and Dawson 2016).

Nest site quality

Following Potti and Montalvo (1991), we calculated "nest site quality" as the number of years a nest site was occupied in relation to the number of years the nest site was available for breeding by Tree Swallows. Our study area was established in 2002, so we used occupancy data from 2003 to 2009 in our calculations. We confirmed whether this measure of occupancy reflected nest site quality in Tree Swallows by testing whether the number of years a nest site was occupied was related to average clutch initiation date at that site (standardized so that day 1 represented the first clutch initiation within each year at the site) and the total number of nestlings fledged from 2004 to 2006 (we restricted our analysis to these years, as experimental manipulations in other years may have influenced fledging success, e.g., Dawson et al. 2005). Overall, box occupancy was negatively correlated with clutch initiation date (Spearman rank correlation: $r_s = -0.27$, $N = 118$ nest sites, $P < 0.01$) and positively correlated with the number of nestlings fledged (Spearman rank correlation: $r_s = 0.57$, $N = 100$ nest sites, $P < 0.0001$). That nest boxes used more frequently are bred in earlier and have a greater number of nestlings fledged indicates that occupancy provides a reasonable proxy for nest site quality. Nest site quality did not significantly differ among treatments prior to manipulation (Kruskal–Wallis ANOVA: $H = 0.49$, df = 2, $P = 0.78$).

Statistical analysis

We tested whether the plumage brightness treatment of female Tree Swallows influenced nest site retention using a logistic regression with nest retention (retained, left) as the binary dependent variable and plumage brightness treatment as a fixed factor. We also included the quality of the nest site and original plumage brightness (PC2) of females as covariates as well as the interaction between treatment and original plumage brightness. Since defence of a territory by individuals may be influenced by age or experience, as demonstrated in male birds (Hyman et al. 2004), we included the capture status of females (previously banded at our study area, newly captured female) as a categorical variable. We included captured status of females rather than age because the exact age ASY female Tree Swallows breeding at our study area for the first time (i.e., unbanded) cannot be determined. We also used a likelihood ratio test to test whether the proportion of females that bred after being manipulated differed by plumage brightness treatment.

For those females that acquired new nest sites after being manipulated, we used a repeated-measures ANOVA to test whether the quality of nest site they subsequently occupied differed from the site occupied before moving. In this analysis, we included time (before and after moving) as the within-subject factor and plumage brightness treatment as the between-subject factor and the interaction between time and plumage brightness treatment.

We tested whether altering the plumage brightness of females influenced their reproductive success using general linear mod-

Fig. 1. A higher percentage of female Tree Swallows (*Tachycineta bicolor*) with experimentally reduced plumage brightness retained their nest site and bred following manipulation compared to females with control and enhanced plumage brightness. Also shown is the percentage of females in each plumage brightness treatment that left their nest site and found a new nest site after being usurped.
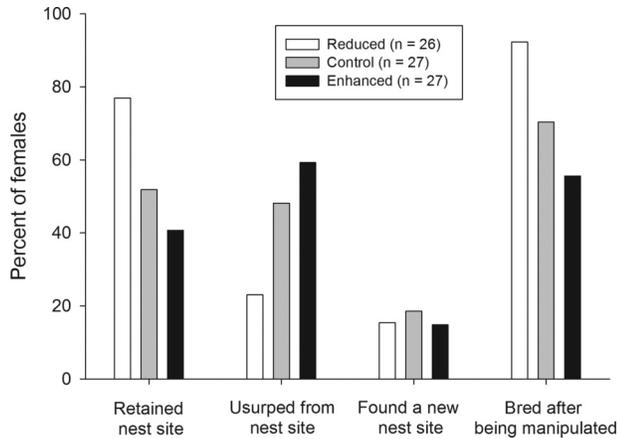
els. First, we tested whether clutch initiation date, standardized to a mean of 0 and a standard deviation of 1 for experimental nests in each year, differed by plumage brightness treatment. In this model, we also included female nest site status (retained, switched nest sites) as a categorical variable, female body mass as a covariate, and the interaction between treatment and nest site status. Second, we also tested whether clutch size and average egg mass differed by the plumage brightness treatment of the female. We included year as a categorical variable and standardized clutch initiation date as a covariate to control for the seasonal decline in clutch size that occurs in Tree Swallows (Winkler et al. 2014).

Nine females were manipulated in both years of the study, and we randomly selected data from one year to use in all analyses. We took this conservative approach to ensure, for example, that our results for nest site retention were not due to the effects of plumage brightness manipulation and not a tendency for some individual females to abandon their nest site after being captured prior to breeding. For all analyses, variables that did not approach significance ($P \geq 0.10$) were removed from models in a backwards, stepwise fashion. We checked the residuals of models for normality and heteroscedasticity (Cleasby and Nakagawa 2011). All statistical tests were two-tailed and results were considered significant at $P \leq 0.05$. Unless stated otherwise, we report least squares means from models ±1 SE (lsmeans: Lenth 2016). The overall significance of omnibus tests was examined using post-hoc tests with false discovery rate adjustment for multiple comparisons (Verhoeven et al. 2005). All statistical analyses were performed using SPSS v20 (IBM Corp. 2011) and R v3.2.3 (R Core Team 2015) statistical software.

Results

Nest site retention, breeding success, and nest site quality

Logistic regression showed that plumage brightness treatment influenced nest site retention by female Tree Swallows ($\chi^2_{[2]} = 8.24$, $P = 0.02$) (Fig. 1). Post-hoc comparisons between treatment groups showed that females with enhanced plumage brightness were no more likely to leave their nest site following manipulation than controls but were more likely to leave their nest site after being manipulated than females with reduced plumage brightness (Table 1). Control females were also more likely to leave their nest sites than females whose plumage was experimentally reduced (Table 1). The logistic regression also showed that females that bred in our study area in previous years were more likely to retain

their nest site than newly captured females (estimate = 1.49 ± 0.57, $\chi^2_{[1]} = 2.60$, $P = 0.009$, odds ratio = 4.43, 95% confidence interval = 1.51–14.60). Quality of the nest site and original plumage brightness (PC2) of females as well as the interaction between treatment and original plumage brightness were not significant predictors of nest site retention (all $P > 0.33$) and were removed from the final model. Since plumage brightness treatment influenced nest site retention of female Tree Swallows, we performed additional analyses to test whether females that retained their nest sites were heavier, in better body condition, or originally displayed brighter plumage than females that left their nest site; these analyses showed no significant differences between females that retained versus left their nest site (all $P > 0.10$).

Although some females in each treatment that lost their nest site were found breeding at new nest sites (Fig. 1), a likelihood ratio test showed that overall the proportion of females that bred successfully following manipulation differed by plumage brightness treatment ($G_{[2]} = 7.67$, $P = 0.02$) (Fig. 1). Subanalyses between pairs of treatment groups showed that a lower proportion of females with enhanced and control plumage brightness bred following manipulation than females in the reduced treatment ($G_1 = 10.00$, $P = 0.002$; $G_{[1]} = 4.42$, $P = 0.04$) (Fig. 1).

For females that switched nest sites following manipulation, repeated-measures ANOVA showed that the quality of the new nest site occupied by females was not significantly influenced by plumage brightness treatment ($F_{[2,13]} = 0.53$, $P = 0.78$); however, the newly acquired nest sites were overall of lower quality than the nest sites occupied by the females prior to manipulation ($F_{[1,15]} = 5.01$, $P = 0.04$) (Fig. 2).

Reproductive success

Clutch initiation date tended to differ by the plumage brightness treatment of the female ($F_{[2,53]} = 2.74$, $P = 0.07$) (Fig. 3a), and post-hoc tests showed that this was due to females in the enhanced plumage brightness treatment tending to initiate clutches approximately 3 days later than females in the control (estimate = −0.64 ± 0.31, $t_{[53]} = −2.04$, $P = 0.07$) (Fig. 3a) and reduced plumage brightness treatment groups (estimate = −0.63 ± 0.30, $t_{[53]} = −2.13$, $P = 0.07$) (Fig. 3a). This analysis also showed that females that switched nest sites after being manipulated initiated clutches approximately 3 days later than females that retained their nest site (estimate = −0.71 ± 0.28, $F_{[1,53]} = 6.62$, $P = 0.01$) (Fig. 3b), and there was some suggestion that females with lower body mass when captured prebreeding also bred later (estimate = −0.14 ± 0.08, $F_{[1,53]} = 3.26$, $P = 0.08$).

As expected, there was a significant decline in clutch size with later dates of clutch initiation (estimate = −0.42 ± 0.12, $F_{[1,53]} = 11.19$, $P < 0.01$) as well as a decline in average egg mass with initiation date (estimate = −0.06 ± 0.02, $F_{[1,55]} = 8.59$, $P < 0.01$). Neither clutch size nor average egg mass significantly differed by the plumage brightness treatment of the female ($F_{[2,54]} = 0.54$, $P = 0.58$ and $F_{[2,55]} = 0.68$, $P = 0.51$, respectively), but clutches tended to be smaller in 2011 than in 2010 (estimate = −0.45 ± 0.24, $F_{[1,54]} = 3.44$, $P = 0.07$).
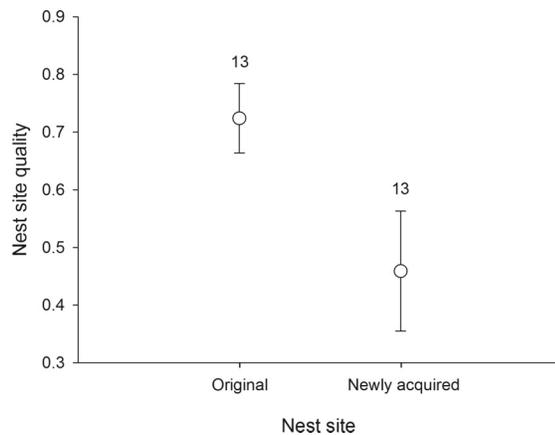
Discussion

We manipulated the plumage brightness of female Tree Swallows to test whether brightness is a signal assessed by conspecific females that influences nest site retention and reproductive success. Our results showed that females in the enhanced plumage brightness treatment were less likely to retain their nest site and breed than females with experimentally reduced plumage brightness (Fig. 1). Control females were also less likely to retain their nest site and breed compared to females with reduced plumage brightness (Fig. 1). These results suggest that our experiment altered social interactions among female Tree Swallows, as similarly reported in male Collared Flycatchers following the ex-

Table 1. Experimentally altered plumage brightness (enhanced or reduced or unchanged) of female Tree Swallows (*Tachycineta bicolor*) influenced nest site retention.

Plumage brightness treatment	Estimate	SE	z	P	Odds ratio (95% confidence interval)
Control vs. enhanced	0.27	0.58	0.46	0.65	1.30 (0.41–4.15)
Reduced vs. enhanced	1.65	0.63	2.59	0.027	5.19 (1.56–19.29)
Reduced vs. control	1.38	0.64	2.15	0.047	3.98 (1.17–14.98)

Note: Results of post-hoc comparisons from a logistic regression show that females with reduced plumage brightness were more likely to retain their nest sites compared to females with control and enhanced plumage brightness. See the Materials and methods for details of the plumage brightness manipulation.
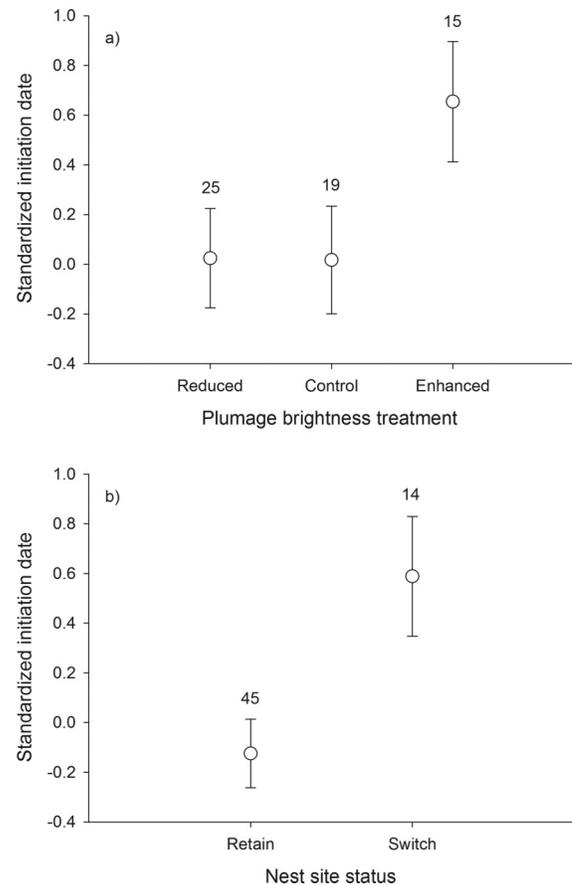
Fig. 2. Female Tree Swallows (*Tachycineta bicolor*) that were usurped from their original nest site bred in lower quality nest sites than their original nest site (mean ± SE). See Materials and methods for details of calculating nest site quality. Sample sizes are given above the error bars.

Fig. 3. Clutch initiation date (mean ± SE) of female Tree Swallows (*Tachycineta bicolor*) (*a*) tended to be later for females with experimentally enhanced plumage brightness compared to those females with reduced and control plumage brightness and (*b*) was later for females that were usurped and switched nest sites after their plumage brightness was manipulated compared to females that retained their nest site. Clutch initiation dates were standardized to a mean of 0 and a standard deviation of 1 for experimental nests separately for each year. Negative values indicate that clutches were initiated early, while positive values indicate that clutches were initiated later in the breeding season. Sample sizes are given above the error bars.

perimental enlargement of the size of their forehead patch (Qvarnström 1997). Since nest usurpation by intruding female conspecifics occurs frequently in Tree Swallows (Leffelaar and Robertson 1985), females that left their nest site after being manipulated were likely unable to defend their nest site from other females; male Tree Swallows are rarely involved in defence against intruding females (see Leffelaar and Robertson 1985; Whittingham and Schwabl 2002; Coady and Dawson 2013). Overall, our finding that plumage brightness influenced nest site retention suggests that social interactions among female Tree Swallows may enforce the honesty of bright plumage, and the cost of dishonestly signalling high quality may be nest usurpation. Since the average life expectancy of Tree Swallows is 2.7 years (Winkler et al. 2011), females unable to retain their nest site may have to forego breeding, thereby imposing fitness costs on unsuccessful females.

Although our results are consistent with altered social interactions influencing nest site retention, three alternative possibilities also exist that may explain why females manipulated to display bright, presumably high-quality plumage ornamentation (enhanced) were less likely to retain their nest site than females with dull, low-quality plumage (reduced). First, lower nest site retention may have occurred if females in the enhanced plumage brightness treatment were more likely to be depredated due to their increased conspicuousness of their plumage (Huhta et al. 2003). If our results for nest site retention were due to predation, then females in the enhanced plumage brightness treatment should have been less likely to retain their nest site than control females, but there was no difference between these treatment groups (Table 1). Second, females in the enhanced plumage brightness treatment may have left their nest site to obtain a higher quality nest site or mate (Otter and Ratcliffe 1996) after being manipulated to signal high quality, but we find it unlikely that a

female would relinquish a limited resource essential for breeding after intense competition with conspecifics (Leffelaar and Robertson 1985; Rosvall 2008). This explanation also cannot account for why control females were more likely to leave their nest site than females in the reduced plumage brightness treatment. Moreover, we found that females that switched nest sites were observed breeding in poorer quality sites than the nest site they originally occupied (Fig. 2) and they initiated their clutches later (Fig. 3b), so

there appears to be little advantage for females that leave their nest site. Third, the differences in nest site retention that we observed could be due to using two different methods to alter plumage brightness; however, both treatments have been successfully used previously with no reported adverse effects on behaviour or feather quality (e.g., Ballentine and Hill 2003; Johnsen et al. 2005). Consequently, it seems unlikely that the actual application of treatments themselves would differentially alter nesting success of females.

That fewer female Tree Swallows in the enhanced plumage brightness treatment retained their nest site, and were able to breed, compared to females with reduced plumage brightness (Fig. 1) is consistent with social mechanisms enforcing the honesty of elaborate ornaments. Although we have no behavioural data to confirm this, our results for nest site retention are consistent with social interactions among conspecifics of similar quality (e.g., high quality versus high quality) enforcing the honesty of ornamentation displayed by individuals (reviewed in Tibbetts 2014). In Gouldian Finches (*Erythrura gouldiae* (Gould, 1844) = *Chloebia gouldiae* (Gould, 1844)), red-headed females engaged in agonistic interactions more aggressively with other red-headed females than with females with other colour morphs (Pryke 2007). Such a social mechanism may operate in female Tree Swallows, if females in the enhanced plumage brightness treatment were challenged aggressively by naturally bright females to test signal quality and were less able to defend their nest site from high-quality intruders of greater competitive ability. Moreover, engaging in agonistic interactions with superior competitors may use resources required for breeding (Fitzpatrick et al. 1995), and provide an explanation for why those females in the enhanced plumage brightness treatment that retained their nest site tended to initiate their clutches later than females in the control and reduced treatments (Fig. 3*a*).

The finding that control females also lost their nest sites is consistent with pervious observations in Tree Swallows (Leffelaar and Robertson 1985) and provides further evidence that plumage brightness of females is a signal of quality that is social enforced by conspecific females. Social interactions occurring among individuals of similar apparent quality would also explain the results for females with reduced plumage brightness if they were better able to defend and retain their nest site if they were challenged by females of lower quality with poorer competitive ability. Although this explanation suggests that dishonestly signalling low quality is advantageous for female Tree Swallows because they are more likely to breed, and reflects the classic "Trojan sparrow" strategy modelled by Owens and Hartley (1991), there may be costs associated with dishonestly signalling low quality in other contexts, such as on wintering roost sites, that were not measured in our study. Because it is not possible to differentiate differences in plumage brightness among interacting female Tree Swallows by observation alone, future studies could use proximity loggers on marked individuals to quantify social interactions (e.g., Levin et al. 2016) and test behavioural mechanisms that enforce the honesty of displaying bright plumage in Tree Swallows and in female birds more generally.

An alternative explanation for why most females in the reduced plumage brightness treatment were able to retain their nest site and breed (Fig. 1) following manipulation is that they were involved in fewer agonistic interactions overall with conspecific females. At our study area, Coady and Dawson (2013) reported that SY female Tree Swallows received less aggressive responses when intruding on the territories of other females and received fewer nest site intrusions as territory owners, suggesting that less-ornamented plumage of SY females signals their low competitive threat. These results were in contrast with Stutchbury and Robertson (1987), who reported that territory-owning female Tree Swallows were equally aggressive to SY and ASY females; however, nest site occupancy at our study area is low (approximately 47% from 2003

to 2009, L.L. Berzins and R.D. Dawson, unpublished data), and so signalling low competitive threat to conspecific females may be beneficial when competition for nest sites is less intense (Coady and Dawson 2013). Consequently, if ASY females displaying reduced plumage brightness were also perceived by conspecifics as a low competitive threat, it would explain why most of these females bred following the manipulation (Fig. 1). It would be interesting to determine whether female Tree Swallows displaying reduced plumage brightness would similarly have higher nesting success in areas with more intense competition for nest sites.

If displaying less-ornamented plumage is beneficial for female Tree Swallows as our results (Fig. 1) and those of Coady and Dawson (2013) suggest, then this raises the question of why female Tree Swallows display bright, presumably high-quality plumage, especially since there appear to be costs associated with the expression of this trait (this study; Coady 2011; Bentz and Siefferman 2013). Although it is currently unknown whether plumage brightness of ASY female Tree Swallows functions as a status signal, the pattern of assortative mating in this species for plumage brightness (Bitton et al. 2008) may suggest that brighter females have greater competitive ability, since plumage brightness does not appear to be used by males in mate choice (Berzins 2016; Berzins and Dawson 2016). Consequently, brighter females may have greater nesting success if they outcompete conspecific females for access to nest sites, especially in high-quality or fully occupied habitats. Moreover, since male Tree Swallows displaying brighter dorsal plumage are preferred as extra-pair mates by females and have higher reproductive success than duller males because they sire more offspring (Bitton et al. 2007; Whittingham and Dunn 2016), females displaying bright plumage that mate with such males also may have greater reproductive success if they produce sons that inherit the bright plumage of their father (e.g., sexy son hypothesis: Weatherhead and Robertson 1979). Overall, the selective advantage to female Tree Swallows displaying bright plumage warrants further investigation, especially in areas that differ in their habitat quality and intensity of female competition (Cain and Langmore 2016).

Several studies have reported that the response of territory-owning females to intruding conspecific females is related to their own ornamentation; for example, female Pied Flycatcher territory owners displaying a forehead patch were more likely than females without forehead patches to attack female intruder decoys (Morales et al. 2014). If plumage brightness of female Tree Swallows is related to how intensely they defend their nest site against intruders, then we expected original plumage brightness of females to influence nest site retention, but this was not observed. While we acknowledge that the degree of incongruence between a female's manipulated plumage brightness and behaviour may have better predicted nest site retention than original plumage brightness, it is alternatively possible that nest site defence by female Tree Swallows is related to other factors, such as prior ownership or the value of the nest site for the female. Our results showed that previously banded female Tree Swallows were more likely to retain their nest site than newly captured females; it is unclear whether females that were previously banded at our study area are older because the exact age of newly captured ASY females cannot be determined, but banded females had previous experience breeding at our study area. Since only 5 of 18 of the banded females in our study bred at the same nest site as the previous year (L.L. Berzins, unpublished data), it is unlikely that banded females retained their nest site simply because of ownership in the previous breeding season. Prior ownership of a nest site also did not influence nest site retention by Tree Swallows from competing Mountain Bluebirds (*Sialia currucoides* (Bechstein, 1798)) (Wiebe 2016). Dale and Slagsvold (1995) reported that the outcome of contests over nest sites in female Pied Flycatchers was determined by the value of the breeding opportunity to the female and not asymmetries in body size, age, or previous owner-

ship. Moreover, Elias et al. (2010) reviewed the few studies on contest behaviour in female animals and similarly reported that success at winning is determined by resource value and not resource holding potential. Our results for female Tree Swallows may similarly suggest that nest sites are perceived as more valuable to returning breeders, but clearly, further research on contest rules in female animals is warranted.

Social costs imposed on dishonest signalers may include increased aggression from conspecifics and lower reproductive success (Kotiaho 2001). Although we were unable to directly observe social interactions among females, manipulating the ornamentation of wild female Tree Swallows prior to breeding allowed us to examine whether conspecific females assess the quality of plumage brightness displayed and whether females displaying enhanced or reduced plumage brightness incurred social costs associated with dishonest signalling (Laubach et al. 2013). Indeed, females in the enhanced plumage brightness treatment that dishonestly signalled high quality suffered costs, since fewer of them were able to retain their nest site and breed (Fig. 1), and those that did breed tended to initiate their clutches later than females in the control and reduced plumage brightness treatments (Fig. 3a). Consequently, females that engage in social interactions with conspecific females may face trade-offs between ornament display and reproduction (Fitzpatrick et al. 1995), as our results suggest. Future studies should examine whether ornamental traits displayed by females mediate social interactions that influence trade-offs with parental care, which may provide insight into why ornamented females of some species produce low-quality offspring (Nordeide et al. 2013).

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References

Ballentine, B., and Hill, G.E. 2003. Female mate choice in relation to structural plumage coloration in blue grosbeaks. Condor, **105**(3): 593–598. doi:10.1650/7234.

Bentz, A.B., and Siefferman, L. 2013. Age-dependent relationships between coloration and reproduction in a species exhibiting delayed plumage maturation in females. J. Avian Biol. **44**(1): 80–88. doi:10.1111/j.1600-048X.2012.05730.x.

Berzins, L.L. 2016. Determinants of mating success in female tree swallows (*Tachycineta bicolor*). Ph.D. dissertation, University of Northern British Columbia, Prince George, B.C. doi:1024124/2017/1338.

Berzins, L.L., and Dawson, R.D. 2016. Experimentally altered plumage brightness of female tree swallows: a test of the differential allocation hypothesis. Behaviour, **153**(5): 525–550. doi:10.1163/1568539X-00003354.

Bitton, P.-P., O'Brien, E.L., and Dawson, R.D. 2007. Plumage brightness and age predict extrapair fertilization success of male tree swallows, *Tachycineta bicolor*. Anim. Behav. **74**(6): 1777–1784. doi:10.1016/j.anbehav.2007.03.018.

Bitton, P.-P., Dawson, R.D., and Ochs, C.L. 2008. Plumage characteristics, reproductive investment and assortative mating in tree swallows *Tachycineta bicolor*. Behav. Ecol. Sociobiol. **62**(10): 1543–1550. doi:10.1007/s00265-008-0583-7.

Cain, K.E., and Langmore, N.E. 2016. Female song and aggression show contrasting relationships to reproductive success when habitat quality differs. Behav. Ecol. Sociobiol. **70**(11): 1867–1877. doi:10.1007/s00265-016-2192-1.

Cleasby, I.R., and Nakagawa, S. 2011. Neglected biological patterns in the residuals. Behav. Ecol. Sociobiol. **65**(12): 2361–2372. doi:10.1007/s00265-011-1254-7.

Clutton-Brock, T. 2009. Sexual selection in females. Anim. Behav. **77**(1): 3–11. doi:10.1016/j.anbehav.2008.08.026.

Coady, C.D. 2011. The signaling function of plumage characteristics in female tree swallows and implications for reproductive success and life-history decisions. M.Sc. thesis, University of Northern British Columbia, Prince George, B.C. doi:1024124/2011/bpgub759.

Coady, C.D., and Dawson, R.D. 2013. Subadult plumage color of female tree swallows (*Tachycineta bicolor*) reduces conspecific aggression during the breeding season. Wilson J. Ornithol. **125**(2): 348–357. doi:10.1676/12-155.1.

Cuthill, I.C., Bennett, A.T.D., Partridge, J.C., and Maier, E.J. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. Am. Nat. **153**(2): 183–200. doi:10.1086/303160.

Dale, S., and Slagsvold, T. 1995. Female contests for nest sites and mates in the pied flycatcher *Ficedula hypoleuca*. Ethology, **99**(3): 209–222. doi:10.1111/j.1439-0310.1995.tb00895.x.

Dawson, R.D., Lawrie, C.C., and O'Brien, E.L. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. Oecologia, **144**(3): 499–507. doi:10.1007/s00442-005-0075-7. PMID:15891832.

Elias, D.O., Botero, C.A., Andrade, M.C.B., Mason, A.C., and Kasumovic, M.M. 2010. High resource valuation fuels "desperado" fighting tactics in female jumping spiders. Behav. Ecol. **21**(4): 868–875. doi:10.1093/beheco/arq073.

Fitzpatrick, S., Berglund, A., and Rosenqvist, G. 1995. Ornaments or offspring: costs to reproductive success restrict sexual selection processes. Biol. J. Linn. Soc. **55**(3): 251–260. doi:10.1111/j.1095-8312.1995.tb01063.x.

Hegyi, G., Garamszegi, L.Z., Eens, M., and Török, J. 2008. Female ornamentation and territorial conflicts in collared flycatchers (*Ficedula albicollis*). Naturwissenschaften, **95**(10): 993–996. doi:10.1007/s00114-008-0408-6. PMID:18548223.

Huhta, E., Rytkönen, S., and Solonen, T. 2003. Plumage brightness of prey increases predation risk: an among-species comparison. Ecology, **84**(7): 1793–1799. doi:10.1890/0012-9658(2003)084[1793:PBOPIP]2.0.CO;2.

Hussell, D.J.T. 1983. Age and plumage color in female tree swallows. J. Field Ornithol. **54**(3): 312–318.

Hyman, J., Hughes, M., Searcy, W.A., and Nowicki, S. 2004. Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. Behaviour, **141**(1): 15–27. doi:10.1163/156853904772746574.

IBM Corp. 2011. IBM SPSS statistics for Windows, version 20.0. IBM Corp. Armonk, N.Y.

Johnsen, A., Delhey, K., Schlicht, E., Peters, A., and Kempenaers, B. 2005. Male sexual attractiveness and parental effort in blue tits: a test of the differential allocation hypothesis. Anim. Behav. **70**(4): 877–888. doi:10.1016/j.anbehav.2005.01.005.

Kotiaho, J.S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. Biol. Rev. Camb. Philos. Soc. **76**(3): 365–376. doi:10.1017/S1464793101005711. PMID:11569789.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution, **34**(2): 292–305. doi:10.2307/2407393. PMID:28563426.

Laubach, Z.M., Blumstein, D.T., Romero, L.M., Sampson, G., and Foufopoulos, J. 2013. Are white-crowned sparrow badges reliable signals? Behav. Ecol. Sociobiol. **67**(3): 481–492. doi:10.1007/s00265-012-1468-3.

Leffelaar, D., and Robertson, R.J. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. Wilson Bull. **97**(2): 221–224.

Lenth, R.V. 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Levin, I.I., Zonana, D.M., Fosdick, B.K., Song, S.J., Knight, R., and Safran, R.J. 2016. Stress response, gut microbial diversity and sexual signals correlate with social interactions. Biol. Lett. **12**(6): 20160352. doi:10.1098/rsbl.2016.0352. PMID:27354713.

López-Idiáquez, D., Vergara, P., Fargallo, J.A., and Martínez-Padilla, J. 2016. Female plumage coloration signals status to conspecifics. Anim. Behav. **121**: 101–106. doi:10.1016/j.anbehav.2016.08.020.

Maia, R., Eliason, C.M., Bitton, P.-P., Doucet, S.M., and Shawkey, M.D. 2013. pavo: an R package for the analysis, visualization and organization of spectral data. Methods Ecol. Evol. **4**(10): 906–913. doi:10.1111/2041-210X.12069.

Møller, A.P. 1987. Social control of deception among status signalling house sparrows *Passer domesticus*. Behav. Ecol. Sociobiol. **20**(5): 307–311. doi:10.1007/BF00300675.

Morales, J., Gordo, O., Lobato, E., Ippi, S., Martinez-de la Puente, J., Tomás, G., Merino, S., and Moreno, J. 2014. Female–female competition is influenced by forehead patch expression in pied flycatcher females. Behav. Ecol. Sociobiol. **68**(7): 1195–1204. doi:10.1007/s00265-014-1730-y.

Moreno, J., Velando, A., Ruiz-de-Castañeda, R., González-Braojos, S., and Cantarero, A. 2013. Oxidative damage in relation to a female plumage badge: evidence for signalling costs. Acta Ethol. **16**(2): 65–75. doi:10.1007/s10211-012-0138-9.

Murphy, T.G., Hernández-Muciño, D., Osorio-Beristain, M., Montgomerie, R., and Omland, K.E. 2009a. Carotenoid-based status signaling by females in the tropical streak-backed oriole. Behav. Ecol. **20**(5): 1000–1006. doi:10.1093/beheco/arp089.

Murphy, T.G., Rosenthal, M.F., Montgomerie, R., and Tarvin, K.A. 2009b. Female American goldfinches use carotenoid-based bill coloration to signal status. Behav. Ecol. **20**(6): 1348–1355. doi:10.1093/beheco/arp140.

Nordeide, J.T., Kekäläinen, J., Janhunen, M., and Kortet, R. 2013. Female orna-

ments revisited — are they correlated with offspring quality? J. Anim. Ecol. **82**(1): 26–38. doi:10.1111/1365-2656.12021. PMID:23194443.

Otter, K., and Ratcliffe, L. 1996. Female initiated divorce in a monogamous songbird: abandoning mates for males of higher quality. Proc. R. Soc. B Biol. Sci. **263**(1368): 351–355. doi:10.1098/rspb.1996.0054.

Owens, I.P., and Hartley, I.R. 1991. "Trojan sparrows": evolutionary consequences of dishonest invasion for the badges-of-status model. Am. Nat. **138**(5): 1187–1205. doi:10.1086/285277.

Potti, J., and Montalvo, S. 1991. Male arrival and female mate choice in pied flycatchers *Ficedula hypoleuca* in Central Spain. Ornis Scand. **22**(1): 45–54. doi:10.2307/3676620.

Pryke, S.R. 2007. Fiery red heads: female dominance among head color morphs in the Gouldian finch. Behav. Ecol. **18**(3): 621–627. doi:10.1093/beheco/arm020.

Qvarnström, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. Proc. R. Soc. B Biol. Sci. **264**(1385): 1225–1231. doi:10.1098/rspb.1997.0169.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Rohwer, S. 1977. Status signaling in Harris sparrows: some experiments in deception. Behaviour, **61**(1): 107–129. doi:10.1163/156853977X00504.

Rohwer, S., and Rohwer, F.C. 1978. Status signalling in Harris sparrows: experimental deceptions achieved. Anim. Behav. **26**(4): 1012–1022. doi:10.1016/0003-3472(78)90090-8.

Rosvall, K.A. 2008. Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. Anim. Behav. **75**(5): 1603–1610. doi:10.1016/j.anbehav.2007.09.038.

Rosvall, K.A. 2011. By any name, female–female competition yields differential mating success. Behav. Ecol. **22**(6): 1144–1146. doi:10.1093/beheco/arr111. PMID:22479138.

Safran, R.J., Adelman, J.S., McGraw, K.J., and Hau, M. 2008. Sexual signal exaggeration affects physiological state in male barn swallows. Curr. Biol. **18**(11): R461–R462. doi:10.1016/j.cub.2008.03.031. PMID:18522812.

Senar, J.C. 2006. Color displays as intrasexual signals of aggression and dominance. *In* Bird coloration. Vol. II: Function and evolution. *Edited by* G.E. Hill and K.J. McGraw. Harvard University Press, Cambridge, Mass. pp. 87–136.

Stutchbury, B.J., and Robertson, R.J. 1985. Floating populations of female tree swallows. Auk, **102**(3): 651–654.

Stutchbury, B.J., and Robertson, R.J. 1987. Signaling subordinate and female status: two hypotheses for the adaptive significance of subadult plumage in female tree swallows. Auk, **104**(4): 717–723.

Tarvin, K.A., and Murphy, T.G. 2012. It isn't always sexy when both are bright and shiny: considering alternatives to sexual selection in elaborate monomorphic species. Ibis, **154**(3): 439–443. doi:10.1111/j.1474-919X.2012.01251.x.

Tibbetts, E.A. 2008. Resource value and the context dependence of receiver behaviour. Proc. R. Soc. B Biol. Sci. **275**(1648): 2201–2206. doi:10.1098/rspb.2008.0477.

Tibbetts, E.A. 2014. The evolution of honest communication: integrating social and physiological costs of ornamentation. Integr. Comp. Biol. **54**(4): 578–590. doi:10.1093/icb/icu083. PMID:24944118.

Tibbetts, E.A., and Izzo, A. 2010. Social punishment of dishonest signalers caused by mismatch between signal and behavior. Curr. Biol. **20**(18): 1637–1640. doi:10.1016/j.cub.2010.07.042. PMID:20727756.

Tibbetts, E.A., and Lindsay, R. 2008. Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. Biol. Lett. **4**(3): 237–239. doi:10.1098/rsbl.2008.0048. PMID:18331973.

Tobias, J.A., Montgomerie, R., and Lyon, B.E. 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Philos. Trans. R. Soc. B Biol. Sci. **367**(1600): 2274–2293. doi:10.1098/rstb.2011.0280.

Verhoeven, K.J.F., Simonsen, K.L., and McIntyre, L.M. 2005. Implementing false discovery rate control: increasing your power. Oikos, **108**(3): 643–647. doi:10.1111/j.0030-1299.2005.13727.x.

Vitousek, M.N., Zonana, D.M., and Safran, R.J. 2014. An integrative view of the signaling phenotype: dynamic links between signals, physiology, behavior and social context. Curr. Zool. **60**(6): 739–754. doi:10.1093/czoolo/60.6.739.

Weatherhead, P.J., and Robertson, R.J. 1979. Offspring quality and the polygyny threshold: the sexy son hypothesis. Am. Nat. **113**(2): 201–208. doi:10.1086/283379.

Whittingham, L.A., and Dunn, P.O. 2016. Experimental evidence that brighter males sire more extra-pair young in tree swallows. Mol. Ecol. **25**(15): 3706–3715. doi:10.1111/mec.13665. PMID:27105297.

Whittingham, L.A., and Schwabl, H. 2002. Maternal testosterone in tree swallow eggs varies with female aggression. Anim. Behav. **63**(1): 63–67. doi:10.1006/anbe.2001.1889.

Wiebe, K.L. 2016. Interspecific competition for nests: prior ownership trumps resource holding potential for mountain bluebird competing with tree swallow. Auk, **133**(3): 512–519. doi:10.1642/AUK-16-25.1.

Winkler, D.W., Hallinger, K.K., Ardia, D.R., Robertson, R.J., Stutchbury, B.J., and Cohen, R.R. 2011. Tree Swallow (*Tachycineta bicolor*), version 2.0. *In* The birds of North America. *Edited by* A.F. Poole. Cornell Lab of Ornithology, Ithaca, N.Y. doi:10.2173/bna.11.

Winkler, D.W., Ringelman, K.M., Dunn, P.O., Whittingham, L., Hussell, D.J.T., Clark, R.G., Dawson, R.D., Johnson, L.S., Rose, A., Austin, S.H., Robinson, W.D., Lombardo, M.P., Thorpe, P.A., Shutler, D., Robertson, R.J., Stager, M., Leonard, M., Horn, A.G., Dickinson, J., Ferretti, V., Massoni, V., Bulit, F., Reboreda, J.C., Liljesthröm, M., Quiroga, M., Rakhimberdiev, E., and Ardia, D.R. 2014. Latitudinal variation in clutch size – lay date regressions in *Tachycineta* swallows: effects of food supply or demography? Ecography, **37**(7): 670–678. doi:10.1111/j.1600-0587.2013.00458.x.