SIGNALING SUBORDINATE AND FEMALE STATUS: TWO HYPOTHESES FOR THE ADAPTIVE SIGNIFICANCE OF SUBADULT PLUMAGE IN FEMALE TREE SWALLOWS

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ABSTRACT.—Delayed plumage maturation in males is relatively common among North American passerines, but the Tree Swallow (*Tachycineta bicolor*) is one of few species in which 1-yr-old females have a distinct subadult plumage. Although they are reproductively mature, most subadult females do not breed in their first year because of intense intrasexual competition for nesting sites. Early in the season, subadult female floaters explore for recently vacated nest sites. The subadult plumage of young females could be adaptive by communicating their low threat to residents, thereby decreasing the cost of this exploration.

To determine whether resident aggression depends on intruder color, we observed live intrusions and conducted model presentations. When the resident female was out of sight or did not respond to intruders, resident males were significantly less aggressive toward subadult females than toward adult intruders in both the nest-building/egg-laying and incubation stages. Early in the season, resident females were equally aggressive toward subadult female and adult intruders. When presented simultaneously with adult and subadult female models, resident males were always more aggressive toward the adult model, whereas females were aggressive toward either model.

We propose two hypotheses for the adaptive significance of subadult plumage in female Tree Swallows: subordinance signaling and sex signaling. Our results suggest that subadult females may reduce resident aggression by signaling their female status to resident males, rather than by signaling their subordinate status to resident females. *Received 18 November 1986, accepted 2 June 1987.*

IN about 30 species of sexually dichromatic North American passerines, males have a dull, often female-like, subadult plumage in their first potential breeding season (Rohwer et al. 1980). Subadult males often do not breed in their first year, even though the delay in plumage maturation is not accompanied by a delay in sexual maturation (Rohwer and Niles 1979, Rohwer et al. 1980, Procter-Gray and Holmes 1981, Flood 1984). Four hypotheses have been proposed to explain the adaptive significance of dull subadult plumages of 1-yr-old males: the cryptic hypothesis (Selander 1965, 1972; Procter-Gray and Holmes 1981), the female-mimicry hypothesis (Rohwer et al. 1980), the status-signaling hypothesis (Lyon and Montgomerie 1986), and the winter-adaptation hypothesis (Rohwer et al. 1983, Rohwer 1986). The summer-adaptation hypotheses assume that young males are at a disadvantage when competing with older males for limited breeding resources, and have a reproductive tactic that favors a dull or female-like plumage rather than the bright plumage of older males. An additional hypothesis, the breeding-threshold hypothesis (Studd and Robertson 1985), predicts that the evolution of delayed plumage maturation in a species depends on the costs to a subadult male of competing with older males for breeding resources, and on the expected benefits of breeding in the first year (i.e. potential lifespan).

Although delayed plumage maturation in males is relatively common, the Tree Swallow (*Tachycineta bicolor*) is one of only a few North American passerines in which a distinct subadult plumage in 1-yr-old females has been well documented (Cohen 1980, Hussell 1983). Subadult females are reproductively mature but have a dull brown-blue plumage on the upperparts, in contrast to the completely iridescent blue plumage of older females and all males. In the Tree Swallow the female delays plumage maturation, rather than the male. Two of the hypotheses for male subadult plumage (female

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mimicry and status signaling) argue that the adaptive significance of the dull plumage of young males is that it evokes less aggression from male residents during competition for territories. Our purpose was to determine whether the dull plumage of first-year female Tree Swallows reduces resident aggression toward these subadult female intruders.

Tree Swallows are secondary cavity nesters, and females compete intensely to obtain limited nesting opportunities (Stutchbury and Robertson 1985), which often results in fights and injuries (Leffelaar and Robertson 1985, Robertson et al. 1986). In our study populations, most subadult females do not breed and are members of a floating population (Stutchbury and Robertson 1985). Thus, subadult female Tree Swallows appear to face selection pressures similar to those for subadult males of other species (Rohwer et al. 1980).

Early in the breeding season, the behavioral tactics of subadult female floaters include extensive exploration of nest sites that are defended by resident pairs (Stutchbury and Robertson 1987b). Subadult females make brief intrusions on many nest sites in succession but rarely gain close access to nest sites. They quickly enter and defend nest sites where resident females have been removed. Subadult females appear to have a facultatively delayed breeding tactic, in that they do not breed unless they can obtain a breeding opportunity that does not involve costly competition with the residents.

Subadults that breed in their first year without incurring the high costs of competition should have a great advantage over subadults that delay breeding for one year (Studd and Robertson 1985). Assuming that the early-season exploratory behavior of subadult female Tree Swallows increases their chances of obtaining a recently vacated nest site, there should be strong selection pressure on those factors that tend to increase the success of the exploratory behavior. Because the costs of an escalated fight are high (Leffelaar and Robertson 1985, Robertson et al. 1986), subadult females could decrease the cost of exploring for nest sites by communicating their low threat to residents (Hansen and Rohwer 1986). To test whether the subadult plumage of females acts as a signal to reduce resident aggression, we examined the response of residents to live and model intruders with adult and subadult plumage.

METHODS

The study was done at the Queen's University Biological Station, near Chaffey's Lock, 50 km north of Kingston, Ontario, during the summers of 1984-1986. Tree Swallows were studied at the New Land (NL) and Northeast Sanctuary (NES) study areas. These populations were about 10 km apart and had been established for at least 8 yr. Throughout this study, the NL had 55-65 breeding pairs, and the NES had 30-40 pairs. The NL had grids of nest boxes mounted on aluminum posts that were distributed over several hayfields with a total area of 10 ha. The NES had both natural nest sites and nest boxes over about 5 ha of shallow, open water.

In all years the contents of each nest site were checked every 3-4 days to determine the nesting stage of the resident pair. Birds were caught with mist nets or nest traps (Stutchbury and Robertson 1986), and each was banded with a Canadian Wildlife Service numbered band and sexed by the presence of a brood patch (female) or a cloacal protuberance (male), or by its behavior at the nest (Cohen 1984). Females with completely iridescent blue plumage on their upperparts were defined as adults, and females with brown-blue plumage on their upperparts were defined as subadults (Hussell 1983). Subadults with less than 50% blue plumage are 1 yr old, and subadult females that have greater than 50% blue plumage (about 20% of all subadults) tend to be 1 or 2 yr old (Hussell 1983). Each captured bird was uniquely marked on the wings or tail with different colors of acrylic paint, so that members of a resident pair could be easily distinguished from a distance.

To observe the response of residents toward intruders, we conducted box watches in the NL and NES in 1984 and the NES in 1985. In each population we observed 10 resident pairs where the female was an adult and where at least one member of the pair was individually marked. Watches were 30 min long and were conducted between 0600 and 1200 every 4-5 days on each of the nest sites throughout the breeding season. An intrusion was recorded when a conspecific entered the territory of the resident pair, defined as an area with a radius of about 15-20 m around the nest site (Robertson and Gibbs 1982, Muldal et al. 1985). For each intrusion we recorded whether the intruder had an adult or subadult plumage and the response of the resident male and female toward the intruder. We classified the behavior of each resident as out of sight (absent, inside nest box), present but no aggressive response, mild response (brief chatter), or strong response (persistent chatter, guarding the nest hole, chasing). Most intruders were not marked with paint, so we could not identify repeated intrusions by the same individual. To minimize the possible lack of independence of those intrusions, we included intrusions in the analysis only if there had not been an intruder of the same color in the previous

5 min. For a given half-hour watch, there were usually only 1 or 2 intrusions by birds of a color that met those criteria; therefore, we considered the response of residents to different intrusions to be independent.

To further quantify resident response to adult and subadult intruders, we presented models to 46 resident pairs in the NL in 1986, where at least one member was marked and the female was an adult. Each resident pair was given one presentation to avoid habituation to the models. Presentations were done between 0600 and 1200 during good weather. We used freeze-dried mounts of a subadult and adult female Tree Swallow in a normal perched posture. Each model was taped to a thin aluminum post 1.5 m high (the height of the nest box) and placed 1 m in front of the nest box with the models 1.5 m apart facing the nest box (Lombardo 1985). We set the models in place when both residents were in sight so each would have an equal opportunity to respond. The position of the models, to the left or right of the nest box, was alternated between presentations. The behavior of the male and female resident toward each of the models was recorded for 5 min using an event-recorder program on a portable Radio Shack TRS80 computer. We defined a resident as being more aggressive toward one model than the other if it spent more time attacking one model or, if there were no attacks, more time hovering over one model. If the difference in time was less than 5 s, then the resident had an equally aggressive response to both models.

RESULTS

Resident response to intruders.—Residents were more aggressive toward an intruder when their mate was not aggressive (out of sight or had no response) than when their mate was aggressive (mild or strong response). For intrusions that occurred when the residents were nest building or egg laying, male response (excluding out of sight) to adult intruders was dependent on the female's behavior (including out of sight) ($\chi^2 = 23.14$, df = 6, $P < 0.001$), but male response to subadult female intruders was independent of female behavior ($\chi^2 = 9.65$, df = 6, $P > 0.10$). Female response (excluding out of sight) was dependent on male behavior (including out of sight) for both adult intruders ($\chi^2 = 35.06$, df = 6, $P < 0.001$) and subadult female intruders ($\chi^2 = 13.26$, df = 6, $P < 0.05$).

To compare resident male and female response to subadult female vs. adult intruders during the nest-building/egg-laying stage, we first controlled for the response of the mate (Table 1). When their mates were not aggressive (out of sight, no response), males were significantly less aggressive toward subadult female than adult intruders ($\chi^2 = 12.89$, df = 2, $P < 0.01$), but females were equally aggressive toward subadult female and adult intruders ($\chi^2 = 0.15$, df = 2, $P > 0.40$). When their mates were aggressive (mild or strong response), neither male nor female response depended on intruder color (males: $\chi^2 = 0.27$, df = 2, $P > 0.50$; females: $\chi^2 = 3.37$, df = 2, $P > 0.10$). For both residents and intruders, chasing is the most costly resident response in terms of risk of injury and energetic cost. When their mates were not aggressive, males chased 23.8% (15/63) of adult intruders, but only 10.4% (5/48) of subadult female intruders ($\chi^2 = 3.31$, df = 1, $0.05 < P < 0.10$). When their mates were aggressive, the frequency of male chases was independent of intruder color (adult: 5/57, subadult: 4/26; $\chi^2 = 0.80$, df = 1, $P > 0.10$). The frequency of chases by female residents was independent of intruder color when the male was not aggressive (adult: 5/36, subadult: 6/26; $\chi^2 = 0.86$, df = 1, $P > 0.10$) and when the male was aggressive (adult: 5/64, subadult: 4/39; $\chi^2 = 0.10$, df = 1, $P > 0.10$).

During the incubation and the nestling stages, male and female responses to intruders were not dependent on each other (χ^2 test, $P > 0.05$), so we did not control for the response of the mate (Table 2). Males were significantly more aggressive toward adult than subadult female

TABLE 1. Percentage of different responses (none, mild, strong) by male and female residents to adult and subadult intruders during the nest-building/egg-laying stage. The total numbers of responses are given in parentheses. Resident responses are separated according to whether the mate was not aggressive (out of sight, present but no response) or aggressive (mild or strong response).

Resident response	Mate not aggressive		Mate aggressive	
	Adult	Subadult	Adult	Subadult
Male	(63)	(48)	(57)	(47)
None	3.2	12.5	45.6	44.7
Mild	39.7	68.8	29.8	34.0
Strong	57.1	18.8	24.6	21.3
Female	(36)	(26)	(64)	(39)
None	5.6	3.8	51.6	33.3
Mild	50.0	53.8	28.1	33.3
Strong	44.4	42.3	20.3	33.3

TABLE 2. Percentage of different resident responses (none, mild, strong) to adult and subadult intruders during the incubation and nestling stages. The total numbers of responses are given in parentheses.

Resident response	Incubation		Nestling	
	Adult	Subadult	Adult	Subadult
Male	(67)	(33)	(50)	(30)
None	7.5	30.3	26.0	26.7
Mild	56.7	45.5	42.0	50.0
Strong	35.8	24.2	32.0	23.3
Female	(17)	(16)	(24)	(18)
None	11.8	12.5	41.7	33.3
Mild	41.2	25.0	20.8	22.2
Strong	47.0	62.5	37.5	44.5

TABLE 3. Frequency distribution of the response [none, more aggressive to adult model (A > SA), more aggressive to subadult model (SA > A), or equally aggressive to both models (A = SA)] of each male and female resident pair toward adult (A) vs. subadult (SA) models presented simultaneously during the nest-building/egg-laying stage.

Male response	Female response			
	None	A > SA	SA > A	A = SA
None	6	6	1	1
A > SA	10	1	5	1
SA > A	0	0	0	0

intruders ($\chi^2 = 27.77$, df = 2, $P < 0.001$) during the incubation stage, but not during the nestling stage ($\chi^2 = 1.14$, df = 2, $P > 0.10$). The lack of a difference in male response to adults vs. subadults in the nestling stage was due to a decrease in male aggression (when their mates were not aggressive) toward adult intruders over the three nesting stages ($\chi^2 = 18.53$, df = 4, $P < 0.001$), rather than an increase in male aggression toward subadult female intruders ($\chi^2 = 4.17$, df = 4, $P > 0.10$).

Resident response to models.—During the nest-building/egg-laying stage, 17 males were more aggressive toward the adult than the subadult model, but no males were more aggressive toward the subadult model (binomial test, $P \ll 0.001$; Table 3). Only 2 of the 31 males tested showed any aggression toward the subadult model (both hovered for less than 10 s), while 7 males attacked the adult model. Female response to the models (excluding ties) depended on whether the male did not respond or was aggressive ($\chi^2 = 7.01$, df = 2, $P < 0.05$). When males did not respond, females tended to be more aggressive toward the adult model (6:1; binomial test, $P = 0.06$), but when males were aggressive toward the adult model, females tended to be more aggressive toward the subadult model (5:1; binomial test, $P = 0.11$). Females attacked the adult model in 2 trials, the subadult model in 4 trials, and both models in 2 trials.

During the incubation stage, we presented models to 15 pairs. Males either had no aggressive response (10), were more aggressive toward the adult model (2), or were equally aggressive toward both models (3). They were never more aggressive toward the subadult model. In contrast, females had no aggressive response (10) or were more aggressive toward the subadult model (5).

We have considered only aggressive responses to the models, but males sometimes attempted to copulate with the models. This behavior could be clearly distinguished from aggressive attacks on the model. A copulating male makes unique vocalizations and holds the nape of the female in its beak while repeatedly attempting to make cloacal contact. Attacking males repeatedly pecked at all areas of the head and neck from either a hovering position or by standing on the model, and never made copulatory vocalizations or attempted cloacal contact. Of the 31 males tested during nest building and egg laying, 6 attempted to copulate with the adult model and 1 with both models. On 4 occasions the male both attacked and attempted to copulate with the adult model, and in 3 of those cases the attack came first. During the incubation stage, 2 males attempted to copulate with the adult model, 1 with the subadult model, and 3 with both models.

DISCUSSION

Resident males were significantly more aggressive toward the iridescent blue adult than toward the brown subadult intruders during both the nest-building/egg-laying and incubation stages. The response of resident females to live intruders did not depend on intruder color, however. Residents' responses to adult and subadult models were consistent with residents' responses to live intruders. Males that were aggressive toward the models were never more aggressive toward the subadult model than the adult model, and in fact rarely showed any aggression toward the subadult model. When males had no response to the models, females tended to be more aggressive toward the adult model, but when males were aggressive toward the adult model, females tended to be more aggressive toward the subadult model. These results provide strong evidence that intruder color has an important influence on the aggressive response of male residents but a relatively small influence on female aggression.

The interpretation of these results is confounded by the fact that the color of the intruder does not always correspond with the sex of the intruder. All subadults are females, but adults could be either male or female (Hussell 1983). It is likely that most adult intruders were males. Most adult intruders did not have paint markings, indicating that they were floaters. In our study populations, the size of the male floating population is probably similar to the size of the female floating population (Stutchbury and Robertson 1985). We found that about 30% of the female floating population was adult females, so the ratio of males to females in the adult floating population should be about 3:1. Assuming that individual adult male and female floaters intrude on nest sites with equal frequency, then the majority of adult intruders were probably males. The extent to which male and female responses to intruders were influenced by the color, as opposed to the sex, of the intruder is difficult to assess. During the model presentations, however, the "intruders" differed only in their color, and males were rarely aggressive toward the subadult model.

The response of resident males to adult and subadult intruders was consistent with the expectation that males should be more aggressive toward male than female intruders. Male intruders are a greater threat to resident males because they could usurp the nest site or attempt to copulate with the resident female. Also, males that allow female intruders access to the territory may have a greater probability of gaining an extrapair copulation (Lombardo 1986). Males sometimes aggressively chased subadult female intruders, however, even when the resident female was out of sight. Resident females were equally likely to be aggressive toward subadult female and adult intruders. Male and female residents defend their nest site from intruders of either sex. Furthermore, there appears to be some division of labor between the sexes in nest-site defense. Residents tended to be more aggressive toward an intruder when their mates were out of sight or had no response than when their mates responded aggressively.

The reduced level of aggression that subadults encounter during intrusions probably is adaptive in that it decreases the cost of exploring for recently vacated nest sites (Stutchbury and Robertson 1987b). How the subadult female plumage acts as a signal to reduce resident aggression is unknown. Lyon and Montgomerie's (1986) status-signaling hypothesis for the adaptive significance of male subadult plumage could apply in part to subadult female Tree Swallows. We suggest that the dull subadult plumage could be an honest signal of subordinate status among females. Because of the intensity of intrasexual competition, resident females should vigorously defend their nest sites from other females (Power and Doner 1980, Gowaty 1981). Subadult females are relatively inexperienced, have a shorter wing length than adult females (Stutchbury and Robertson 1987a), and rarely evict resident females successfully (but see Leffelaar and Robertson 1985). A critical prediction of this hypothesis is that resident females are less aggressive toward subadult female than adult female intruders. Although we did not know the sex of adult intruders, however, our results suggest that female response does not depend on intruder color.

An alternative hypothesis is that the subadult plumage is a signal of female status to resident males. Because adult Tree Swallows are sexually monochromatic, males may have difficulty determining the sex of adult intruders and therefore may treat all adults as threatening intruders (Weatherhead and Robertson 1980). Males probably can identify the sex of adult intruders from behavioral and vocal cues, but this may require relatively long periods of assessment. Assuming that males are less aggressive toward intruders they can identify as females, then a distinctive subadult female plumage could facilitate sex recognition and decrease the aggressive response of resident males to subadult female intruders. A critical prediction of this hypothesis is that males are less aggressive toward subadult female than adult female intruders. Indeed, we found that males were more aggressive toward adult intruders of unknown sex than subadult female intruders, which suggests that sex signaling may be occurring.

These two hypotheses are not mutually exclusive, because subadult females could benefit from signaling both their subordinate status to resident females and their female status to resident males. Other hypotheses to consider for the adaptive significance of subadult plumage in female Tree Swallows include those proposed for subadult plumage in males of other species. Subadult females are not deceptively mimicking the opposite sex (Rohwer et al. 1980) because males have no brown plumage. The cryptic hypothesis (Selander 1965, 1972) predicts that 1-yr-old females with subadult plumage have a lower risk of predation than 1-yr-old females with adult plumage. Because subadult behavior is conspicuous, it is unlikely that the sole benefit of a subadult plumage is to increase crypticity. The winter-adaptation hypothesis (Rohwer et al. 1983, Rohwer 1986) does not seem applicable with respect to competition for food, because in the winter Tree Swallows aggregate in large flocks (Kuerzi 1941), in which adults are unlikely to defend aerial insect food resources from subadult females (Robertson unpubl. data).

If a dull subadult plumage is adaptive for 1-yr-old female floaters, then why do 1-yr-old males lack a subadult plumage? There must be some asymmetry between young males and females in the costs of competing with adults or in their reproductive tactics. Young males may not face as intense competition for nest sites and therefore may have a higher probability of breeding in their first year. Our observations do not support this interpretation, however. The very intense level of intrasexual competition among female Tree Swallows is probably comparable to levels of competition among males. In our study populations, we found floating populations of males (Stutchbury and Robertson 1985), indicating a limitation of breeding opportunities for males, just as for females. Assuming that young males are competitively inferior to older males and that most 1-yr-old males are floaters and explore for vacant nest sites, as do subadult females (Stutchbury and Robertson 1987b), it is unclear why male and female reproductive tactics should differ with respect to plumage color in their first year. Without information on the success of young males in obtaining breeding opportunities and on the behavioral tactics of floater males, it is difficult to develop useful hypotheses for why male Tree Swallows do not have a delay in plumage maturation.

There are many similarities between the reproductive tactics of subadult female Tree Swallows and subadult males of other species. Subadult female Tree Swallows face intense intrasexual competition for mating opportunities, and most subadult females do not breed in their first breeding season (Stutchbury and Robertson 1985). Although the behavioral tactics of subadult male floaters have not been well documented for any species, there is evidence that subadult males actively explore for vacant territories and can quickly replace resident males that are removed (Rohwer 1982), as we have shown for subadult female Tree Swallows (Stutchbury and Robertson 1987b). These similarities suggest that further study of the sex reversal of delayed plumage maturation in Tree Swallows may reveal much about the evolution of delayed plumage maturation in general.

ACKNOWLEDGMENTS

Over the course of this study, we had excellent field assistance from Cathy Cameron, Janet Cox, Anne Davies, Andy McClure, and Tracey Wood. We thank Terry Armstrong, Andy Hurly, and Jim Mountjoy for their comments on the manuscript, and Michael Lombardo for his helpful review. The Queen's University Biological Station provided logistic support, and the Natural Sciences and Engineering Research Council of Canada provided financial support.

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