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SUBADULT PLUMAGE COLOR OF FEMALE TREE SWALLOWS (*TACHYCINETA BICOLOR*) REDUCES CONSPECIFIC AGGRESSION DURING THE BREEDING SEASON

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ABSTRACT.—Delayed plumage maturation (DPM) in young males (in their second year of life: SY) of some species of birds has been found to reduce aggression directed at these younger males. Tree Swallows (*Tachycineta bicolor*) are unusual because it is SY females rather than males that display DPM; however, the functional significance for DPM remains equivocal. During the breeding season, we tested whether both male and female Tree Swallows behaved differently towards SY and older (after second year: ASY) female Tree Swallow models. When presented as a territory intruder, we predicted that ASY models would receive more aggression from resident pairs if ASY females are perceived as a greater competitive threat. When presented as a territory owner, we predicted that SY models would experience more territorial intrusions if SY plumage is perceived as a signal of inexperience in territory defense. When models were presented as intruders, resident females were more aggressive towards ASY models compared to SY models. When presented as territory owners, ASY models received more aggression than SY models from intruding Tree Swallows, although we suspect that intruders were neighboring Tree Swallows with already established territories, as opposed to birds seeking to settle within the territories of our models. Overall, our results suggest that DPM in female Tree Swallows is an adaptive trait that potentially reduces intrasexual competition for SY females during the breeding season. *Received 25 September 2012. Accepted 19 December 2012.*

Key words: aggression, competition, delayed plumage maturation, territory, Tree Swallow.

Much attention has focused on the fitness benefits of elaborate plumage of male birds with respect to sexual signaling (e.g., Badyaev et al. 2001). Plumage ornaments, however, have also been found to signal such characteristics as age, aggressiveness, or social-dominance (Korsten et al. 2007, Quesada and Senar 2007) and so potentially display individual quality and degree of threat as a competitor to conspecifics. Most commonly exhibited by males, delayed plumage maturation (DPM), is defined as the delay in the acquisition of adult plumage traits without a delay in sexual maturity, resulting in a 'subadult' plumage (Rohwer et al. 1980). Hypotheses for the adaptive significance of DPM in passerine birds suggest that it may have evolved by communicating a lowered competitive threat to conspecifics and thus reducing aggression and competition for mates and resources, increasing the fitness of the bearer (Lyon and Montgomerie 1986, Rohwer and Butcher 1988).

The status-signaling hypothesis is arguably among the most well supported of the hypotheses for DPM and suggests that males displaying DPM during their second year of life (SY), and first potential breeding season, are honestly signaling their subordinate status to older males (after second year: ASY). Thus, DPM may result in a reduction in male aggression towards SY males, potentially allowing young males easier access to females (Lyon and Montgomerie 1986). Pertaining specifically to dichromatic species, the female mimicry hypothesis suggests that DPM in males may deceptively communicate female-status to ASY males, thus allowing SY males to avoid costly agonistic interactions with older males (Rohwer et al. 1980). Regardless of the mechanism, both of these hypotheses suggest that DPM communicates a lowered competitive threat to conspecifics. While there is evidence to support the potential adaptive functions of DPM (reviewed in Beauchamp 2003), several studies have shown that individuals displaying DPM have reduced reproductive success and obtain fewer resources compared to older individuals (Enstrom 1992, Conover et al. 2000). These studies illustrate the necessity of investigating both potential advantages and disadvantages of DPM in a given study.

Tree Swallows (*Tachycineta bicolor*) are one of only two species of North American passerines where females exhibit DPM rather than males (Rohwer et al. 1980). ASY females in at least their second breeding season, as well as all males, have predominately iridescent blue-green dorsal plum-

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age (Hussell 1983). SY females that are entering their first potential breeding season may also have some iridescent blue-green dorsal feathers, but in the majority of SY females these constitute much less than 50% of dorsal feathers and so the subadult plumage is predominately brown. Of the few studies that have investigated the functional significance of DPM in female Tree Swallows (Stutchbury and Robertson 1987a, Lozano and Handford 1995), Stutchbury and Robertson (1987a) suggested a gender-signaling hypothesis for the adaptive significance of subadult plumage in this species. They found that males were less aggressive towards intruding SY females compared to ASY females, suggesting that subadult plumage may aid in nest-site exploration for these females, many of which do not breed in their first potential breeding season because of competition from older, more experienced females (Stutchbury and Robertson 1985).

Tree Swallows are obligate cavity nesters that frequently use artificial nest boxes. Although fierce competition for nest sites among males begins early in the breeding season (Kuerzi 1941) with males returning to breeding grounds prior to females and claiming a nest site (Cohen 1987), females also participate in aggressive interactions as they compete for suitable mates and nest sites. Since many nest sites can remain unoccupied throughout the breeding season, it is believed that females compete for males with nest sites rather than vacant nest sites alone (Leffelaar and Robertson 1985), and aggressive interactions among females can lead to severe injury or death (Leffelaar and Robertson 1985 and CDC, pers. obs.). As DPM has been found to function by reducing intrasexual aggression during the breeding season in males of many species (Lyon and Montgomerie 1986), DPM in female Tree Swallows could also function by reducing aggression from conspecific females. Although Stutchbury and Robertson (1987a) found that resident female Tree Swallows were equally aggressive to female intruders regardless of age, other studies have commonly found female ornaments to be signals of status in species with high levels of female-female competition for resources and mates (Johnsen et al. 1996, Murphy et al. 2009). As Stutchbury and Robertson's (1987a) study is the only experimental test of the potential signaling function of DPM in Tree Swallows, the hypothesis that DPM is an adaptive intrasexual signal of subordinance in SY female Tree Swallows is worthy of further investigation.

While displaying subadult plumage could be beneficial for young females, Whittingham and Schwabl (2002) found that SY female Tree Swallows experienced more nest-site intrusions compared to ASY females. Similarly, Lozano and Handford (1995) suggested that adult-colored plumage in female Tree Swallows is an honest signal of dominance and condition, and thus could be an adaptive signal of fighting ability in intrasexual interactions. SY females therefore may be displaying their inexperience in territory and nest defense via their plumage coloration, creating the perception of an easily attainable nest site to intruders. This notion stems from the theory of contest asymmetries, where individuals with more elaborate ornaments should be less contested by conspecifics because their perceived condition is greater compared to less-ornamented individuals (Reichert 1998). In Song Sparrows (*Melospiza melodia*) for example, younger, more inexperienced males are poorer territory defenders (Hyman et al. 2004) and are more frequently intruded upon by unmated 'floating' males (Arcese 1987). If plumage coloration is an intrasexual signal of competitive fighting ability as seen in other species (Hegyi et al. 2008b), potential intruders may intrude more frequently into territories occupied by SY females and avoid territories occupied by adult-colored ASY females if the intruder has a greater risk of losing a contest (Rohwer 1982).

As there has been relatively little research carried out on the functional significance of DPM in Tree Swallows, we experimentally tested whether resident Tree Swallows perceive SY and ASY female intruders differently during the breeding season. Stutchbury and Robertson (1987a) also studied a relatively dense population of Tree Swallows with a high frequency of intrusions into nest sites, and a known 'floating' population of females that were unable to acquire nest sites (Stutchbury and Robertson 1985). In our study area, competition for nest sites is potentially less pronounced, with as many as 45% of the nest sites remaining vacant for the duration of the breeding season (O'Brien and Dawson 2007), potentially allowing for the benefits of subadult plumage during intrasexual interactions to be more evident. We also expanded on Stutchbury and Robertson's study by including a second set of experiments designed to test whether subadult plumage of SY female Tree Swallows is perceived by competing Tree Swallows as a signal of

inexperience in nest-site defense (Whittingham and Schwabl 2002) and reduced fighting ability (Lozano and Handford 1995). If so, we predicted that territories occupied by SY females would have a higher rate of intrusions compared to those occupied by ASY females. This result would indicate that DPM in Tree Swallows may not be an adaptive signal during the breeding season and rather DPM may have signaling potential during other periods of the annual cycle (see Beauchamp 2003).

METHODS

We studied Tree Swallows breeding in nest boxes during 2008 at two study sites; one located 25 km west of Prince George, BC, Canada (53° 50′ N , 123° 2′ W), and the other 25 km south of Prince George (53° 45′ N, 122° 33′ W). Both study sites consisted of open agricultural fields mixed with patches of coniferous and deciduous forest, and small wetlands. Experiments were performed between 0900–1600 PST from early to mid-May, when Tree Swallows in our region are establishing territories and building nests. We used three ASY and two SY freeze-dried female Tree Swallows as our models for all experiments. These models were constructed with close attention to detail so that they were as identical in appearance as possible for body posture, head position, etc. We certainly recognize some of the potential issues associated with using few exemplars to test hypotheses about responses to general classes of stimuli, such as can occur in avian song playback experiments when examining responses to various song dialects (e.g., McGregor et al. 1992, Kroodsma et al. 2001). While it is possible that subtle differences among the models in our study, such as posture, could have induced different behavioral responses from Tree Swallows, we feel that this was very unlikely. In contrast to many playback experiments that test responses to slight differences in song structure, our study tested for responses to models that differed immensely in plumage color, and so we believe that the responses we detected in our study were because of age differences between models as opposed to subtle variation in model posture, etc. Furthermore, because we relied on using dead female Tree Swallows as models, the number of specimens available to us was necessarily limited. We felt that because the plumage differences between ASY and SY models were so pronounced, collecting more adults to use as additional models was not ethically justified.

Model Intruder Plumage Color and Resident Behavior

To investigate whether the subadult plumage of SY females reduced aggression from conspecifics during the breeding season, we placed models of both SY and ASY females within territories of resident pairs during two experiments (details below). The amount of aggression elicited from residents was measured based on the number of times a male or female resident attacked or hovered over each model. Although we were unable to time the length of each hover or attack, a hover was considered so if a Tree Swallow was directly above the model for at least 2 secs and was <60 cm above the model. An attack was considered to have occurred if a Tree Swallow visibly contacted the model.

The first experiment investigated the responses of resident pairs ($n = 26$) to SY and ASY models when presented simultaneously. Tree Swallows are known to aggressively defend a territory within a 6–8 m radius of their nest, and may defend as far as an 18 m radius around their nest box (Robertson and Gibbs 1982). Models were placed on 1.5 m high wooden poles approximately 1.5 m apart and 1.5 m in front of resident pairs' nest boxes, facing the nest box to ensure the residents perceived the models as intruders on their territories (similar to the design of Stutchbury and Robertson 1987a). Presentations were 5 mins in length and began when one or both of the residents entered the vicinity of the nest box after we placed the model in front of the resident's nest box. The position of the ASY model to the left or right of the nest box was alternated between observations, and models were only presented once to any given resident pair. The second experiment examined the response of resident pairs ($n = 14$) when models were presented separately. Models were mounted directly on top of nest boxes to simulate more aggressive intrusions into territories, and presentations were again 5 mins in length, commencing when one or both residents entered the vicinity of the nest box. At the first nest used in this experiment, we randomly chose to present an ASY model first, followed by an SY model. We then alternated presenting the SY or ASY model first at each nest subsequently used in the experiment. The time

TABLE 1. Intruder behavior scoring system for model-occupied territories of Tree Swallows (adapted from Duckworth 2006).

Score	'Intruder' behavior and distance from nest box	No. of 'intruder' attacks on model
1	10-5 m from nest box	0
2	<5 m from nest box/hovering over model	0
3	Inspecting interior of nest box	0
4	Sitting on nest box and/or hovering over model	1 to 2
5	Sitting on nest box and/or hovering over model	3 to 5
6	Sitting on nest box and/or hovering over model	>5

between model presentations for a given resident pair ranged from 1.5–3.5 hrs.

Model Resident Plumage Color and Intruder Behavior

To investigate if intruders respond differently according to the age of resident female Tree Swallows, which could indicate differences in intruder perception of the nest defense capabilities of female Tree Swallows, we separately placed both SY and ASY female models in unoccupied territories ($n = 21$) for 20 mins to simulate their ownership of that territory. For all of the presentations, this unoccupied territory was a nest box that was erected immediately prior to the presentation and taken down immediately after the presentation. Models were placed on a nest box attached to a metal pole or a fence post approximately 1.5 m high and at least 20 m from already established pairs. We attempted to minimize the influence of neighboring Tree Swallows entering our simulated territory in defense of their own by remaining outside the maximum range that Tree Swallows have been found to defend (Robertson and Gibbs 1982), while ensuring that our model territory was still visible to Tree Swallows in the area. A neighboring nest box was considered 'established' if a pair was seen occupying the area in the vicinity of the nest box (i.e., within ~10 m of the nest box), and if the nest was approximately midway or farther though the nest-building stage. Each time a Tree Swallow entered the model territory (i.e., within 10 m of the model mounted to the nest box), we used a 6 point scoring system (Table 1) similar to Duckworth (2006) and assigned a single score to each individual to categorize the nature of the intrusion, with higher scores representing the most aggressive intrusions. As multiple Tree Swallows would often simultaneously enter the territory of the models, it was not always possible to track an individual intruder if it left the territory; therefore, if an intruder left and later returned to the territory, it was treated as a separate intrusion. Some presentations had to be abruptly stopped if intruders began to severely attack the models, although in no cases were models visibly damaged before a trial was stopped. Therefore, as some presentations did not last a full 20 mins due to the model being attacked, we calculated a mean intrusion score for each model presentation at the end of the observation period. Similarly, for each presentation, we also calculated the number of scores that included attacks on the model (i.e., score of four or higher; see Table 1) and divided that by the total number of scores for a given presentation to get the proportion of scores that included attacks on the models.

For experiments on resident and intruder behavior, observations were made using binoculars from a distance of ~30 m from the model set up and as far as possible from any neighboring nest sites. Observations were dictated into digital recorders and later transcribed. For all experiments, we endeavored to identify the sex of each bird interacting with our models using plumage characteristics (e.g., females have greener dorsal plumage and their white chest coloration tends to be sootier than males). In most cases, we are confident in our assignment of sex to each individual. During routine field work trapping adult Tree Swallows at nest boxes from a similar distance as in our experiments (30 m), we always targeted the male parent first as birds entered the next box. As evidence of our ability to identify the sex of birds while in flight from 30 m away, we have been able to correctly identify the sex of birds on the wing in 93.5% of these cases ($n = 171$ captures during the 2008–2010 breeding seasons; RDD, unpubl. data). For the intrusion experiments, however, when multiple Tree Swallows simultaneously entered the model territory,

we often were unable to identify the sex of the individual intruders. Nonetheless, only during four of the presentations did we identify an SY female entering the model territory; therefore, the remaining intruders were either males or ASY females.

Statistical Analyses

Model Intruder Experiments.—To investigate whether resident birds responded differently to SY and ASY female models, we separately analyzed the number of hovers and attacks on models using a repeated measures design, with SY and ASY models as the repeated measure. We analyzed data from resident males and resident females separately, and for both sexes pooled. We present results from analyses of each sex separately, however, as stated above in some cases the sex of residents could not be identified and so our sample sizes were smaller than for analyses of the sexes pooled. In cases where our results for analyses of each sex differed from those where the sexes were pooled, we present both results.

Tree swallows are known to be most active and defensive around their nest sites in the early morning when the majority of territorial behavior, courtship and nest building occur (Cohen 1984a, Whittingham et al. 1994), so we also used the start time of the presentation and the stage of nest construction as covariates in analyses. Stage of nest construction was scored on a 5 point scale, ranging from a few blades of grass (1) to a completely constructed nest (5). Both intrusion experiments were performed over only a 2-day period, so we did not examine how behavior varied with presentation date. When we presented the models directly on the nest boxes of resident pairs to simulate a more aggressive territorial intrusion, we also included which model (SY or ASY) was presented first and the elapsed time between the presentations, which could influence factors such as the hormonal levels of the resident pairs and thus the aggressiveness of their responses to the intruding models (reviewed in Wingfield et al. 1987). We classified resident females as SY or ASY by their plumage coloration (Hussell 1983), and included female age as a factor in the analyses.

Model Resident Experiment.—We used analyses of covariance (ANCOVA) to examine the effects of model age on the mean intrusion scores, proportion of scores per presentation that included attacks, proportion of scores per presentation that included nest box inspections and number of intrusions per minute into the model territories. To meet assumptions of parametric analyses, we performed inverse-log transformations on the mean intrusion scores, and arcsine-square root transformations on the proportion of scores that included attacks on models. As we were often unable to accurately identify the sex of the intruders, we analyzed data for this experiment without specifically examining the behavior of males and females individually. We examined the level of establishment of neighboring nest boxes by including the highest nest stage (on a 5 point scale; see above) of the two nest sites within closest proximity to our model territories to determine whether intrusions into our model territories could be neighboring Tree Swallows defending their own territories. As presentations were performed over multiple days, we also included date as a covariate because more intrusions may have occurred during earlier presentation dates if more Tree Swallows have not yet acquired nest sites.

All statistical analyses were performed using SPSS (Norušis 2000). Results of two-tailed tests were considered significant at the 0.05 level and means presented ± 1 standard error (SE).

RESULTS

Effects of Intruder Plumage Color on Resident Behavior

Simultaneous Presentations.—When SY and ASY models were presented simultaneously as intruders on poles in front of resident pairs' nest boxes, there were no significant differences in the number of hovers over ASY versus SY models for either resident females (ASY models: 0.82 ± 0.32; SY models: 0.88 ± 0.38; $F_{[1,16]} = 0.05$, $P = 0.83$) or males (ASY models: 1.00 ± 0.32; SY models: 0.59 ± 0.36; $F_{[1,16]} = 1.91$, $P = 0.19$). These results may be the consequence of reduced sample sizes caused by our uncertainty in identification of the sex of residents, because when data were pooled we found that overall, resident pairs hovered significantly more over ASY models (2.19 ± 0.42 hovers) compared to SY models (1.35 ± 0.42 hovers; $F_{[1,25]} = 4.42$, $P = 0.046$). Time of day of presentation ($P = 0.68$), stage of nest construction ($P = 0.59$) and age of the resident female ($P = 0.81$) did not influence the number of hovers. We found that resident females attacked ASY models (3.32 ±

1.53 attacks) more than SY models (0.40 ± 0.24 attacks; $F_{[1,19]} = 9.07$, $P = 0.007$), and that SY resident females attacked both models more, regardless of model age, compared to ASY resident females ($F_{[1,19]} = 9.21$, $P = 0.007$). This analysis also showed that there was an interaction between model age and time of day of presentation ($F_{[1,19]} = 4.97$, $P = 0.038$), and between model age and the resident pair's stage of nest construction ($F_{[1,19]} = 5.71$, $P = 0.027$). To further investigate these interactions, we analyzed data separately for each model age. We found that attacks by resident females on ASY models decreased with time of day of presentation ($F_{[1,19]} = 5.01$, $P = 0.037$), but no relationship was found for SY models ($F_{[1,19]} = 0.01$, $P = 0.98$). Similarly, resident females attacked ASY models more often during earlier stages of nest construction ($F_{[1,19]} = 5.24$, $P = 0.034$), while no relationship was found for SY models ($F_{[1,19]} = 0.26$, $P = 0.62$). Among the resident birds of which we were able to determine their sex, we only observed the resident male attacking an ASY model during one of 25 presentations; although resident males were present in all of these trials, they generally perched on fence lines close to their box and did not attack any of the models.

Separate Presentations.—By presenting ASY and SY models separately as intruders on resident pairs' nest boxes, we further investigated whether intruder plumage color influenced resident behavior by simulating more aggressive territorial intrusions. Resident males did not differ in the number of hovers over ASY (3.17 ± 1.45 hovers) and SY models (1.25 ± 0.69 hovers; $F_{[1,11]} = 1.34$, $P = 0.27$), however, we found a trend for resident females to hover more over ASY models compared to SY models ($F_{[1,11]} = 4.22$, $P = 0.065$; Fig. 1). When we examined residents with sexes pooled we found that they hovered significantly more over ASY models (12.0 ± 2.59 hovers) compared to SY models (5.23 ± 1.33 hovers; $F_{[1,10]} = 8.09$, $P = 0.017$). This relationship also was influenced by which model was presented first to the pairs, such that residents hovered more over the models when ASY models were presented first ($F_{[1,10]} = 7.19$, $P = 0.023$). The age of the resident females, time between the model presentations, and stage of nest construction did not influence the number of hovers over models (all $P > 0.30$). We found that resident females attacked ASY models more than SY models ($F_{[1,11]} = 11.36$, $P = 0.006$; Fig. 2), and

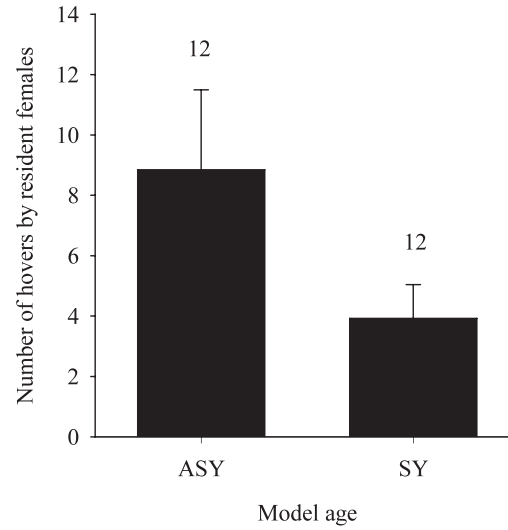

FIG. 1. Mean number of hovers (± SE) by resident female Tree Swallows, over female models with SY or ASY plumage. Models were separately placed directly on resident pairs' nest boxes to simulate an aggressive territorial intrusion. Sample sizes are indicated above error bars. Differences are significant at the $P = 0.05$ level.

that resident females tended to attack more if ASY models were presented first ($F_{[1,11]} = 4.49$, $P = 0.058$). No differences according to model age were found for the number of attacks by resident males (ASY models: 1.26 ± 0.89 attacks; SY models: 0.07 ± 0.07 attacks; $F_{[1,13]} = 2.05$, $P = 0.18$).

Effects of Model Resident Plumage Color on Intruder Behavior

When examining the influence of resident plumage color on intruder behavior, we found that ASY models elicited significantly higher mean intrusion scores ($F_{[1,25]} = 8.76$, $P = 0.007$; Fig. 3b) and a higher number of scores that included attacks by intruding Tree Swallows compared to SY models ($F_{[1,25]} = 25.3$, $P < 0.001$; Fig. 3a). When models were presented near neighboring nest sites at earlier stages of nest construction, they also suffered more aggressive intrusions, as both measures of intrusion were negatively related to the highest nest stage of the two closest neighboring nest sites (mean intrusion score: $F_{[1,25]} = 4.48$, $P = 0.044$; proportion of scores with attacks: $F_{[1,25]} = 6.07$, $P = 0.021$). We did not find any effects of time or date of presentation on mean intrusion scores or the proportion of scores that included attacks on

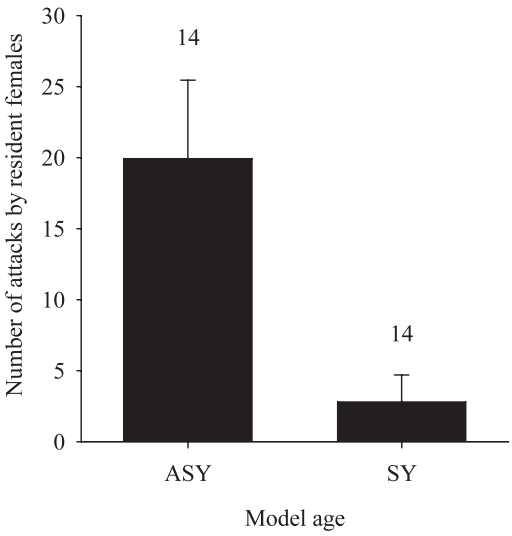

FIG. 2. Mean number of attacks (± SE) by resident female Tree Swallows on female models with SY or ASY plumage when separately placed directly on resident pairs' nest boxes to simulate an aggressive territorial intrusion. Sample sizes are indicated above error bars. Differences are significant at the $P = 0.05$ level.

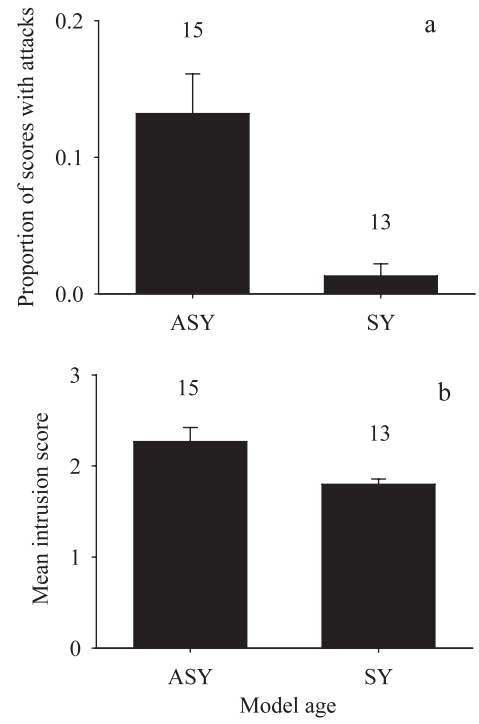

FIG. 3. The mean (± SE) (a) proportion of intrusion scores with attacks and (b) intrusion score of Tree Swallows entering territories with female models having either SY or ASY plumage as territory holders. Differences are significant at the $P = 0.05$ level. Sample sizes are indicated over error bars. See METHODS for details on intrusion scores.

models (all $P > 0.13$). Furthermore, we did not find any relationship between the age of the models and the proportion of scores that included nest box inspections by intruders ($F_{[1,23]} < 0.01$, $P = 0.99$), or the number of intrusions per minute ($F_{[1,23]} < 0.01$, $P = 0.99$).

DISCUSSION

Model Intruder Plumage Color and Resident Female Behavior.—When examining the influence of model plumage color on behavior of resident Tree Swallows, we found that resident females were significantly more aggressive towards ASY models compared to SY models, supporting our prediction (Fig. 1). Our results differ from those of Stutchbury and Robertson (1987a), who found that resident females were equally aggressive to ASY and SY models, and may be because of territories in our population being easier for females to obtain and maintain. During the breeding season, unoccupied nest boxes are dispersed throughout our study sites, with as many as 45% of the nest sites remaining vacant for the duration of the breeding season (O'Brien and Dawson 2007). The increased distance from one occupied territory to another in our population may result in fewer intrusions into occupied territories and may reduce the defensive behavior of females at their nest sites during an intrusion. Therefore, while females in densely populated areas may vigorously defend their nest sites from all intruders, lower density populations such as ours, which are less hostile and have potentially less-defensive resident females, may allow for any potential adaptive function of subadult plumage to be more evident.

The aggressive behavior of female Tree Swallows towards intruding females during the breeding season is believed either to be a means of securing a socially monogamous mate or to prevent territory eviction, neither of which is directly related to the quality of the nest site in terms of habitat or resources (Muldal et al. 1985). The aggressive behavior of resident females towards ASY models supports the hypothesis that ASY female Tree Swallows are perceived as greater territorial threats compared to SY females and therefore elicit more aggressive territorial defensive behavior from resident females. In

female Collared Flycatchers (*Ficedula albicollis*), wing patch size is an honest signal of age and body condition, and predicts the mating strategy of males (i.e., monogamy versus polygyny; Hegyi et al. 2008a). Hegyi et al. (2008b) found that when resident female Collared Flycatchers were presented with model females with varying wing patch size, resident females were more aggressive towards models with larger wing patch size. Since female plumage color is an honest signal of age in Tree Swallows (Hussell 1983), resident females may be more aggressive when defending their nest site against ASY females that are potentially more experienced competitors.

When models were presented simultaneously on poles in front of the resident pairs' nest boxes, we found that SY resident females were significantly more aggressive towards the models compared to ASY resident females. In other species, less experienced breeders have been found to be much more aggressive territory defenders (Landmann and Kollinsky 1995, Schwartz et al. 2007), potentially because of their tenuous ownership of their territories compared to more experienced breeders. There were very few SY resident females (four of 25) in this experiment, however, and while more SYs were present in the second experiment where models were presented separately on nest boxes (six of 14), resident female age was not a factor in their behavior towards the models. Further investigation is required to determine how age of resident females influences their response to intrusions within their territories.

We also found resident females that occupied nests in earlier stages of nest construction were more aggressive towards ASY model intruders when models were presented simultaneously on poles in front of resident pair nest boxes. In Tree Swallows (Whittingham et al. 1994) and other species (e.g., Sandell and Smith 1997) where females are competing for male-occupied territories, as opposed to territories alone, resident females are more aggressive towards intruders during the pre-laying and laying stages of reproduction compared to later in the breeding season. Resident females are believed to be more territorial at this time to prevent nest usurpation from intruding females and to secure their occupancy at their nest site, prior to the pair's further investment in reproduction (i.e., egg laying and nestling stages). If females at earlier nest stages are less secure of their ownership of a nest site, it would seem reasonable for those females to be more aggressive toward any intruders that could potentially usurp their nest site compared to a female that has spent more time securing the pair bond with her mate.

Model Intruder Plumage Color and Resident Male Behavior.—In contrast to Stutchbury and Robertson (1987a), who found that males were less aggressive towards SY females intruding into their territories compared to ASY female intruders, we did not find a significant effect of model age on behavior of resident males. We were unable to determine the sex of residents during some observations, and the possibility that males were more aggressive towards one of the models therefore cannot be eliminated. Nonetheless, non-aggressive behavior of resident males toward the models may be attributable to population differences between our study sites and those of Stutchbury and Robertson (1987a). Stutchbury and Robertson's (1987b) population had a large number of floating females that occupied newly vacant nest boxes within a matter of 10–15 mins after removal of the resident female. Their population also had floating males, indicating limited breeding opportunities for both sexes, and an increased potential for heightened territorial behavior of males in their population (Stutchbury and Robertson 1987b). The males in Stutchbury and Robertson's population may have been highly sensitive to any intruders, regardless of their sex. If so, a male's immediate aggressive response to intruders may increase his chances of remaining at that nest site (Parker 1976) and would outweigh the costs associated with increased territorial aggression (Studd and Robertson 1988, Stutchbury 1992). Furthermore, Leffelaar and Robertson (1985) found that when female Tree Swallows intruded into occupied territories, males would not equally participate in territory defense and would, at times, attempt to copulate with the intruding females. Although socially monogamous, Tree Swallows engage in extra-pair copulations (Lifjeld et al. 1993, O'Brien and Dawson 2007), and a male's lack of defensive behavior at his nest site may indicate his interest in gaining an extra-pair mate or a new social mate, further supporting a role for female aggression in this species.

Model Resident Plumage Color and Intruder Perception of Models.—When examining the influence of plumage color of territory owners on intruder behavior, we found that ASY models suffered significantly more aggressive intrusions

compared to SY models (Fig. 3a, b). We also found, however, higher mean intrusion scores and a higher proportion of scores that included attacks on the models when model territories were situated near neighboring Tree Swallows at earlier stages of nest building. We found similar results when models were presented as intruders and suggest this may be because of tenuous ownership of their territories; it may be that the Tree Swallows that entered the model territories during this experiment were neighboring birds defending their own territories as opposed to birds actively searching for nest sites. Similar to Stutchbury and Robertson's (1987a) results, ours are confounded by the fact that we were unable to identify the sex of all intruding Tree Swallows because of multiple birds simultaneously entering our model territories. Regardless, this does not diminish the fact that ASY models received much more aggressive encounters compared to SY models.

Overall, our findings suggest that subadult plumage is beneficial for SY female Tree Swallows by reducing aggression from conspecific females during the breeding season. Our findings do not address the question of why female Tree Swallows molt into predominantly iridescent blue-green plumage after their first breeding season when it elicits a much more aggressive response from conspecifics. ASY female Tree Swallows with bluer plumage have been found to have higher fledging success and assortatively mate with males based on plumage brightness (Bitton et al. 2008). If males are adjusting their reproductive effort based on their assessment of female quality from plumage characteristics, this may indicate an adaptive function of plumage coloration in ASY females. Further studies should examine the influence of female plumage coloration in terms of territory acquisition and status signaling as well as the influence of plumage coloration with respect to sexual selection using mate-choice experiments.

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