FEMALE-LIKE PLUMAGE OF SUBADULT MALE AMERICAN REDSTARTS DOES NOT REDUCE AGGRESSION FROM OTHER MALES

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ABSTRACT.—I used models to test the effectiveness of female-like plumage in protecting second-year male American Redstarts (*Setophaga ruticilla*) from attacks by other males. Territorial males attacked both second-year and after-second-year male models placed in their territories when these models were accompanied by recorded male song. There was no significant difference in the response time nor in the intensity of the attack toward either model. I suggest that the plumage alone of second-year male redstarts does not guarantee reduced aggression from other males as predicted by the Female Mimicry, Juvenile Mimicry, and Status Signaling hypotheses of delayed plumage maturation. *Received 27 July 1990, accepted 26 March 1991.*

MALE American Redstarts (*Setophaga ruticilla*) exhibit delayed plumage maturation. In their first potential breeding season, the plumage of young males is very similar to that of adult females. In spite of their appearance, these males are sexually mature, and some establish territories, mate, and fledge young (Bent 1953, Ficken and Ficken 1967, Procter-Gray and Holmes 1981). Males attain bright orange and black definitive plumage in the subsequent (second) prebasic molt (Dwight 1900, Rohwer et al. 1983).

Delayed plumage maturation occurs in males of 31 of 105 sexually dichromatic passerine species in North America (Rohwer et al. 1980). However, the role of female-like plumage in young males is unclear. Three hypotheses concerning delayed plumage maturation share a critical assumption which is the focus of this experiment. The common critical assumption is that the proximate function of dull or female-like plumage in sexually mature young males provides them protection from the attacks of other males.

The *Female Mimicry Hypothesis* (Rohwer 1978, Rohwer and Niles 1979, Rohwer et al. 1980) proposes that the dull plumage of young males allows them to mimic females, and thus benefit from the tendency of adult males not to attack females. The reduction of aggression by female-like plumage accordingly frees young males to acquire information to be used in future breeding seasons or to enter breeding habitat, where they may establish site dominance and may attract a mate (Rohwer 1983).

The *Juvenile Mimicry Hypothesis* proposes that when dull, juvenile-like plumage is retained in young but sexually mature adults, it deceitfully signals that the subadults are not yet prepared to breed (Foster 1987). Thus they are perceived as less of a competitive threat by older males, who allow the subadults greater access to breeding sites, females, or both than they would if the subadults possessed the definitive male plumage. Although the plumage of second-year (SY) male redstarts is more female-like than juvenile-like, the Juvenile Mimicry Hypothesis could possibly explain or partially explain the adaptive significance of that dull plumage, again, if the critical assumption that older males are more tolerant of birds in second-year plumage is met.

The *Status Signaling Hypothesis* (Lyon and Montgomerie 1986) differs from the mimicry hypotheses in that the dull, female-like plumage of second-year males is regarded as a reliable signal of subordinate status rather than as a deceptive signal. This hypothesis assumes that females will prefer to mate with a bright male rather than a dull one. Because SY males would thus be less attractive to females than after-second-year (ASY) males, the ASYs would achieve little mating benefit by repelling SYs. Therefore they tolerate SYs in dull plumage. This hypothesis assumes further that SYs that "cheated" by wearing bright plumage would lose in contests with older, more experienced males and would have little chance of breeding anyway. The benefit they receive from reduced attacks

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when in dull plumage must outweigh any increased chance of breeding that they might have in bright plumage.

I attempted to test the shared critical assumption of the Female Mimicry Hypothesis, the Juvenile Mimicry Hypothesis, and the Status Signaling Hypothesis in the case of the American Redstart. I tested whether the single factor of plumage coloration, all other factors being equal, could affect the aggressive response of males toward models. If so, then reduction of aggression would appear to be a proximate function of the female-like plumage of SY male redstarts.

METHODS

This study was conducted in 1985 in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, on the gridded study plot described by Holmes et al. (1986).

After-second-year male redstarts began to arrive at the study area on 11 May, although they did not remain in fixed territories until 19 May or later. Females began to arrive on 20 May, and second-year males on 23 May. Model experiments were performed between 21 May and 8 June. These dates included the territory-establishment, mating, nest-building, and early incubation stages of the redstart breeding cycle.

The two models used in the experiment were stuffed mounts of an ASY male redstart and a female redstart. The female was painted slightly orange on its upper flanks with several small black spots on the neck. To the human eye this appeared to be a mount of an SY male redstart. (SY males resemble females in having a drab olive-brown color on the back, but they differ in having an orange tinge on the sides where females have yellow. Second-year males have a variable amount of black spotting on the throat, which is unspotted in females.) Unfortunately, no SY skin was available at the time of the experiment, so a female skin had to be used. Any bias introduced by this substitution would favor the Female Mimicry Hypothesis; compared with the majority of living SYs, this model was more female-like. Both models were mounted in a flight posture with wings spread.

I mapped territories of the color-banded male redstarts resident at the study plot by recording their movements on a gridded map and then connecting the outermost perches observed. Then, for each male tested, one of the models (ASY or SY) was placed in the approximate center of the territory, attached to a branch at a height of 1–2 m. I attempted to place the model in a spot visible from the canopy. I chose the center of the territory to maximize the chance of getting a response from the study male, as boundaries tended to shift on a daily basis, especially in the early, territory-establishment stage of the season. A Mineroff Electronics, Inc., SP5 speaker was concealed beneath leaf litter below the model. A cable connected this speaker to a Sony TCM-5000EV cassette player controlled by the observer, approximately 7 m away from the model.

The experiment commenced when I turned on the cassette player, which played male American Redstart chip notes, accented-ending songs, and unaccented-ending songs (Ficken 1962) for 10 min. These sounds were recorded at Hubbard Brook in previous years. As soon as the tape began, I continuously recorded the location and behavior of the territory owner; and I noted (1) the estimated distance from the model and (2) aggressive displays such as bill wipes, circle flights (Ficken 1962), wing flicks, and pecks. Observations continued for 5 min after the song playbacks ended, and the complete experiment lasted 15 min. The model was then removed.

The experiment was repeated 24 h later in exactly the same location. I played the same taped song sequence at the same volume, but I used the model of the other plumage type. To prevent any bias due to habituation to models or song playbacks, I alternated the order in which the models were presented, so that the number of males that saw the SY model first equaled the number that saw the ASY model first. I tested 21 male redstarts in this manner: 16 ASYs and 5 SYs. If the male did not show any response to the models, that male was not tested further.

The results were analyzed using paired *t*-tests, and the probabilities reported are from a two-tailed Student's *t*-distribution.

RESULTS

General responses to the models.—Nearly all males tested showed some response to the models and recorded song. Only 2 ASYs and one SY did not approach within sight of the observer (2 on the first presentation and 1 on the second), and these birds were omitted from the analyses. Possibly these males had moved off their territories at the time of model presentation. The responses of the remaining males varied in intensity. Some flew to the model within 1 min of the start of an experiment and immediately landed on the model, pecking it on the head and wings and pulling out its feathers. Others approached more cautiously, hopping back and forth on branches above the model, or performing aerial glides over the model. Males sometimes perched near the model and rapidly flicked their wings or wiped their bills on the substrate. Males never appeared to attempt copulation with any model. Attacks were directed at the model itself rather than at the speaker hidden below, and attacks continued

TABLE 1. Time elapsed (s) between initial approach and closest approach to models by individual after-second-year (ASY) and second-year (SY) males during territory establishment and mating (T), nest building (B), and early incubation (I).

Breeding stage	ASY model	SY model	Difference
	After-second-year males		
T	75	16	−59
T	40	7	−33
T	487	265	−222
T	8	2	−6
T	39	5	−34
B	214	0	−214
B	400	35	−365
B	0	653	653
B	430	27	−403
B	170	537	367
B	155	0	−155
B	5	398	393
I	197	197	0
I	316	401	85
Mean (±SE)	181 ± 162	182 ± 221	1 ± 286
	Second-year-males		
B	175	11	−164
B	570	120	−450
B	187	232	45
I	720	398	−322
Mean (±SE)	413 ± 238	190 ± 143	−223 ± 185
	All males		
Mean (±SE)	233 ± 206	184 ± 206	−49 ± 282

after the song ceased. However, responses to the model (SY or ASY) could not be elicited without first drawing the male's attention by playing the song. Apparently males could not see the model until song drew them to the immediate area.

Comparison of responses to ASY and SY models.—If the function of female-like plumage in SY male redstarts is to lower the aggressiveness of males that they encounter, according to the hypotheses being tested, some measurable difference in the intensity of attacks toward the two types of models ought to be evident. There was no obvious, qualitative difference in the behavior of males toward the ASY and SY models, but in order to evaluate the agonistic behaviors quantitatively, I examined three specific parameters:

(1) I measured the interval between the initial approach to the model (within 15 m) and the closest approach. A male's attention is drawn by the recorded song, and then he sees the model. The hypotheses predict that if the model is female-like or juvenile-like, the male ought to hesitate before rushing to attack, either because the identity of the intruder must be more carefully determined or simply because the bright orange and black stimuli that would trigger maximum aggression are absent. In my experiment, this measure varies from 0 s (when the male flew immediately to the model) to 720 s. Contrary to the prediction, the time elapsed was not significantly shorter for the response to the ASY model (Table 1, $t = 0.51$, $P > 0.6$). On average, in fact, the time for attack was shorter for the SY model than for the ASY model, when all responding males are considered. Among ASY males only, the mean time for attack was virtually the same for both models. Thus dull plumage on a singing intruder does not cause male redstarts to hesitate before attacking.

(2) I calculated the proportion of time after initial approach that the male stood on the model and pecked it. Pecking was the most aggressive response of males to the models. If SYs benefited from female mimicry, juvenile mimicry, or subordinate status signaling, SYs ought to elicit less of this response than ASYs. Again there was no significant difference in the behavior of males toward the ASY and SY models

TABLE 2. Fraction of observation period during which males pecked on models. Abbreviations: ASY = after second year; SY = second year; T = territory establishment and mating; B = nest building; and I = early incubation.

Breeding stage	ASY model	SY model	Difference
	After-second-year males		
T	0	0	0
T	0.641	0.489	0.152
T	0	0	0
T	0.632	0.021	0.611
T	0.842	0.807	0.035
B	0	0	0
B	0.150	0.597	−0.447
B	0	0.213	−0.213
B	0	0.379	−0.379
B	0	0	0
B	0	0.075	−0.075
B	0.537	0.233	0.304
I	0	0	0
I	0	0	0
Mean (±SE)	0.200 ± 0.301	0.201 ± 0.258	−0.001 ± 0.251
	Second-year males		
B	0.425	0.409	0.016
B	0.203	0.332	−0.129
B	0.003	0	0.003
I	0	0	0
Mean (±SE)	0.158 ± 0.175	0.185 ± 0.187	−0.028 ± 0.059
	All males		
Mean (±SE)	0.191 ± 0.279	0.198 ± 0.244	−0.007 ± 0.224

(Table 2, $t = 0.09$, $P > 0.9$). Seven males did not peck either model, although they approached them and displayed aggression. Of the remaining 11 males, 6 pecked the ASY model longer and 5 pecked the SY model longer. One male pecked the ASY model but not the SY, and three pecked the SY but not the ASY. The mean difference (Sokal and Rohlf 1969: 331) in paired comparisons between the time spent on ASY and SY models is extremely close to zero (both for all males and for ASY males only), with—on average—very slightly more time spent on the SY model (Table 2). Again, the critical assumption that dull, female-like intruders elicit less aggression than those in ASY male plumage was not supported.

(3) As an index of the average distance of a male from a model throughout an entire presentation period, I used the "distance-of-approach" (D_a) of Studd and Robertson (1985a). The distance scores, which are averaged to yield D_a, are assigned from a logarithmic scale, with the highest score of 10 being an approach of <0.2 m from the model, and the lowest score, zero, being >30.0 m from the model (Studd and Robertson 1985a). Thus the greater D_a, the shorter the average distance from the model or the greater degree of response. Because the behaviors of males near the models were agonistic rather than courtship-oriented, I interpreted a greater D_a as a higher degree of aggression toward the model.

On average the D_a score was slightly higher for the SY model than for the ASY model. Eight of males remained closer to the ASY model, and 10 were closer to the SY model through the period (Table 3). As with the two measures discussed above, there was no statistically significant difference in males' behavior toward the two models ($t = 0.163$, $P > 0.8$). This measure, like the others, indicates no lessening of aggression toward males in dull, female-like plumage.

Behaviors of SY males toward the models.—Four of the males that responded to models in this study were SYs. Three of the four approached the SY model more rapidly than the ASY model (Table 1), which may indicate some hesitancy to attack an older, more experienced male. This implies that female-like plumage does not protect an SY male from attacks from fellow SYs, but it is consistent with the idea that SYs might

TABLE 3. Distance scores averaged over entire 15-min model presentation periods (D_a, Studd and Robertson 1985a). Abbreviations: ASY = after second year; SY = second year; T = territory establishment and mating; B = nest building; and I = early incubation.

Breeding stage	ASY model	SY model	Difference
After-second-year males			
T	2.97	1.53	1.44
T	7.31	6.90	0.41
T	4.97	1.42	3.54
T	8.65	5.64	3.01
T	8.50	9.13	−0.63
B	1.33	1.27	0.07
B	5.22	7.20	−1.99
B	0.64	4.60	−3.96
B	1.25	6.63	−5.38
B	1.53	2.44	−0.91
B	4.14	4.17	−0.03
B	7.76	4.11	3.66
I	0.95	1.63	−0.68
I	2.86	3.19	−0.33
Mean (±SE)	4.15 ± 2.84	4.28 ± 2.43	−0.13 ± 2.50
Second-year males			
B	6.20	7.59	−1.39
B	4.18	6.40	−2.22
B	2.49	1.80	0.69
I	4.53	2.22	2.31
Mean (±SE)	4.35 ± 1.32	4.50 ± 2.53	−0.15 ± 1.78
All males			
Mean (±SE)	4.19 ± 2.58	4.33 ± 2.46	−0.13 ± 2.36

be inferior to ASYs in competition (which is a tenet common to many theories about delayed maturation). One of the SYs did not peck either model, another pecked only the ASY model very briefly, and the other two pecked each model approximately equally (Table 2), in agreement with the general results of this experiment. As a group, SY males had approximately equal average distance-of-approach scores for the ASY and SY models (Table 3). Given the small number of SYs involved, additional study is needed before firm conclusions can be drawn about their responses to models in female-like and ASY-like plumage.

DISCUSSION

The results of my study do not support the critical assumption of the Female Mimicry, Juvenile Mimicry, and Status Signaling Hypotheses. The model in female-like plumage was attacked as quickly and severely as the model in full adult male plumage when shown with song to territory-defending males. There was no indication that the males were "deceived" into treating the SY model as a female or juvenile or that their aggression was allayed by the absence of bright orange and black plumage on the SY model.

This result stands in contrast to several other recent studies of birds' responses to models. Male Red-winged Blackbirds (*Agelaius phoeniceus;* Rohwer 1978), Northern Orioles (*Icterus galbula;* Flood 1984), Yellow Warblers (*Dendroica petechia;* Studd and Robertson 1985a), and Black-headed Grosbeaks (*Pheucticus melanocephalus;* Hill 1989) responded less aggressively to dull or female-like models than to bright adult-male-like models of their respective species.

It was unfortunate that in the dense cover of the Hubbard Brook Forest it was necessary to use song to attract attention to the models. Song clearly is an important cue in eliciting aggressive reactions in birds (see Chantrey and Workman 1984). It might be argued that in natural conditions, SY male American Redstarts might benefit from reduced aggression through female mimicry, juvenile mimicry, or signaling subordinate status if they keep completely quiet or sing very infrequently or differently from ASY males. Perhaps by playing song with the model I "blew the cover" of the SY and prevented mimicry from being effective, or I signaled a higher status than an SY would normally do, bringing on an attack of intensity appropriate for an ASY intruder. However, there are three problems with this argument: (1) Studd and Robertson (1985a) and Hill (1989) also used recorded song in presenting models, and the males tested in their experiments discriminated between dull and bright models. (2) American Redstart second-year males will sing in the wild and will use both the unaccented-ending song and the more aggressively oriented accented-ending song (Ficken 1962). Procter-Gray and Holmes (1981) found that before mating (i.e. when competition to establish territories and obtain mates is most intense) there was no significant difference in the singing frequencies of ASY and SY males. In contrast, females never sing. (3) All three of the hypotheses tested, in attempting to explain the proximate function of delayed plumage maturation, predict that male plumage *alone* should have some effect on the aggression of other males.

Given that the behavior of American Redstarts does not satisfy the critical assumption of the Female Mimicry Hypothesis, Juvenile Mimicry Hypothesis, and Status Signaling Hypothesis, these hypotheses are not likely to explain the adaptive significance of delayed plumage maturation for redstarts, although they may certainly be valid for other species. If the proximate function of female-like plumage is not the reduction of aggression in rival males on the breeding grounds, an alternative explanation is required.

One alternative, the Winter Adaptation Hypothesis, is that the female-like plumage of SY males serves its primary (but unknown) function on the wintering grounds, and that young males are simply stuck with that plumage in the first spring because either insufficient energy is available for a full prealternate molt or such a molt has been difficult to evolve (Rohwer et al. 1983, Rohwer and Butcher 1988). American Redstarts winter in Central America and the Caribbean, where both sexes defend territories (Holmes et al. 1989). Aggressive interactions occur within and between the sexes, although sometimes a male and a female overlap in territory, whereas ASY males never do. It is conceivable that young males could benefit from resembling females on the winter grounds, and female mimicry would be more "convincing" there, because the birds do not sing (Holmes et al. 1989). The Winter Adaptation Hypothesis deserves further study, although it does seem difficult to believe that young males would expend the tremendous amount of energy to fly north to their breeding areas and yet forego a late winter molt, which occurs in several other parulids (Rohwer et al. 1983), unless there were some advantage to their keeping a female-like plumage during the spring.

Ficken and Ficken (1967) attempted to explain the female-like plumage of second-year male American Redstarts as a by-product of delayed sexual maturation (the Delayed Maturation Hypothesis). If there were a high risk of mortality during reproduction, and if young males were generally much less successful in breeding than older males, selection could favor the postponement of breeding attempts until later years (Lack 1954, Selander 1965). This postponement could be achieved by a decrease in the levels of male hormones; reduced aggressiveness, reduced sex drive, and a female-like plumage would result. The problem with this hypothesis is that many SY redstarts breed successfully, and many more attempt to breed. In other words, if selection favors a delay of breeding attempts, it does not work very well.

As another alternative, Procter-Gray and Holmes (1981) suggested that the female-like plumage of young male redstarts is a reflection of a reduced investment (though not complete postponement) in breeding by young males, who because of inexperience are at a competitive disadvantage against older males. Studd and Robertson (1985b) called this the Reduced Investment Hypothesis and greatly improved upon it. If a species has a relatively long lifespan and high levels of competition for breeding in which young males are at a selective disadvantage, then selection should favor reduced investment. This is a lower-cost alternative in which the young males are sexually ready but do not make a full reproductive effort. This reduced investment is reflected in the later arrival of young males at the breeding grounds, and in their dull plumage. Studd and Robertson (1985b) did not specify a function for the dull plumage. Procter-Gray and Holmes (1981) suggested that, because it is more cryptic, dull plumage decreases the risk of predation (leading some authors to call this the Cryptic Hypothesis) (Rohwer et al. 1983). Adult males willing or able to fight harder have a plumage that signals dominance. This hypothesis does not predict that SYs are necessarily given deferential treatment by older males.

The main objection to the Reduced Investment Hypothesis has been that if the function of the young male plumage is simply crypsis, why is it so female-like (Rohwer et al. 1980)? It does not explain why the juvenile plumage is simply retained at the time of the prebasic molt. It could be that some female mimicry occurs in a place other than the breeding grounds (Rohwer et al. 1983, Brown 1984), and this plumage is sufficiently cryptic to serve for concealment in the spring, as according to the Reduced Investment Hypothesis. Alternatively it is easier for young males to molt into a female-like plumage at the time when young females do than for them to molt into a second juvenile-like plumage. Lawton and Lawton (1986) envision that in the ancestral state, both sexes looked alike (resembling adult females of today). Then sexual selection (epigamic or intrasexual) led to male differentiation, so that now males in definitive plumage look very different from females. According to this scenario, male American Redstarts are simply retaining an ancestral plumage pattern in their first year, or they have reverted to it as the simplest path to a relatively cryptic plumage for their second spring.

The proximate function(s) of SY plumage in American Redstarts could be elucidated further by artificially altering the coloration of males in the wild (i.e. painting SYs to look like ASYs, and vice versa), and comparing their breeding success, agonistic interactions, and loss to predation with those of control males. My main proposition is that delayed plumage maturation almost certainly has different functions in different species: the hypothesis that best explains the SY plumage of American Redstarts may not account for the phenomenon in Red-winged Blackbirds, for instance. Further comparative studies of life histories and social structures (e.g. Ekman and Askenmo 1986, Montgomerie and Lyon 1986, Foster 1987, Rohwer and Butcher 1988) are necessary to explain these interspecific differences and to reveal why delayed plumage maturation is found in only a minority of species.

ACKNOWLEDGMENTS

I thank Richard T. Holmes and Thomas W. Sherry for their comments on this manuscript and for helpful discussions as the study was being carried out. T. W. Sherry also provided the models and recordings that were crucial to the experiment. I appreciated the field observations made by Walter Ellison, Whitman Miller, Kevin Omland, Scott Schwenk, Eyal Shy, and Peter Yaukey. These observations enabled me to find enough study animals to conduct the experiment. This study was supported in part by a grant from the National Science Foundation to Dartmouth College. I thank the Northeast Forest Experiment Station, U.S. Forest Service, for permission to work in the Hubbard Brook Experimental Forest.

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