

IS THE SONG OF BLACK REDSTART MALES AN HONEST SIGNAL OF STATUS?¹

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Abstract. We analyzed song differences between adults and subadults of the Black Redstart (*Phoenicurus ochruros*) breeding in the Western Alps and found differences both among individuals and between the two age categories. The song parameters utilized for differentiation of individuals were different from those used for adults and subadults. A playback experiment simulating territory intrusion revealed that adults reacted more quickly to the broadcast of an adult song, whereas the reverse was found for subadults. Females did not react to the playback. The results of this study do not support the hypothesis that subadult males mimic female or juvenile behavior (Female or Juvenile Mimicry Hypothesis) nor the Non-adaptive Hypothesis which predicts an equal response to adult and subadult intrusions. We suggest that subadult Black Redstarts honestly signal their status with both visual and acoustic cues. The Status Signaling and the Polyterritorial Deception Hypotheses both seem to explain the data collected for this species.

Key words: age difference, Black Redstart, delayed maturation, *Phoenicurus ochruros*, vocalizations.

In some passerine species, breeding subadult males are clearly distinguishable from adults by their different, typically dull, plumage. Various hypotheses have been proposed to explain the delayed plumage maturation of males. A first set of hypotheses is based on possible adaptations during the reproductive period. According to the Cryptic (Selander 1972), Reduced Investment (Procter-Gray and Holmes 1981), and Breeding Threshold (Studd and Robertson 1985) hypotheses, subadults are not subjected to the ecological (higher visibility to predators) and physiological (lowered immunity) costs connected with bright plumage, but they have to minimize or completely postpone their reproduction. Other hypotheses of an adaptation to the reproductive period propose that dull yearling-plumage evolved to serve a communicative function. Subadult plumages are supposed to reduce the aggression of adult males by deception (Female Mimicry Hypothesis: Rohwer et al. 1980; Juvenile Mimicry Hypothesis: Foster 1978) or by honest signaling of subordinate status (Status Signaling Hypothesis: Lyon and Montgomerie 1986), and subadult males are able to reproduce. Lastly, according to the Polyterritorial Deception Hypothesis (Alatalo et al. 1990), delayed plumage matu-

ration could be maintained if the advantage of male ornamentation was reduced by female choice of less vigorous, but not polygynous, dull males.

A second set of hypotheses concerns the nonreproductive period. According to the Male Competition Hypothesis (Rohwer 1975), the delayed plumage maturation is an adaptation that reduces aggression by adults in the winter territory, whereas in the Molt Constraint Hypothesis (Rohwer and Butcher 1988) this trait is nonadaptive and reflects the fact that yearlings cannot bear the cost of molting the feathers.

The number of hypotheses proposed could lead to uncertainties and be difficult to test because they sometimes lead to similar (or not contrasting) predictions or could be at work simultaneously. Moreover, delayed plumage maturation is likely to have evolved independently in several lines of passerine birds (Stutchbury 1991), thus the explanation of this trait could be different in various species. Weggler (1997) pointed out that some hypotheses (Reduced Investment and Breeding Threshold Hypotheses) try to explore why delayed plumage maturation evolved in some passerine species but not in others, and thus must be tested by cross-species comparisons. The aim of the other hypotheses is to explain the function of dull plumage in subadults and must be tested by intraspecific across-male comparisons.

In the above hypotheses, birds use visual cues in assessing the status of the male. The existence of an acoustic cue that might accompany or replace the visual difference between adult and subadult males has been little studied. Lemon et al. (1994) found that in the American Redstart (*Setophaga ruticilla*), birds can change their vocal repertoire between years, with either additions or deletions of song types. All birds that were subadults dropped some songs used in their first year and added new songs used by adults. In Red-winged Blackbirds (*Agelaius phoeniceus*), repertoire size increases with age and is correlated with reproductive success (Yasukawa et al. 1980), whereas Great Tits (*Parus major*) and Song Sparrows (*Melospiza melodia*) exhibit no change of repertoire size with age (Hiebert et al. 1989, McGregor and Krebs 1989). Payne et al. (1988) found that Indigo Bunting (*Passerina cyanea*) subadults that had the song of a neighboring adult tended to be more successful than first-year males that retained an individual song.

The Black Redstart *Phoenicurus ochruros* is a small passerine that exhibits delayed plumage maturation. Although dull reproducing males were considered extremely rare in the past, it has been recognized in the last few decades that this trait is widespread (Cucco

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and Malacarne 1995). According to Landmann and Kollinsky (1995b), dull plumage in Black Redstart does not reduce aggression toward intruders and is not a signal of fighting ability or aggressive motivation. The Cryptic, Reduced Investment, and Breeding Threshold Hypotheses are not applicable to Black Redstart because subadults regularly breed and do not minimize their reproduction (Cucco and Malacarne 1995, Landmann and Kollinsky 1995a). The dull plumage does not reduce the attack rate by adults in winter (Cuadrado 1995), thus the Male Competition Hypothesis is not applicable. Even if subadults sometimes occupy more peripheral territories (Andersson 1995), they do not try to conceal themselves (Juvenile and Female Mimicry Hypotheses). Thus delayed plumage maturation has been supposed to be nonadaptive in this species (Landmann and Kollinsky 1995a).

In this study, we investigate whether the difference in plumage between subadults and adults is correlated to differential song structure, and if the song of each individual has distinct frequency and time values. Landmann and Kollinsky (1995b) found a similar degree of aggression by adult Black Redstarts to stuffed adult and subadult intruders, but in their experiment the intruder models were placed close to the nests and the cue was visual. Here we have simulated intrusion in male territories with a song playback experiment in order to re-examine from an acoustic point of view the predictions of the Nonadaptive Hypothesis and the Status Signaling Hypothesis that subadult males receive equal (Nonadaptive) or less (Status Signaling) aggression from adults.

METHODS

The research was conducted in the Alps (Susa Valley, NW Italy) during the breeding season from 1993 to 1995. The study area, located between 1,200 and 2,020 m elevation, contains mountain villages where Black Redstarts establish their territories and build their nests in cavities in the external walls of buildings (Cucco and Malacarne 1995, Cucco and Malacarne 1997).

After their arrival from the wintering quarters, birds were captured by mist-nets or spring traps baited with a mealworm, and then individually color-ringed. Subadult males entering their second year of life are clearly distinguishable from adult males, the former having dull brown and the latter black plumage. Subadults regularly breed.

Songs were recorded in 1994 and 1995 with a Sony TC-D5pro recorder with a Sennheiser K3 microphone and an Ecosson 45-cm parabolic reflector. Spectrograms were obtained with the Canary software of Cornell University, Ithaca, New York. From the spectrograms, we measured 11 parameters (Fig. 1): 4 frequencies (F1–F4, Hz), 5 durations (T1–T5, msec), and 2 counts of repeated elements (N1: during T1; N2: during T3).

The identity of perched birds was ascertained from their color-ring combination observed at a distance (about 30–40 m, with 10× binoculars). Usually the recorded individuals were not neighbors (only three adults and two subadults lived in the same village the same year) and all of them were in the before-breeding stage (no activity at the nest). From field tape record-

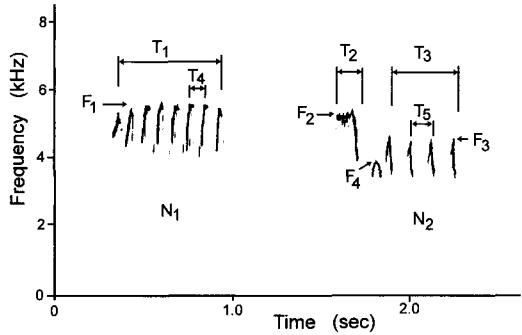


FIGURE 1. Spectrogram of a song of the Black Redstart with the parameters measured in this study (grid resolution set: ± 87 Hz).

ings, we selected 10 vocalizations for each of 20 adults and 20 subadults to be processed by Canary. The 10 vocalizations were chosen from recordings made on different days. For 20 individuals (10 adults and 10 subadults out of the individuals previously considered), a further 10 supplementary vocalizations were recorded to be utilized for cross-validation statistics. Some of the supplementary vocalizations (28% of cases) were recorded on the same day provided they were separated by at least 4 hr.

Statistical analyses were performed by SYSTAT. We conducted discriminant analyses to classify individuals on the basis of the parameters measured on spectrograms. A cross-validation procedure was then performed on the supplementary record set to check the success of classification.

PLAYBACK EXPERIMENT

From a 1993 sample of vocalizations of Black Redstarts, one song of an adult and one of a subadult were selected to be utilized in playback experiments. The selected songs had the lowest background noise. Because we did not utilize more than one exemplar of each class of vocalization (see McGregor et al. 1992), and to avoid the possibility that our exemplars were not representative, we tested whether or not their time and frequency values belonged to the two male categories by comparing the expression: (selected song value – mean category value)/SD, to the tabular t_{α} value (Sokal and Rohlf 1995). The mean category values for subadults and adults are reported in Table 1. None of the frequencies and times differed from the mean values ($P > 0.10$). The two songs were transferred to a Kenwood DX7 digital tape recorder (DAT) and, in the field, the DAT was connected to a Sony SRS-77G amplified speaker for broadcasting. The output level was set at 70 dB at 1 m distance (measured with a Bruel and Kjaer 2230 sound level meter), a value that matched by ear the amplitude of natural singers. Experiments took place in the 1995 breeding season. Tested birds were unlikely to be familiar with the songs presented because the two recordings were made two years before the experiment and most tested territories were located in different villages.

In the three days preceding the playback, at least

TABLE 1. Parameters of the songs of 20 adult and 20 subadult male Black Redstarts.

Parameter	Adults ^a ($\bar{x} \pm SD$)	Subadults ^a ($\bar{x} \pm SD$)	<i>t</i> (or <i>U</i> ^b)	<i>P</i>
T1 (msec)	731 \pm 188	541 \pm 139	3.6	<0.001
T2 (msec)	212 \pm 121	152 \pm 96	1.7	ns
T3 (msec)	226 \pm 144	708 \pm 157	10.1	<0.001
T4 (msec)	79 \pm 5.2	78 \pm 30	0.09 ^b	ns
T5 (msec)	125 \pm 63	124 \pm 20	0.49 ^b	ns
F1 (kHz)	5.50 \pm 0.12	5.47 \pm 0.23	0.21 ^b	ns
F2 (kHz)	5.06 \pm 0.11	4.62 \pm 0.19	29.0 ^b	<0.001
F3 (kHz)	4.43 \pm 0.19	5.23 \pm 0.16	14.6	<0.001
F4 (kHz)	3.90 \pm 0.09	3.79 \pm 0.23	4.1 ^b	<0.05
N1 (N)	8.27 \pm 1.02	5.57 \pm 0.71	9.7	<0.001
N2 (N)	2.66 \pm 0.21	5.45 \pm 0.56	29.3 ^b	<0.001

^a Each individual contributed only one value (the mean of all its songs) to the statistical analysis.

^b Chi-square values from the Mann-Whitney *U*-test are reported because variances were not homogeneous.

two inspections were made in each Black Redstart territory in order to detect the males that were actively singing and their singing posts. Playbacks were broadcasted for 5 min from a central location with respect to the singing posts. The response to the stimulus was registered in the field as the time elapsed before the territory owner replied by singing to the taped song. The distance of the bird to the speaker was not recorded because it was found that the males usually responded from any prominent point they could find near the area where they were at the start of playback and rarely approached the speaker location. Each individual was subjected to only one test.

Males were assigned to four playback categories: (1) adult subjected to adult playback, (2) adult subjected to subadult playback, (3) subadult subjected to subadult playback, (4) subadult subjected to adult playback.

RESULTS

DIFFERENCE BETWEEN ADULT AND SUBADULT SONG

Adult male song differed significantly from subadult song in 7 of the 11 parameters (Table 1). Adult males had a longer first part of the song (T1), whereas subadults had a longer final part (T3). These different lengths were due only to a correspondingly higher number of N1 elements and a lower N2 number in adults, because the time elapsed between elements (T4 and T5) was not different in the two male categories. Frequency values did not differ in the first part of the song (F1), but were significantly different in the middle and last parts (F2, F3, and F4).

In the discriminant analysis, only one canonical factor was extracted for separation of age-class. The parameters that loaded highest were N2, F3, T3, F2, and N1 (loadings: -0.592, -0.488, -0.400, 0.330, and 0.327, respectively). The success of classification of age-class from the songs was high: 99.5% of songs were correctly assigned to adults and 100% to subadults. Indeed, only 1 out of 400 songs was incorrectly classified. When the cross-validation procedure was performed on the adult and subadult supplementary record sets, all 200 songs were correctly classified.

The most important frequency and time parameters

for discrimination of age-class were not the same ones that discriminated individuals. For adult males, the highest loading parameters that differentiated individuals were T1, F1, F4, T5, and T4 (in order of magnitude), whereas in subadult males the parameters were F1, T1, T4, T2, and F4. The success of classification of individuals from their songs was high: 88% of songs were correctly assigned to individuals in adults ($\chi^2_1 = 93$, $P < 0.001$) and 85.3% of songs in subadults ($\chi^2_1 = 148$, $P < 0.001$). When the cross-validation procedure was performed on the supplementary record set, a high success in classification also was found both for adults (65% correct; $\chi^2_1 = 8.4$, $P < 0.001$) and for subadults (79% correct; $\chi^2_1 = 32$, $P < 0.001$).

PLAYBACK EXPERIMENT

Only males responded to the playback. The response percentage was high, ranging from 66.7% of individuals for broadcasting of adult song to 85.2% for subadult song (Fig. 2). The latency to respond to the playback differed between adult and subadult male Black Redstarts. These two age-categories responded more quickly to the playback of the song of the same age category. When the adult song was broadcasted, 56% of adults but only 22% of subadults replied within 3 min ($\chi^2_1 = 6.3$, $P < 0.05$). When the subadult song was broadcasted, only 44% of adults replied quickly, whereas 82% of the subadults responded within 3 min ($\chi^2_1 = 7.9$, $P < 0.005$; Fig. 2).

DISCUSSION

The song of Black Redstart subadult males have frequency and time values very different from those of adult males; thus these two age-categories are clearly statistically discriminable. In our playback experiment, adult males showed more rapid response to the adult song, whereas subadults replied more quickly to subadult song.

The differences in song parameters between age-classes seems to be well established in our study population. Some confounding factors proposed to explain differences in song (such as differential mating status, different breeding stage, physical properties of the habitat, repertoire matching between neighboring birds) are unlikely to operate in our study area. Differences

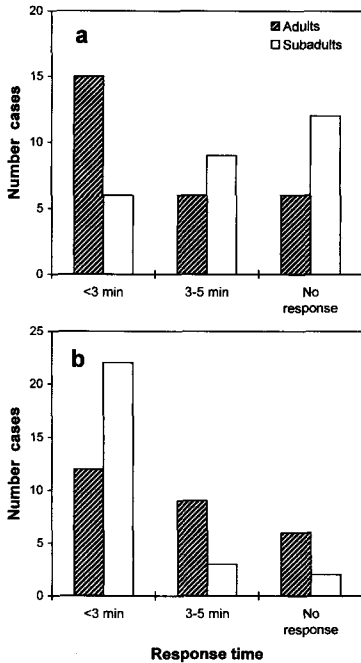


FIGURE 2. Response of adult and subadult male Black Redstarts to the playback of the song of (a) an adult male and (b) a subadult male.

in mating status (Staicer 1996) and breeding stage (Brindley 1996) could affect the song characteristics of the Black Redstart, in which a high number of unmated subadults is observed (Andersson 1995, Landmann and Kollinsky 1995a, Weggler 1997). However, our study concerned only before-mating males. Differences in the physical properties of the habitat (Williams and Slater 1993) can be excluded because there were no differences in the territories occupied by the two male categories (Cucco and Malacarne 1995). Repertoire matching (McGregor 1986) should affect mainly birds living in clumped territories, a situation that does not apply to our Black Redstart study as we recorded individuals located in villages far from each other.

As reported by Landmann and Kollinsky (1995b) for their experiment with Black Redstart stuffed intruders, we observed a strong male response to intrusions, but in our study the cue for detection of strangers was acoustic. Nevertheless, it should be emphasized that Landmann and Kollinsky did not find any influence of the age of the intruders (assessed by the plumage of stuffed males) on the reaction of the territory owners. In contrast, we did find a different response in relation to the age of the intruder (assessed by the song utilized in the playback).

There could be various reasons for the different results of the two studies. First, the three protocols employed by Landmann and Kollinsky had some characteristics that could make it difficult to interpret the results: in two experiments the birds were attracted to-

ward the stuffed males by the broadcasting of a tape recording, but the song utilized was always that of an adult male (Landmann, pers. comm.); thus there was no matching of the visual and acoustic stimuli. The similar aggressiveness toward dull or black stuffed birds, after the song-attracted territory owners had reached the dummies, could have been caused by a previous acoustic perception of an adult intruder in both situations. In a third experiment, the visual stimulus was not accompanied by the acoustic one, but the stuffed males were mounted in a conspicuous position near the nest (2–3 m distance). In this experimental condition, it might be difficult to differentiate aggressiveness in relation to intruder age, because all birds should react equally to the intruders so near their nest.

Another explanation for the different results could be the difference in territory quality in the two study areas. In the Austrian Alps, the adult males were reported to occupy better, more central territories than the subadults (Landmann and Kollinsky 1995a), whereas in the Italian Alps no difference in territory centrality was found (Cucco and Malacarne 1995). In the first area, adult males could be more motivated to defend their high-quality territories and subadults could tend to invade them more frequently, thus eliciting a high aggressiveness from the adults. In the second area, the adult territories do not have a higher quality than the others and the subadults could have a lower intrusion rate, thus being more easily tolerated. Whatever the explanation, it is difficult to draw decisive conclusions from the present data.

From a comparison of the results of Landmann and Kollinsky (1995a, 1995b) and the present study, it could be inferred that in the Black Redstart the song is as important as chromatism for the assessment of territorial intrusion. In the Pied Flycatcher (*Ficedula hypoleuca*), when the acoustic and visual stimuli presented to territory owners in intrusion experiments pertained to the same age category, the subadult intruders elicited less aggression than the adult ones (Huhta and Alatalo 1993). In another experimental study, on the Black-headed Grosbeak (*Phaeucticus melanocephalus*), there was no voice and plumage matching because adults and subadults appeared to have similar songs (Hill 1989). Unfortunately, no other studies have investigated the existence of a different response to songs between age-categories in species with delayed plumage maturation. However, because differences in voice features have been described in another two species, the Indigo Bunting (Payne 1982) and the American Redstart (Lemon et al. 1994), we predict that this trait should be widespread in species with male dichromatism. We expect that the visual signal of status (plumage) is not contradicted by the acoustic signal. In contrast, in the species without delay in plumage maturation, there are only small, if any, differences in song between age classes. Although it has been found that the song is an important cue in male quality assessment (Lambrechts 1992), a clear-cut difference between first-year and older males has not been recognized in non-dichromatic species.

In conclusion, we highlight two characteristics of the Black Redstart: there is no deceptive mimicry of songs (*sensu* McGregor and Krebs 1984), and subadult

Black Redstarts honestly signal their age, both with visual and acoustic cues. The Status Signaling Hypothesis (Lyon and Montgomerie 1986) and the Polyterritorial Deception Hypothesis (Alatalo et al. 1990) could explain the data. Paternity assessment and experiments on female preference are needed to decide between these two adaptive hypotheses.

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DISTRIBUTION AND DIURNAL BEHAVIOR OF STELLER'S EIDERS WINTERING ON THE ALASKA PENINSULA¹

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Abstract. We studied the distribution and activities of adult Steller's Eiders (*Polysticta stelleri*) during winter and spring on a deep-water embayment and a shallow lagoon along the Alaska Peninsula from September 1980 to May 1981. During the remigial molt, eiders were observed on Izembek Lagoon but not on Cold Bay. Following the flightless period, Izembek Lagoon continued to support 63–100% of eiders encountered during surveys. As ice cover on Izembek Lagoon increased, the number of birds decreased on Izembek Lagoon but increased on Cold Bay, suggesting that some eiders disperse to nearshore, deep-water habitats in close proximity to Izembek Lagoon during severe weather. Diurnal activity budgets indicated that the amount of time resting or engaged in aggression and alert activities was similar among locations, seasons, tidal stages, and sexes. In contrast, time spent foraging differed among seasons and locations but did not differ among tidal stages or sexes. Although time spent foraging was similar during winter and spring on Izembek Lagoon, eiders on Cold Bay foraged more during winter compared to spring. Synchronous diving was the dominant foraging strategy.

Key words: Alaska Peninsula, Izembek Lagoon, *Polysticta stelleri*, population distribution, Steller's Eiders, winter habitat use.

Steller's Eiders (*Polysticta stelleri*) winter in three geographic areas: Alaska, northeast Asia, and northern Europe. Of these, the Alaskan population is the largest. Jones (1965) estimated 200,000 Steller's Eiders once

wintered along the Alaska Peninsula, but estimates declined to less than 65,000 in 1991 (Kertell 1991). In 1997 the U.S. Fish and Wildlife Service (USFWS) listed the Alaska breeding population as threatened (USFWS 1997).

The Alaskan wintering range extends from Kodiak Island (Islieb and Kessel 1973) west along the northern and southern sides of the Alaska Peninsula (Jones 1965, Petersen 1981) to the eastern Aleutian Islands (Troy and Johnson 1987). Within this region, most Steller's that breed in Siberia molt in the shallow embayments of Nelson Lagoon and Izembek Lagoon (Petersen 1981). Izembek Lagoon also is one of the major wintering areas in the world (Jones 1965).

This study was conducted on Izembek Lagoon and adjacent Cold Bay from September 1980–May 1981. The objectives were to (1) use aerial surveys to document the chronology of use and importance of different wetland types (bays, shallow lagoons) for postbreeding Steller's Eiders and (2) determine whether diurnal activities of adult Steller's Eiders differed among wetland types. Although shallow lagoons are heavily used by postbreeding eiders (Jones 1965, Petersen 1980, 1981), bays also are utilized (Bauer and Glutz von Blotzheim 1969, Troy and Johnson 1987) but have received little research emphasis. In particular, investigations regarding the use of eelgrass (*Zostera marina*) lagoons and bays in close juxtaposition have not been published, and detailed studies of the world's largest postbreeding population of Steller's Eiders are lacking (Jones 1965).

METHODS

STUDY AREA

Izembek Lagoon, a shallow embayment on the north shore of the Alaska Peninsula, is 41 km long, varies

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