A TEST OF AN ASSUMPTION OF DELAYED PLUMAGE MATURATION HYPOTHESES USING FEMALE TREE SWALLOWS

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ABSTRACT.—The Tree Swallow (*Tachycineta bicolor*) is one of only two North American birds in which females, and not males, have delayed plumage maturation. The hypothesis that plumage differences are the result of differences in competitive abilities among individuals is tested by comparing brown and blue Tree Swallow females in terms of foraging abilities, as determined by the growth of nestlings under their care without the help of the males, and in terms of body size and nutritional condition. Blue and brown females were not different when comparing the growth and fledging success of nestlings under their care. Blue females were larger and, even after accounting for body size differences, heavier and in better body condition than brown females. While brown plumage serves to reduce male aggression, blue plumage probably serves as a signal of dominant status in intrasexual confrontations. This signalling system is not open to cheating because of the larger size and better body condition of blue females. *Received 26 Aug. 1993, accepted 30 Jan. 1994.*

About 35 species of sexually dichromatic North American passerines have delayed plumage maturation in which males have a dull, sometimes female-like plumage during their first potential breeding season (Rohwer et al. 1980). Although these males attain sexual maturity after one year, they often fail to breed during their first potential breeding season (e.g., Rohwer et al. 1980, Procter-Gray and Holmes 1981, Studd and Robertson 1985, Lyon and Montgomerie 1986). Delayed plumage maturation of females and not males has been reported only for Hooded Warblers (*Wilsonia citrina*) (Morton 1989) and Tree Swallows (*Tachycineta bicolor*) (Hussell 1983). Tree Swallows also differ from other North American passerines that show delayed plumage maturation in that most adults over two years old are sexually monochromatic. Most females in their first potential breeding season are dull brown, but a few are iridescent blue-green, like most older females and all males (Hussell 1983). Although these brown females are sexually mature (DeSteven 1978), few manage to become breeders (Kuerzi 1941, Stutchbury and Robertson 1985).

Several hypotheses have been proposed to explain the adaptive significance of delayed plumage maturation: (1) cryptic (Selander 1965, 1972; Procter-Gray and Holmes 1981), (2) female-mimicry (Rohwer et al. 1980), (3) breeding threshhold (Studd and Robertson 1985) and (4) status signalling (Lyon and Montgomerie 1986) hypotheses. One assumption

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common to these is that differences in plumage are the result of variation in the ability of individuals to obtain breeding opportunities. Using female Tree Swallows, we tested this assumption by examining two factors that could affect both how early females can arrive to the breeding grounds to obtain territories, and their ability to defend these territories thereafter. Blue and brown females are compared in terms of size, nutritional condition, and their ability to raise offspring without male help. We assumed that differences in their ability to raise offspring would be a reflection of the females' foraging abilities. Foraging ability is important when food availability is low, and would affect how early in the spring females can arrive to the breeding grounds.

METHODS

We conducted the study in 1990 at a Tree Swallow colony surrounding two sewage lagoons near Tweed, Ontario, Canada (44°29'N, 77°26'W). This colony has been occupied since 1983. Fifty-three nest boxes (14 × 14 × 33 cm, 3.85 cm diameter entry hole) were available, plus another twelve smaller boxes that were not used in any experiments, although some nestlings from these boxes were used in the first experiment. Each large box was fitted with a bird trap and was approximately 1.5 m above ground, attached to metal or wooden poles. To prevent predation, the poles were fitted with conical metal shields or maintained with copious amounts of grease for the duration of the breeding season. The boxes were placed around the lagoons at approximately 20 m intervals, with the entrance holes all facing south.

The first experiment tested whether blue females were better than brown females at raising offspring. Because the abundance of flying insects changes during the breeding season (Quinney et al. 1986), the procedure involved locating pairs of boxes, one of each pair being occupied by a brown and the other by a blue female, whose eggs had hatched on the same day. The sample size was limited by the availability of such pairs. Females whose plumage was intermediate between brown and blue were not used.

For each such pair, on the morning of day 4 (hatch = day one), nestlings of these two boxes plus all other nestlings in the colony at the same stage of development were weighed and individually marked. In the afternoon of day 4, the two experimental boxes were randomly assigned six young each taken from this pool. One pair of nests received only five young each because only 10 nestlings were available. Assigned young were obtained from the subset of those nestlings banded in the morning that excluded both extremely large and small chicks. Therefore, each female ended up raising relatively uniform-sized young, some of which may have been originally her own. This removed any potential correlations between the quality of parents and their young. The following morning the young were visually checked to confirm that the parents had accepted all young as their own. To remove any confounding effect males might have, by compensatory feeding for example, they were removed on the afternoon of day 5.

Nestlings were checked daily until they fledged or died, and on days 10 and 15 the mass, wing chord, and ninth primary feather length of each young were measured. Differences in the survival and growth of the young at days 10 and 15 and the fledging success were assessed using a Wilcoxon Matched-pairs Signed-ranks test.

Starting in the last week of April 1990, females were sequentially removed from nest boxes. These birds were not the same used in the previous experiment, and again, females

of intermediate plumage were not used. Dissections were carried out to confirm the birds' sex. The birds were then weighed, bagged, and frozen. Birds were collected only during the mornings. All females collected were measured and analyzed to determine if blue females are larger and/or in better nutritional condition than brown females. For each carcass the following structural measurements were recorded: wing chord (mm), ninth primary (mm), left tarsus (0.01 mm), keel length (0.01 mm), body length (mm), and middle rectrix (mm). The birds were then weighed to the nearest 0.01 g, and reweighed after being plucked and after the reproductive organs and contents of the intestinal tract had been removed. The carcass and reproductive organs were dried to a constant mass, extracted with petroleum ether in a Soxhlet apparatus, and then burned overnight in a muffle furnace to determine the amount of ash. The ash value was subtracted from the residue of the ether extraction to determine the ash free lean dry weight, which was used as an index of protein for each bird (Dobush et al. 1985).

Differences in size were analyzed with a MANOVA using all six morphological measurements. To account for body size when comparing body composition and nutrient reserves, a principal components analysis (PCA) was carried out on the correlation matrix of the six morphological measurements, and then each body composition variable was regressed against the resulting first principal component (PC1), which was taken to be an indicator of size (Rising and Somers 1989). The residuals of all significant regressions were added to the respective mean to obtain body condition values adjusted for size (Steel and Torrie 1980). These adjusted values were used to test the effects of plumage color on body composition, using type III sums of squares ANCOVAs with plumage color, date of capture, and color-date of capture interaction effects. Interaction effects were included to test if the effect of color differed depending on the date of capture, and were removed from the model if not significant.

RESULTS

Fourteen clutches were available for this experiment. Two of these, both belonging to blue females, were lost to predators. To obtain balanced analyses, data for the corresponding brown female boxes were removed from all comparisons between the two treatments. Young in any one box were a subset of all those form the colony at the same developmental stage, some of which might have been originally from that same box. It is possible that females preferentially fed their own young; however, there were no significant differences in survivorship between the chicks that remained in the box where they hatched and those that were moved (day 10 $\chi^2 = 0.032$, 1 df, $P > 0.90$; day 15 $\chi^2 = 0.371$, 1 df, $P > 0.50$; fledging $\chi^2 = 0.513$, 1 df, $P > 0.25$).

No differences between brown and blue nests were found in the percent of nestlings surviving to day 10 (Wilcoxon Matched-pairs Signed-rank test, $Z = 1.000$, $P = 0.3173$) or day 15 ($Z = 1.000$, $P = 0.3173$), nor in the number ($Z = 1.4832$, $P = 0.1380$) or percent ($Z = 1.4832$, $P = 0.1380$) of young fledged. However, in four out of five pairs blue females fledged more young than brown females (Table 1).

To account for the initial variation in size when comparing the growth of nestlings, masses, wing chord and ninth primary feather lengths of the

TABLE 1

SURVIVAL OF TREE SWALLOW NESTLINGS RAISED BY BROWN (BR) OR BLUE (BL) FEMALES

Hatch date (June)	Number per nest	Number alive							
		Day 10		Day 15		Fledged		Percent fledged	
		BR	BL	BR	BL	BR	BL	BR	BL
5	6	6	6	6	6	4	6	0.666	1.000
6	6	6	6	6	6	4	5	0.666	0.833
7	6	6	5	6	2	0	2	0.000	0.333
7	5	5	5	5	5	4	5	0.800	1.000
13	6	6	6	3	3	2	1	0.333	0.166

nestlings at days 10 and 15 were regressed separately against masses at day 4. Values adjusted for initial size were obtained using the residuals of these regressions, from which a mean for each nest was calculated. These means were used in Wilcoxon Matched-pairs Signed-ranks tests. No differences in wing chord lengths were found at day 10 ($Z = 1.21136$, $P = 0.2249$) nor day 15 ($Z = 0.4045$, $P = 0.6858$). Comparisons using the ninth primary feather lengths did not produce significant differences either ($P > 0.30$), and showed the same pattern.

Only for mass at day 10 (Fig. 1) was the difference between the two treatments significant ($Z = 2.0226$, $P = 0.0431$). On day 10, nestlings being raised by brown females were heavier than those being raised by blue females. This is the exact opposite of the expected result. These differences, however, were not evident by day 15 ($Z = 0.4045$, $P = 6858$) (Fig. 1).

Blue females were bigger than brown ones when taking all variables into account (MANOVA $P = 0.03$). Except for keel length, the means of blue females were higher than those of brown females and, using univariate tests, only the length of the 9th primary feather differed significantly (Table 2).

To account for body size when comparing body composition and nutrient reserves, a principal components analysis (PCA) was carried out on the correlation matrices of the six morphological measurements. The first principal component (PC1) was positively correlated with all morphological measurements and accounted for 44.8% of the total variance. Except for gonad weight, all regressions of body composition variables against PC1 were significant (Table 3). Values adjusted for size (PC1) were used on all subsequent analyses.

When comparing these size-adjusted values, there were significant color·date interaction effects for carcass weight (Table 4). This indicates that
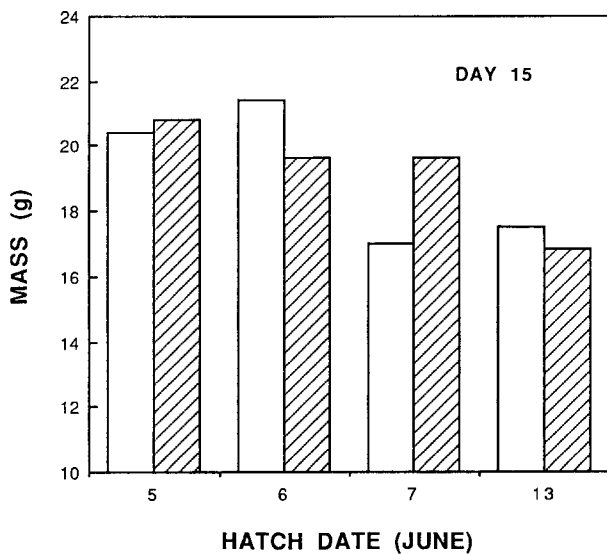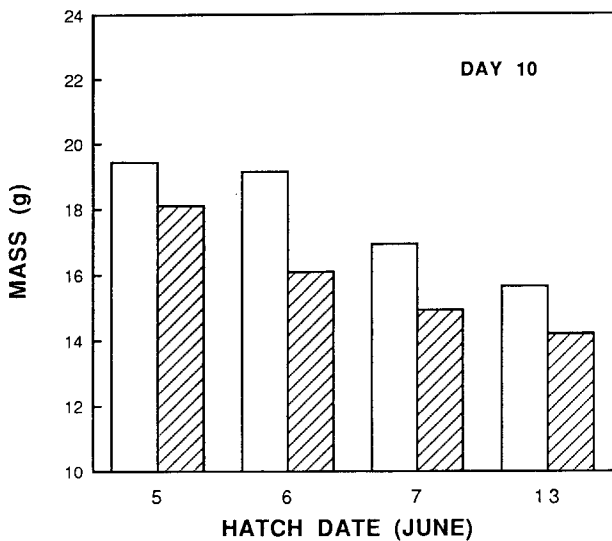
FIG. 1. Mass of Tree Swallow nestlings at 10 and 15 days after hatch. Values were adjusted for mass at day 4. Open bars = brown females, Lined bars = blue females.

TABLE 2
SIZE OF BROWN AND BLUE FEMALE TREE SWALLOWS[a]

Variable	Brown females	Blue females	P
Wing chord	115.9 (0.526)	116.8 (0.436)	0.205
Ninth primary	89.75 (0.445)	91.50 (0.469)	0.009
Keel*	20.64 (0.113)	20.39 (0.100)	0.102
Tarsus	12.16 (0.077)	12.24 (0.079)	0.686
Body	149.64 (0.559)	150.75 (0.442)	0.147
Rectrix	46.64 (0.360)	46.97 (0.309)	0.523

* N = 57 because of one brown female with a broken keel.
[a] A MANOVA using all morphological variables yielded a P value of 0.030. Shown are the mean lengths (mm), SE and P values from univariate F-tests (N = 58; 26 brown, 32 blue).

the effect of plumage color was dependent on the capture date. This was because the mass of blue females did not change during the removal period (linear regression, $P = 0.3248$), but there was a significant drop in mass with time for brown females ($P = 0.038$) (Fig. 2). Similarly, the color·date of capture interaction effects were also significant for both dry mass and fat content (Table 4), but in both cases there were significant ($P < 0.05$) seasonal declines for both brown and blue females.

For ash and protein measures, there were no significant color·date interaction effects. Blue female values were significantly greater than those of brown females (Table 4, Figs. 3, 4). For protein there was a significant seasonal decline ($P < 0.001$, Fig. 3), whereas ash content was significantly higher ($P = 0.016$) in those birds captured later in the season (Fig. 4). There were no differences in gonad mass (Table 4).

TABLE 3
RELATION OF BODY COMPOSITION AND NUTRIENT RESERVES TO SIZE (PC1) IN FEMALE TREE SWALLOWS

Variable	Slope	P	r^2
Gonad mass	0.001	0.939	0.00011
Carcass mass*	0.655	<0.001	0.29122
Dry mass	0.338	0.007	0.19260
Fat	0.165	0.035	0.07968
Ash	0.022	0.015	0.10518
Protein	0.155	<0.001	0.28263

* Feathers, gonads and contents of the alimentary tract excluded; N = 58.

TABLE 4

THE EFFECT OF PLUMAGE COLOR AND DATE OF CAPTURE ON THE BODY COMPOSITION AND
NUTRIENT RESERVES OF FEMALE TREE SWALLOWS VALUES ADJUSTED FOR BODY SIZE WERE
USED IN ALL CASES[a]

Variable	Plumage color	Date of capture	Color-date interaction	r^2
Carcass mass*	0.588	0.068	0.055	0.283
Dry mass	0.032	<0.001	0.006	0.493
Fat	0.013	<0.001	0.019	0.438
Ash	0.003	0.016	—	0.197
Protein	0.050	<0.001	—	0.302
Gonad mass	0.132	0.002	—	0.177

* Feathers, gonads and contents of the alimentary tract excluded.
[a] The interaction term was removed from the model if not significant (N = 58; 26 brown, 32 blue).

DISCUSSION

Differences in foraging ability could be one way in which blue females might have a competitive advantage over brown ones. Brown females are known to have lower egg mass, clutch size, brood size, and fledging
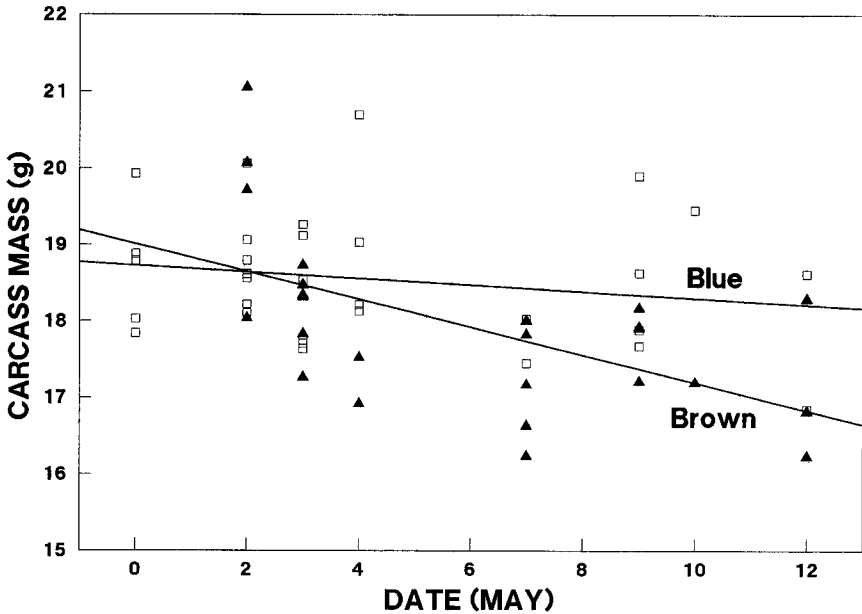

FIG. 2. Mass of Tree Swallow females with respect to plumage color and date of capture. Brown = ▲, blue = □.
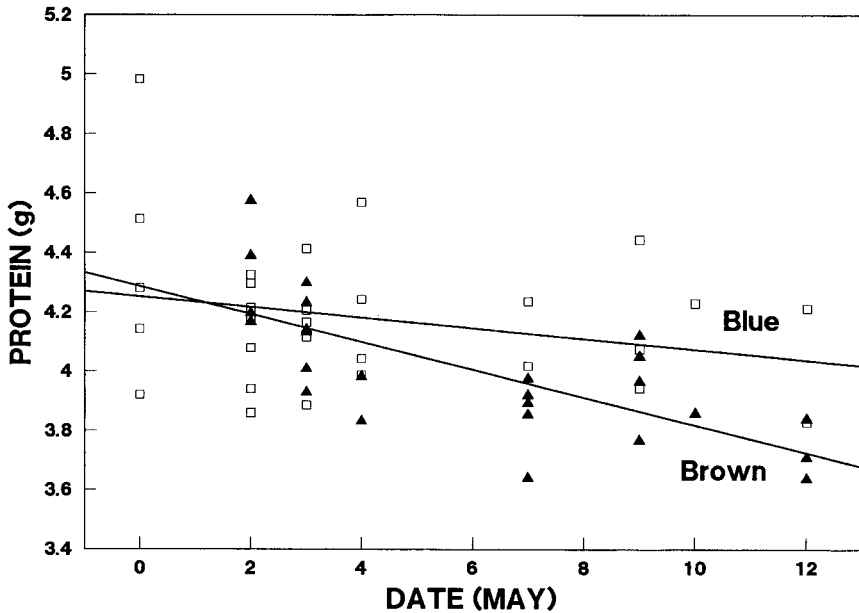
FIG. 3.   Protein of Tree Swallow females with respect to plumage color and date of capture. Brown = ▲, blue = □.

success (DeSteven 1978), but DeSteven (1980) concluded that these were not caused by differences in foraging efficiency because both brown and blue females could easily rear additional young. Her study (DeSteven 1980), however, failed to account for the possibility that males could have compensated for any foraging ability differences that might have existed among females.

In this study the males were removed first, and only then was the growth of nestlings compared. There were no replacement males in any of the experimental nests. Because feather growth of nestling Tree Swallows continues after mass gain has been completed (Zach and Mayoh 1982), it was expected that mass differences would more likely be detected at day 10, and feather growth differences at day 15. Consistent with this, the clearest result across the entire hatch date range was obtained for mass at day 10, but contrary to the predictions, nestlings raised by brown females were heavier than those being raised by blue females. These differences, however, had disappeared by day 15. These results show that brown females who manage to breed are able to deliver food to their young as well as, and sometimes even better than, blue females.

If we accept the notion that, if not due to senility, foraging ability
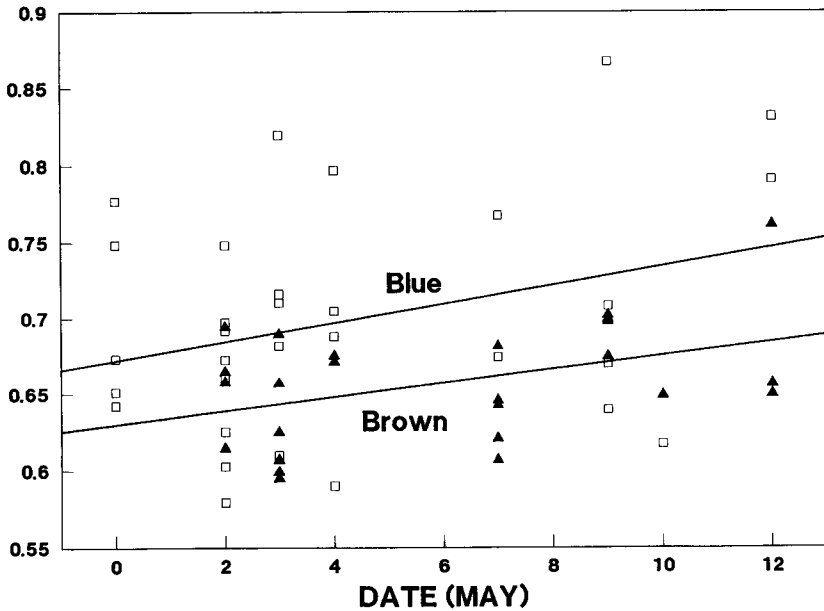
FIG. 4.   Ash content of Tree Swallow females with respect to plumage color and date of capture. Brown = ▲, blue = □.

cannot possibly decrease with age, why did some young raised by brown females grow faster? One possible explanation is that we did not measure foraging ability per se but rather differences in levels of maternal care. There is great variation in feeding rates in swallows as responses to various weather conditions, artificially manipulated brood sizes, and temporary removals of mates (Kuerzi 1941, Leffelaar and Robertson 1986). It is possible that blue females maintain an optimum feeding rate for the conditions in which they find themselves, while brown females simply feed their young at the maximum rate they can. The greater effort of brown females seems to be futile because by day 15 any differences that were observed at day 10 no longer occurred. More importantly, there were no differences in the survival to days 10 and 15, nor in the fledging success.

Another way in which brown females might be at a competitive disadvantage could be in terms of size and nutritional condition. For this part of the study females were collected prior to engaging in reproduction; this eliminated any effects different patterns of maternal care might have on their nutritional condition.

When comparing size, only the length of the primary feather was sig-

nificantly larger in blue females, but the means of all the other variables, except keel length, were also higher for blue females (Table 3). With respect to nutrient reserves, later in the season blue females were heavier and fatter than brown females, but there were no differences earlier in the season. This could be because brown females captured earlier in the season were replacements of previously removed birds, and they are being compared to blue females that had arrived earlier and taken on the costs of nest defense for up to several days, having thus exhausted their reserves. Because the birds were captured as soon as nest building was initiated they were still far from egg laying and no differences in gonad masses were expected. However, differences in protein and ash content indicate that blue females had more resources available to allocate to egg production than brown females. Therefore, blue females could have engaged in reproduction faster than brown females, as soon as the conditions became favorable.

These comparisons were made after correcting for body size, so it is not merely that larger birds are heavier and in better nutritional status. These results indicate that, for any given size, blue females are in better condition than brown females. This could have many implications for their reproductive tactics, perhaps explaining the lower clutch size of brown females (Stutchbury and Robertson 1988). In terms of intrasexual competition for breeding opportunities, a larger and heavier body could affect both the thermoregulation and the fighting ability of females.

Larger birds carry more energy relative to their size and therefore can better tolerate periods of food shortage (Blem 1990). In the study area, night temperatures during April can be low enough for frost to build. These low temperatures, often combined with rain, not only decrease the number and activity of flying insects, but also put swallows under severe thermal stress. Swallows may reduce the demands of thermoregulation by roosting (Stutchbury and Robertson 1990), but continued or extremely low temperatures will unavoidably result in death (Weatherhead et al. 1985, Lombardo 1986a). The larger body size and better condition of blue females should better enable them to withstand these conditions. This also explains why blue females arrive at the breeding grounds earlier than brown females (Kuerzi 1941).

One important advantage of an early arrival is the increased likelihood of obtaining one of the limited number of nest sites. Tree Swallows often engage in violent fights for the possession of nest boxes, which may result in evictions of resident birds (Kuerzi 1941, Leffelaar and Robertson 1985) and sometimes even in deaths (Kuerzi 1941, Lombardo 1986b). There is some anecdotal evidence (Leffelaar and Robertson 1985) showing that, while ignoring empty nest boxes, females fight among themselves for nest

boxes already occupied by males; this suggests that males obtain the nesting cavities first and that females then choose among them. Therefore females may not be limited by the availability of nest boxes per se, but rather by the availability of nest sites with males. Blue females, being in better condition and slightly bigger than brown females, would be at an advantage in any physical confrontations for such nest sites.

Resident male Tree Swallows do not show much hostility towards brown conspecifics, but resident females are equally aggressive towards all intruders (Stutchbury and Robertson 1987). This provides a proximate function for the brown plumage, but it fails to explain why females moult into a blue plumage before their second potential breeding season. Given that brown plumage decreases the aggression from conspecific males, Stutchbury and Robertson's findings have changed the question from: "Why should a female be brown in her first year?", to: "Why should a female be blue in her second year?". There must be some advantage(s) to being blue that outweigh(s) the costs of increased male aggression. While brown plumage serves to decrease aggression from males (Stutchbury and Robertson 1987), blue plumage may function as a signal of dominant status towards females in intrasexual confrontations (Lyon and Montgomerie 1986). For such a signalling system to be stable and not open to cheating, differences in plumage would have to be associated with competitive differences (Rohwer 1982). The fact that blue females were found to be slightly larger and in better body condition than brown females supports this idea.

By definition, color and age are correlated in species with delayed plumage maturation so these results do not negate age as a factor; they simply provide a possible explanation for what it is about age that generally causes Tree Swallow females to be brown in their first potential breeding season and blue thereafter. It would be interesting to determine if blue females are also bigger and in better nutritional status than brown ones among yearlings.

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