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PASSERINE SUBADULT PLUMAGES AND THE DECEPTIVE ACQUISITION OF RESOURCES: TEST OF A CRITICAL ASSUMPTION

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Males of most species of passerines achieve plumage maturity when less than a year old. However, in 30 of 105 dichromatic species of North American passerines, males in their first potential breeding season either are colored like adult females or are intermediate in appearance between older males and adult females. Two hypotheses have been advanced to explain such subadult plumages: the cryptic hypothesis, best developed by Selander (1965, 1972), and the female-mimicry hypothesis, developed by Rohwer et al. (*in press*). These hypotheses are not mutually exclusive (Rohwer et al. *in press*; Rohwer and Niles *in press*).

According to the cryptic hypothesis, year-old males have a low probability of breeding when competing with older, more experienced males. For this reason they assume a drab plumage, presumably to improve their chances of surviving predation in their first summer. This interpretation has several complications. First, young males of all North American passerines known to have a subadult plumage have mature reproductive tracts and, in many of these species, they regularly hold territories and breed. Second, in all of those which are migrants, the subadult males do return to the breeding ground, thus undergoing the risk of migration despite the presumed poor chance of breeding. Third, in all species having a subadult male plumage, the subadults resemble adult females in every way that they differ from older males; yet in many of these species there appears to be an even more cryptic juvenile plumage. If indeed the subadult plumage represents a cryptic habit, it is hard to explain why the adult female plumage rather than the juvenile plumage is the pattern assumed by subadult males.

These complications suggested to Rohwer et al. (*in press*) that the predominant selective pressure favoring a subadult plumage was an improved chance of breeding when only a year old rather than an improved chance of surviving predation. Under certain circumstances subadult males can improve their resource holding potential by mimicking females and thereby "squeezing" into the best habitat occupied by adult males. This hypothesis requires that: (1) adult males, take prior possession of the best resources needed to breed, thus placing subadults at a competitive disadvantage; and (2) females choose mates by the resources they hold rather than by their coloration. These requisites are supported by the evidence available (Rohwer et al. *in press*).

Copulating with many females must always be an advantage to male passerines. Furthermore, even in species which are normally monogamous, polygyny must often be an advantage to males (but not females), because much of the reproductive effort made by males can readily be divided among several females (Trivers 1972). These considerations suggest that males should be strongly selected not to attack other females who enter their territories. Thus, by mimicking females, subadult males may gain entry into habitat held by adults. This initial residency is thought to give them sufficient site-related dominance advantages that they are eventually able to hold territories among old males and to breed as subadults (Rohwer and Niles *in press*).

Another strategically similar but conceptually different advantage of mimicking females may be that subadults profit from entering the territories of old males without attempting to establish a territory amidst those of older males. At least three mechanisms are possible. (1) Subadults may be present to "steal" copulations. However, it is difficult to imagine how cuckoldry could be evolutionarily stable: lacking a penis, male passerines probably cannot force copulations because female cooperation is likely necessary for sperm transfer. This means that females ultimately control who mates with them. Even if infidelity is sometimes advantageous to females, it is doubtful that they would benefit from infidelity with subadults rather than older, more proven males. (2) Even if females mated to older males occasionally do breed with subadults, such cuckoldry may be so rare that the cost to older males of driving away subadults may outweigh their genetic loss. This is more likely in highly polygynous than in monogamous species, because each individual offspring is a smaller fraction of the season's genetic and parental investment. (3) Subadults may profit from entering the territories of older males by gaining useful information. They could be assessing territories for the following summer or learning by watching older birds.

Perhaps the most dubious assumption of female-mimicry is that older males can be fooled. Deception of older males seems particularly unlikely when subadults are intermediate in appearance between older males and females (see Table 1 in Rohwer et al. *in press*). If anything it seems more likely that an intermediate appearance would signal a status inferior to that of adults. This seems particularly true considering that plumage variability accurately signals dominance status in some species (Rohwer 1975, 1977, Rohwer and Niles in press). If subadults are inferior to adults in escalated fights, the intermediate appearance of subadults should enable adults to perceive that the risk involved in a direct attack upon a subadult is low. If so, the expulsion of a subadult intruder might be even more prompt and vigorous than the expulsion of an adult intruder.

This paper reports a direct test of the assumption that older males can really be deceived by a female-like plumage. The test was performed by presenting adult territorial males of Red-winged Blackbirds (*Agelaius phoeniceus*) with a series of conspecific mounted specimens of both subadult and adult males. According to the female-mimicry hypothesis, specimens of adults would be most strongly attacked, those of more adult-male-like ("studly") subadults next most strongly attacked, and those of more female-like ("unstudly") subadults least strongly attacked. Red-winged Blackbirds were chosen for the test because subadult males look more like adult males than females and because subadults vary in appearance. The fact that subadult Red-winged Blackbirds more nearly resemble older males than females rendered these tests particularly strong because the likelihood that older males really are deceived by such a poor mimic seemed particularly slim. The variable appearance of subadults allowed me to examine whether or not responses from territorial adults were graded according to the brightness of the subadult presented. Besides contrasting aggressive responses to the mounts, I also looked carefully for evidence of the subadult mounts being treated like females.

METHODS

Factors such as individual differences in aggresiveness, weather conditions, and habituation to the mounts contribute noise to the measurement of aggressiveness. Aggressive differences among males were controlled by within-male comparisons. Thus, all differences were analyzed by comparing the responses of the same male to different mounts with paired comparison *t*-tests (Nie et al. 1975). Effects of slight daily variations in weather conditions and possible habituation to the mounts were randomized by alternating, from one territory to the next, the sequence in which the specimens were presented. I attempted to minimize habituation by presenting only a single mount to a territorial male each day. Alternation of the mounts from one territory to the next was not perfect because an adult-subadult comparison was always achieved in the first two days of field work. Thus, in case major weather changes (strong winds or rain) stopped the third day of field work, the fundamental prediction had been tested.

Data were collected in three 3-day periods of field work: 16–18 April, 23–25 April, 21–23 May 1976. In the first two periods, field work was conducted along Winchester Wasteway, 10 km S and 18 km W of Moses Lake, in Grant County, Washington. In the third period, I worked along Frenchman Hills Wasteway, 18 km S and 30 km W of Moses Lake. Because of locality differences and of seasonal changes in aggressiveness, data for the three periods of field work probably should not be compared.

From about 20 subadult male Red-winged Blackbirds, the two studliest and the two unstudliest subadults were chosen for mounting. These were repaired whenever damaged by gluing on matching patches of skin and feathers from other subadults. Since all adult males look similar, repairs were less important for damaged mounts of adults because other mounts could be used equally as well. This was fortunate because the mounts of adults were rapidly destroyed. The birds were mounted on T-shaped bars of wooden doweling that could be inserted into 0.5-in metal conduit pipe for positioning in the field. All were mounted in the song-spread posture because it is the most common territorial display (Orians and Christman 1968).

Field sketches of the experimental territories enabled us to make each presentation in exactly the same place on a territory. Mounts were usually presented within one-half hour of the same time each day. However, on one day of deteriorating weather conditions, the schedule of presentations was advanced about 2 h for the last males tested. As soon as a mount was placed, we would move 40 to 60 m away to an inconspicuous observation post off the territory. On initiation of response to the mount, the timing, intensity, and number of displays in the next 15 min were recorded. We waited up to 30 min for males who were away from their territories when the mount was placed to return and respond. Males present when the mount was placed often began responding immediately, but some required several minutes to cease alarm calling and to direct their attention at the mount.

The following variables were measured. Those which are ritualized displays are described by Orians and Christman (1968) or Nero (1956).

Turns (TURNS)—the number of times the male turned to face in the opposite direction on his perch.

Flight songs (FS)—the number of times a male gave a flight song while over his territory.

Climbs (CLIMBS)—the number of separate bouts of crawling in the vegetation on his territory. Each sequence of movement after a brief pause was counted as a climb.

Flutter flights (FF)—the number of these display flights performed, regardless of their length.

Hits (HITS)—the number of times the male struck the mount. A hit was recorded only if initiated from off the mount; thus, cases where the male simply lost his balance and recovered back onto the mount were not counted.

Song spreads (TOTAL SS)—the number of song spread displays.

Average intensity of song spreads (AV SS)—the average of the intensity of all song spreads seen well enough to score. Intensities were scored on a 1–3 scale, where: 1 was with epaulets scarcely exposed or raised, tail hardly spread, and a vocalization of routine loudness; 3 was with epaulets dramatically raised, wings and tail broadly spread and a loud and complete vocalization; and, 2 was intermediate.

Time in crouch (CROUCH)—the number of seconds the bird spent in the crouch display without regard to intensity.

Time in bill-up (BILL UP)—the number of seconds spent in bill-up display at the mount.

Time on mount (ON MOUNT)—time spent on the mount either pecking at it or displaying from it.

Number of call notes—we were able to distinguish three types of call notes which were described as low chink, high chink, and the flight call. The latter seemed identical to the flight calls normally given by birds in winter flocks as they pass overhead. Following the terminology of Orians and Christman (1968), these seemed to represent, respectively, their *check*, *chick*, and probably *cut*. The number of each of these vocalizations was counted. As Orians and Christman (1968) reported, *check* was far the most frequent of these calls.

Time out of view in cattails (CATTAILS)—often, when displaying or moving in the cattails around a mount, males would slide or hop down into the cattails for varying periods of time; frequently they landed on the ground. Most males disappeared this way in a crouch, with epaulets exposed and somewhat elevated.

Time in brush (BRUSH)—some males simply ceased displaying at the mount and flew off into the surrounding desert brushland. In all cases where such males were seen they were foraging. Sometimes they would leave to accompany (presumably to guard) a female; unfortunately, we did not distinguish these few cases from those in which the male left spontaneously.

ANALYTIC PROCEDURES AND RESULTS

In the 15 min given to respond to a mount, different males performed varying numbers of the preceding 15 behaviors. Some gave mainly bill-ups, some mostly gave song spreads, and others spent most of the time on the mount pecking vigorously at its crown, glass eyes, or clavicular region. To obtain comparable aggressive scores for every type of response to a mount, multivariate statistical procedures were used to linearly combine the original variables into a reduced number of new variables. Such a procedure is useful only when intercorrelations among the original variables indicate a redundancy of ways to measure the same underlying variable. Some of the variables were rather highly correlated. For example, the total number of song spreads was inversely correlated with time spent in the brush ($r = -.61$), and time spent on the mount correlated directly with the number hits ($r = .70$). These, however, were the highest correlations obtained; most were no higher than $|.35|$. Because the data were far from normally distributed, I used Spearman Rank correlation coefficients among variables.

Two multivariate procedures were used in this analysis: (1) principal axes were extracted from the Spearman Rank correlation matrix; and (2) these axes were rotated to a simpler structure using a varimax rotation (Nie et al. 1975, Cooley and Lohnes 1962). Multivariate data reductions are meaningful only if the new combinatory variables are interpretable. Interpreting such factors depends upon at least a partial knowledge of the meaning of the original variables. Variables, such as time on the mount (usually spent vigorously pecking it) or hits cannot be other than a measure of aggression. This is also true of time males spent in the bill up display, since this behavior is directed solely at other males (Orians and Christman 1968). Likewise, the time a male spent foraging in the surrounding upland cannot be considered an aggressive response.

In this study, the problem variables are those used both in courtship and in male-male aggressive interactions, such as number and intensity of song spreads and time spent in the crouch posture. Others such as the number of climbs and turns were also enigmatic. Combinatory variables produced by factor analyses are interpreted by the pattern of loadings given to variables of known meaning. These loadings, together with the loadings given to enigmatic variables, supply secondary hypotheses about the meaning of the enigmatic variables. These secondary hypotheses are usually accepted without testing, but are of course subject to testing. In this study I tested my interpretation of varimax factor I by presenting a mounted female to seven territorial adult males (see below).

The first principal axis is, by definition, that which summarizes the maximum amount of variance. In general, the first principal axis weights all the variables heavily, and such was the case in this analysis. This relatively equal weighting of the original variables often means that they are not being divided into functional groups. On the first principal axis for my data, displays used in aggression between males received positive signs, and those

TABLE 1. Coefficients for factor I from the principal axis analysis and the varimax rotation.[a]

Variable	Coefficients: Principal axis	Coefficients: Varimax rotation
TURNS	–.261	–.374
FS	–.537	–.668
CLIMBS	.286	.199
FF	–.250	–.223
HITS	.753	.769
TOTAL SS	.748	.502
AV SS	.447	.099
CROUCH	.524	.167
BILL UP	.471	.533
ON MOUNT	.788	.795
CHECK	–.293	–.004
CHICK	–.041	–.023
CUT	–.042	–.330
CATTAILS	–.117	–.144
BRUSH	–.721	–.698

[a] The varimax coefficients are from the factor structure matrix and cannot be used to obtain scores (see Nie et al. 1975). In the principal axis analysis, factor I accounted for 23.8% of the total variance.

indicating disinterest in the mount (time in brush) or general agitation (the alarm calls) received negative signs (Table 1). The problem was that no contrast was achieved between displays used both in courtship and in aggression and those used solely in aggression. Thus, time on the mount, number of hits, and time in the bill-up display received high positive coefficients; but the number and intensity of song spreads, as well as time spent in the crouch display, also received high positive coefficients (Table 1). Consequently, purely aggressive responses and responses potentially related to courtship were not distinguished by the first principal axis. This seemed inappropriate for my purposes, since I was testing the prediction that subadult mounts would be treated more like females than the adult mounts. Therefore, the principal axes were rotated to a simple structure. I used a varimax rotation because of the greater simplicity of orthogonal axes; luckily, the plot of character loadings on varimax axes I and II showed no need for a non-orthogonal rotation.

The varimax rotation produced a pattern of positive and negative signs similar to that of the principal axes (Table 1), but the weight given some of the variables known to be used both in courtship and in intermale aggression was greatly diminished. For example, the importance given the average intensity of the song spread (but not the total number of song spreads) and the time spent in the crouch was greatly reduced. Furthermore, the value of some variables of unknown significance, such as the *check* and *chick* alarm calls, diminished in importance, while that of others, such as the *cut* call note and the number of turns, increased. This suggests that functional distinctions among these variables were uncovered by the rotation.

RESPONSES TO THE FEMALE MOUNT

The preceding analysis was based on the intercorrelations among the variables measuring the responses of territorial males to mounts of other males, either adult or subadult. To confirm the validity of my interpretation of the first varimax axis, I presented a studly female (reddish epaulets) to seven territorial males; she was mounted in the song spread posture. The prediction that the response to the adult female should yield high negative scores on the axis was confirmed (Tables 2 and 3).

Males most often responded to the female mount using behaviors associated with both courtship and aggression (average intensity of the song spread, and time in crouch)—the variables of positive sign (i.e., more aggressiveness) which were diminished in importance by the varimax rotation. Generally, soon after the mount was positioned, the male alighted near it and gave a series of intense song spreads (often with wings fully extended); throughout their response, most males remained in a strong crouch. However, direct response to the female mount was often brief, after which the male disappeared into the cattails or left to forage in the sage.

The low weight given the average intensity of the song spreads on varimax factor I, when compared to the high weight for number of song spreads, suggests that aggression is better measured by the number of song spreads than their intensity. This was confirmed by two observations. First, the most intense song spreads were directed at the female mount. Second, those males who spent the most time perched on the mount usually gave the greatest number of song spreads ($r = .47$); they also gave very abbreviated songs, often barely spreading their wings, so the correlation between time on the mount and average intensity of song spreads was nearly zero ($r = .08$). (Attacking males seemed so choked with rage that noisy vocalizations and loose movements were impossible.) We scored such song spreads as of low intensity, despite the fact that the quality of the vocalization indicated great excitement.

RESPONSES TO ADULT VERSUS SUBADULT MOUNTS

The data in Tables 2 and 3 confirm the fundamental assumption of the female mimicry

TABLE 2. Factor I scores from the varimax analysis. Highly positive scores represent more aggressive responses.[a]

Territory number	Adult	Studly subadult	Unstudly subadult	Studly female
1	.676	–.650	.025	–
2	.733	–.030	–.209	–
3	–.803	–.488	–.145	–
4	.661	–	–.198	–
7	.991	–.364	–	–
8	.787	–	.351	–
9	.805	–	.371	–
10	1.041	.826	–	–
12	.900	–.225	–	–
20	–1.771	–.353	–.297	–
21	–1.718	–.049	–1.349	–
22	.608	.631	.692	–
23	1.124	1.793	–.382	–
24	–.188	–.448	–.533	–
25	–.857	–.822	–1.044	–
26	.993	.879	.876	–
27	.888	.354	.406	–
31	–	–	–1.567	–1.350
33	1.619	–	.849	–.638
34	–.419	–	–1.877	–1.024
35	–.779	–	1.308	–1.229
36	–1.325	–	–1.250	–1.253
37	.094	–	–1.000	–1.973
38	–.786	–	–1.650	–1.509
42	–.502	.468	–	–
50	.759	.655	–	–
51	.914	.292	–	–
Mean	.171	.145	–.403	–1.282

[a] In each row are the responses of a single territorial, adult male to the various mounts. Results are listed from earliest to latest, with numbers 1 to 12 from the first study period, 20 to 27 from the second, and 31 to 51 from the third.

hypothesis tested by this work. Adult territorial males responded more aggressively to mounts of other adult males than they did to mounts of subadult males. Furthermore, this was a graded response, the intensity of which was directly related to the degree to which the subadult mount resembled an adult male. Thus, the average difference in the intensity of responses elicited by mounts of adults and of studly subadults was only .078 units on the varimax axis, and not statistically significant ($P = 0.36$; df $= 16$); but the average difference in the intensity of response elicited by mounts of adults and of unstudly subadults was .362 units and significant ($P = .012$; df $=$ 19; see Table 3). Means for TOTAL SS and (time) ON MOUNT—two variables contributing importantly to varimax axis I—help elucidate these differences. TOTAL SS means for the adult, studly subadult, unstudly subadult, and female mounts were 36.1, 34.1, 24.0, and 11.6, respectively; for ON MOUNT they were 371, 209, 112, and 0.

These results also suggest why subadult Red-winged Blackbirds are mostly black. In quantifying the appearance of subadults for North American passerines, Rohwer et al. (in press) scored subadult Red-winged Blackbirds as more adult-male-like than female-like in appearance. To be consistent through the species, the black coloration of adult males had to be presumed to be a signaling color. But subadult Red-winged Blackbirds are much less variable in general body color than in epaulet color and they are much more female-like in epaulet color than in body color. This observation, coupled with the treatment of the unstudly subadult much like a female, suggests that the epaulet is more important as an aggressive signal than black body coloration (Smith 1972, Peek 1972). Possibly black has evolved as the basic body coloration of males, for all temperate marsh-nesting blackbirds, either for the absorption of solar radiation in early spring when food is limiting (Hamilton 1973, Searcy unpubl.) and/or for more effective cooling in windy environments (Walsberg et al. in press).

The fact that the intensity of the aggressive response elicited from adult males ranged from a high directed at the adult male to a low directed at the female mount confirms the anticipated graded response (see the means in Table 2 and, particularly, the averages of paired differences in Table 3). Thus, the seemingly plausible alternative hypothe-

TABLE 3. Average differences in varimax factor I scores (above diagonal) for all combinations of the four mounts and one-tailed probabilities (below) from paired comparison *t*-tests.[a]

	Adult male	Studly subadult male	Unstudly subadult male	Studly female
Adult male	—	.078	.362	1.005
Studly subadult male	.360(17)	—	.183	no data
Unstudly subadult male	.012(20)	.179(11)	—	.168
Studly female	.028(6)	no data	.298(7)	—

[a] Sample sizes are given in parentheses. Differences were obtained by subtracting the score for the mount predicted to elicit less aggression from the score for the mount predicted to elicit more aggression.

sis, that lowered potential risk would evoke a stronger aggressive response, is rejected. Furthermore, the test represents a strong evaluation of the female mimicry hypothesis since an intruding subadult need not (and usually does not) expose his epaulets to the adult male.

I also expected under the female mimicry hypothesis to see evidence of the subadults actually being treated as females. Direct copulation attempts were possible and may have happened on two occasions; however, in neither was I certain that the male was not simply falling down on his tarsi to remain balanced on the mount to peck it.

However, the unstudly subadult male seemed to have been mistaken for a female by some males who happened to be foraging in the sage when it was positioned. On returning to their territories, such males suddenly shifted into a more deliberate and rapid flight when the mount was sighted. At the distance sighted (from 50 to 150 m), all of the male mounts resembled intruding adult males because of their large and dark appearance. If the mount in fact was an adult male, the territorial male usually flew directly into it, striking it violently, and often knocking it askew. On several occasions, when the mount was the unstudly subadult male, the returning male would suddenly brake and wheel frantically in air within a few meters of the mount. Subsequently it would perch nearby and give song spreads of great intensity, similar to those given the female mount.

By examining museum specimens with good skull ossification data, Payne (1969:57) showed that females with reddish epaulets are usually two or more years old, whereas, those without red are usually one-year olds. In many species, including Red-winged Blackbirds, older females produce larger clutches and raise young more successfully than yearling females; thus males should prefer older females as mates (Nice 1937, Lack 1954, Coulson and White 1961, Crawford 1977). This may explain the sudden wheeling of those returning males just before striking the unstudly subadult male mount. Imagine a male attacking the most wonderful female ever attracted to his territory!

SUMMARY

The subadult plumage of year-old males of certain temperate passerines has been hypothesized to be a female-mimicry feature which deceives older males and, thus, enables young males to settle in good habitat. Adult male Red-winged Blackbirds seem to be deceived, despite the fact that subadult Red-winged Blackbirds are poor female mimics. Adults responded very aggressively to mounts of older males and with much less aggression to mounts of subadult males that best resembled females. Bright subadults were treated with intermediate levels of aggression. A system of converting multiple measures of aggression into a single variable by using factor scores from a varimax rotation of principal axes is described. The first rotated axis elucidated an interpretable pattern in the character coefficients; this interpretation was confirmed by a test performed by presenting adult males with a mounted female.

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