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Territory Defence in Black Redstarts, *Phoenicurus ochruros*: Effects of Intruder and Owner Age?

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LANDMANN, A. & KOLLINSKY, C. 1995: Territory defence in black redstarts, *Phoenicurus ochruros*: effects of intruder and owner age? *Ethology* 101, 121–129.

Abstract

European black redstarts, *Phoenicurus ochruros*, vigorously defend all-purpose territories and exhibit delayed plumage maturation, most subadult males looking exactly female-like in their first breeding season. We tested the hypotheses that such dull subadult male plumages are beneficial in order to reduce aggression of adult males either by deception or by honest signalling of subordination status, and that, in turn, conspicuous (adult) plumage colorations are able to intimidate contenders because they act as a signal of fighting ability and aggressive motivation. Adult and dull yearling black redstart territory owners were confronted with intruders mimicked by stuffed mounts of either a conspicuous adult or a dull subadult male. Our results do not support the hypotheses tested: dull plumages of young intruders did not reduce aggression from adult territory owners and aggressiveness towards intruders was significantly higher in yearling territory owners as compared with adult owners. Conspicuous intruders did not deter dull territory owners and we found no indications that conspicuous male coloration is a signal of fighting ability or aggressive motivation in this species. Instead, the amount of aggressive response to intruders showed considerable individual variance within age classes regardless of the plumage of the intruder and the status of the owner.

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Introduction

The phenomenon of delayed plumage maturation (DPM) in birds, where males do not develop fully adult plumage until their second year of life but are sexually mature and capable of breeding as yearlings, has provoked many conflicting hypotheses in order to understand the evolution and possible functions of predefinitive, mostly dull male plumages (ROHWER & BUTCHER 1988; ENSTROM 1992). Most theories which claim an adaptive value of DPM in the breeding season propose that dull subadult male plumages have evolved to serve an intraspecific

communication function, i.e. to reduce aggression of adult males either by deception (female mimicry, ROHWER et al. 1980) or by honest signalling of subordination status (LYON & MONTGOMERIE 1986). Basically, both hypotheses predict that young males in dull plumage elicit less aggression and are thus more successful e.g. in obtaining territories and mates than they would be if they had an adult (or more adult-like) plumage. From the viewpoint of a territory owner, on the other hand, a conspicuous (adult) plumage coloration is expected to be beneficial, if plumage brightness acts as signal of fighting ability (ROHWER 1982) and/or aggressive motivation (STUDD & ROBERTSON 1985), because owners that are good fighters will intimidate intruders. For conspicuous coloration to maintain this intimidation function, the badge must be a reliable signal of fighting ability and aggressiveness. Therefore it is also predicted that dull-coloured young territorial males are less aggressive towards intruders than conspicuous adult males (STUDD & ROBERTSON 1985).

In several passerine species, dummy model and live bird presentations to territory owners as well as plumage-dyeing experiments have been used to test for these communication functions. However, most of these studies refer to semicolonial and colonial breeding species or/and to species mainly defending small nest site areas (ROHWER 1978; FLOOD 1984; STUTCHBURY 1991, 1992; ENSTROM 1992; HUHTA & ALATALO 1993) and only few experiments (STUDD & ROBERTSON 1985; PROCTER-GRAY 1991) have involved species with all-purpose territories, where aggressiveness may have different levels or functions. European black redstarts, *Phoenicurus ochruros*, vigorously defend all-purpose territories and exhibit DPM where about 90 % to 95 % of subadult males look like females in their first breeding season (LANDMANN 1987b). In a long-term population study with this species we have found no support that dull subadult plumages are of benefit in the first breeding season because dull yearling males, in contrast to the few brighter-coloured subadults, were forced to settle in peripheral and in lower-quality habitat where mating and reproductive success was lowered (LANDMANN & KOLLINSKY 1995).

Here we present preliminary results of model experiments with stuffed male dummies presented to conspicuous adult and dull yearling territory owners. We investigated: 1. whether adult territory owners behave more aggressively towards intruders than young territory owners; and 2. whether dull models are treated less aggressively than bright models by adult and young males respectively.

Methods

Our study was carried out in 1991 near Innsbruck, Austria, in two adjoining mountain villages. Males were trapped and colour banded as soon as possible after their arrival from wintering grounds and territories were intensely surveyed during the entire breeding season.

Experiment 1

Our main experiment (exp. 1) took place between territory establishment and incubation and thus includes the time of highest territorial aggressiveness (LANDMANN, unpubl. data). Males were tested within 14 d after territory acquisition. As adult males on average arrive 2 wk earlier on the breeding

grounds than young males (LANDMANN 1987a; LANDMANN & KOLLINSKY 1995), this experimental period lasted from 1 to 28 Apr.

Stuffed mounts of either an adult male black redstart or a female-like dull subadult male were presented to territory owners, while at the same time broadcasting redstart song phrases. To avoid risks of pseudoreplication we used only two stuffed models of each type, each of them mounted in identical neutral postures. Models were placed in the approximate centre of a male territory and mounted on a 1.5 m stand with a compact speaker attached to the stand below the dummy, and a tape recorder at the bottom of the stand. Each trial lasted 9 min. The experiment commenced after the observer had retreated to a concealed position 15–20 m from the mount. The presentation started with the broadcasting of a 90-s sequence of redstart song phrases (12 bouts) through the speaker, which in many cases was essential to attract the territory owner. For the remaining trial time 30-s song phrases (four bouts) alternated with 30-s sequences without a playback. Model presentation in human settlements proved to be difficult because of frequent disturbance by humans, noise or feral cats, and because some territories were unsuitable for experiments due to the complex arrangement of habitat structures (buildings, walls, hedges). Therefore, valid repeats of the experiment with the model of the other plumage type were gained with only eight adult and three young territorial males, but, in addition, presentation with either an adult or a yearling model could be performed with another ten adult and eleven young males. In the cases of repeated presentation, trials were separated by at least 3 d, and the order in which the models were presented was changed.

The location and behaviour of focal males were continuously recorded and records of response were divided into 30-s periods. As a measure of aggressiveness we used: 1. The average distance of aggressive approach (D_a) to the model in a modified version of STUDD & ROBERTSON's (1985). Distance scores are assigned from a 10-point scale, with the lowest score, zero, being >30 m from the model, or out of sight, the mean score five being distances between 5 and 2 m, and the highest score of ten being a zero distance, when the male stood on the model and attacked. D_a was calculated by averaging

the distances over the entire presentation, according to: $D_a = \sum_i (D_p \times T_p) / t_i$, where D_p is the distance

score during a specific period, t_p is the duration in s of each of the n periods, and t_i is the total duration of the presentation. To save the models, presentations were interrupted when intense attacks occurred, and such cases were therefore calculated as 30 s with zero distance; 2. An index of the intensity of response (I_r) for the entire presentation was calculated by summing up separate scores (each on a five-point scale) of (a) the intensity of movements (number of position shifts, where <5 movements is score one, and >12 shifts accompanied by at least one swoop over the model is score five), (b) the intensity and frequency of vocalizations (number of alarm calls, song bouts, where <5 bouts is score one, and >20 bouts accompanied by alarm calls is score five), and (c) the frequency of nervous and/or aggressive displays (bill wipes, tail flicks, aggressive plumage swells, where <5 displays without swells is score one, and >10 nervous displays accompanied by continuous swells is score five). The maximum response score (=15) was awarded when the territory owner being tested alighted on the model and began vigorous attacks (pecking, tearing); 3. For more general comparisons we only distinguished whether or not an attack or at least a close and clearly aggressive approach (<3 m) occurred.

Intrusions may be of different character and may cause different reactions by owners at different times of the season. We therefore made additional dummy presentations later in the season, using altered experimental settings. Although sample sizes are rather low, the results of these trials are incorporated in this paper as well, because they offer additional hints about the aggressive motivation of adult and young territorial males.

Experiment 2

In exp. 2, eight adult and five yearling males were presented with a stimulus set consisting of models of both types mounted 3 m apart and accompanied by the same taped song sequence as in exp. 1. These presentations were made between the end of Apr. and the end of May (incubation, early nestling period). All males used in this experiment had been tested previously with single-model presentations.

Experiment 3

In exp. 3 we tested reactions of adult males ($n = 8$) to intruders during the stage of nestling feeding

Table 1: Number of attacks or at least close aggressive approaches (distance to model <3 m; repeated aggressive displays) made on experimental dummies by territorial adult male and yearling male black redstarts in relation to plumage colour (age) of intruders. The columns attack/no attack, and close approach/weak response, respectively, refer to the same males. All differences within age classes are not significant (Fisher's exact tests, $p > 0.1$)

	Attack	No attack	Close approach	Weak response
Adult male				
Adult dummy	2	11	7	6
Yearling dummy	3	10	8	5
Yearling male				
Adult dummy	6	3	9	0
Yearling dummy	6	2	7	1

(mid-May to mid-Jul.). A dummy (either adult or yearling) was mounted in a conspicuous position near the nest (2–3 m distance) without broadcasting song phrases, and presented for 9 min to the males approaching the nest with food for the nestlings.

Results

Age-specific Differences in Aggressiveness

Aggressiveness towards intruders, expressed by the proportion of males which attacked or showed close aggressive approach, was significantly higher in yearling territory owners as compared with adult owners when results of all trials (regardless of type of model) were combined (χ^2 , Yates corrected, = 9.29, $p < 0.01$ for attacks; and = 5.08, $p < 0.05$ for close approaches; Table 1). Young territory owners behaved more aggressively as well when both model types were presented simultaneously later in the season (exp. 2): young males attacked models in three of five presentations whereas in eight presentations to adult males only, one aerial swoop-attack but no aggressive alights on any of the simultaneously presented model types were observed ($p = 0.02$, Fisher's exact test).

No Influence of Intruder Status on Owner Response

The plumage colour (age) of the intruder had no significant influence on the aggressiveness of the territory owner in either of the male age classes (Table 1). Although adult males which were presented with both model types in successive trials showed slight tendencies to spend more time closer to, and to respond with higher intensity towards, dull brown models than to conspicuous black (adult) dummies (Fig. 1), differences in D_a and in I_r scores are not significant (Wilcoxon tests, ns). However, the median shortest distance of approach of adult males during the 9-min trials in exp. 1 was lower towards yearling dummies (4 m vs. 7 m for adult dummies) and the time elapsed between the initial approach to the model and the closest approach was considerably shorter in four of eight cases with yearling dummies involved, but only in two cases with adult dummies. Similarly, when adult males had to choose between two intruder males of different

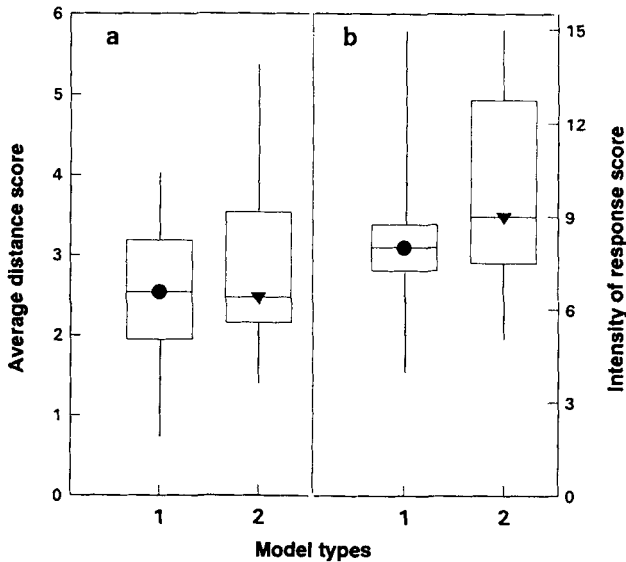


Fig. 1: Reaction of eight adult male territory holders to (1) adult and (2) dull yearling models in successive presentations in the early breeding season (exp.1). Assessment of aggressiveness (a) by an index of the average distance of a male from the model throughout the entire presentation period, and (b) by the intensity of aggressive response, i.e. the number and intensity of movements, vocalizations and other aggressive displays. Symbols represent the median score; the open boxes encompass 50 % of the observations centred on the median; and the solid lines indicate the range of scores

age (exp. 2), adult dummies did not elicit more aggression than yearling models. In five of eight trials, there was no clear preference for one model type, although owners showed general aggressive displays towards the stimulus set. In addition, when models were mounted near the nest of adult males without broadcasting songs (exp. 3), three attacks and five trials without response occurred in eight cases with adult models involved, but three attacks and one close aggressive approach, and only two trials without responses were observed in six cases with dull models (differences not significant: $p > 0.1$, Fisher's exact test).

Age-independent Variation in Individual Response to Intruders

For the eight adult and three yearling males which were tested with both model types in experiment 1, D_a as well as I_r scores reached in trials with adult and yearling models, respectively, were significantly correlated ($r = 0.69$ and 0.70 respectively; $p < 0.05$, two-tailed, Fig. 2) and the correlation is especially clear for D_a scores when only adult male experiments are considered ($n = 8$, $r = 0.85$, $p < 0.01$). This indicates that the amount of aggressive response to intruders was more strongly influenced by the individual aggressive motivation of the owners than by the plumage (age) of the intruder or owner.

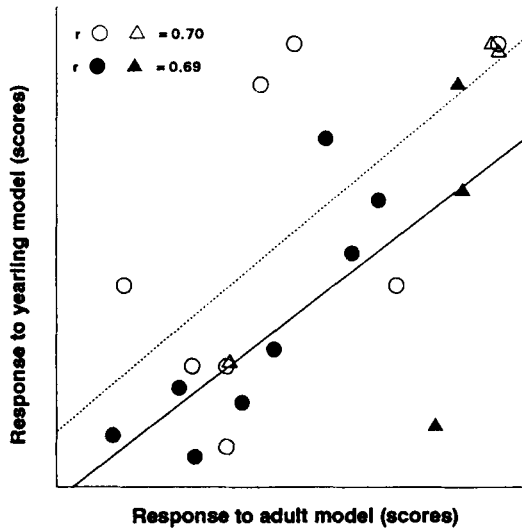


Fig. 2: Correlation between aggressiveness scores reached by eight individual adult (circles) and three yearling (triangles) males in successive trials with adult and yearling models respectively. Filled symbols and solid regression line: average distance scores; open symbols and dotted regression line: intensity of response scores

Discussion

Our results do not support the idea that dull subadult plumages are adaptive with respect to communication as a proximate function in black redstarts; in addition, our results do not support the hypothesis that conspicuous male coloration is a clear signal of fighting ability or aggressive motivation.

Dull plumages of young intruders did not reduce aggression from adult territory owners and there was no indication that female-like appearance was able to deceive adult owners into treating the model as a female. One could argue that in our experiments the intruding female-like male behaves as a territorial male, and hence the potential effect of female mimicry could be destroyed. However, there are several problems with this argument.

Firstly, all breeding season communication hypotheses predict that dull male plumages alone should have some effect on the aggression of dominant adult males. The fact that young-male models were approached less hesitantly and were treated with at least the same (if not stronger) aggressiveness than adult-male models, and that young males were still attacked in the stage of nestling feeding even when presented without song, is inconsistent with both the status signalling (LYON & MONTGOMERIE 1986) and female mimicry hypotheses (ROHWER et al. 1980). Similar results have been reported for the American redstart, *Setophaga ruticilla*, another species with all-purpose territories (PROCTER-GRAY 1991), but were found as well for species mainly defending nest-site areas (ENSTROM 1992; STUTCHBURY 1992).

Secondly, these findings contrast with those of experiments conducted with other species where duller intruders did elicit less aggression than brighter ones

(FLOOD 1984; STUDD & ROBERTSON 1985; HILL 1989; HUHTA & ALATALO 1993), although in most of these studies model presentations were accompanied by recorded songs as well.

Thirdly, yearling black redstart males do sing in the wild (even during intrusions into adult male territories early in the season, pers. obs.) and start performing immediately after arrival from wintering grounds, i.e. they do not attempt to conceal their gender, and, in fact, normally are not successful at carving out portions of adult male territories or in establishing themselves near adult territories (LANDMANN & KOLLINSKY 1995) as predicted by the female mimicry hypothesis.

The subordination status signalling hypothesis (LYON & MONTGOMERIE 1986) proposes that young (dull) intruders would be treated less aggressively by adult owners because they pose less of a reproductive threat than intruders in bright plumage. According to the fighting ability hypothesis (RHOWER 1982), conspicuous intruders in turn should be treated with more care (i.e. less aggressively) by dull young owners to reduce the risk of injuries if bright male colour is a reliable signal of fighting ability. Both predictions were not fulfilled in our experiments.

In the black redstart populations investigated, females are usually in short supply and territory possession and quality seem to be important in determining mating success, i.e. females do not seem to choose males primarily on the basis of plumage coloration (LANDMANN & KOLLINSKY 1995). In such a situation any intruder should be regarded as a potential threat regardless of plumage colour and age. For adult males it could pay to respond aggressively when a young intruder is detected, even if bright plumages are preferred by females and even if already paired, because this could reduce the motivation of a defeated intruder for successive intrusions and thereby reduce the risk of extra-pair copulations by inconspicuous sneaky males later in the season (e.g. before second brood; see results of exp. 3). If, in addition, young males are at an intrinsic disadvantage in competition with adults, the risk of attacking a subadult intruder is lower than the risk of attacking an adult intruder (ENSTROM 1992).

The strong response of young territory owners against intruders of both plumage types suggests that male colour is not a reliable signal of fighting ability or aggressive motivation (e.g. STUDD & ROBERTSON 1985 for yellow warblers) in black redstarts (see as well BREIEHAGEN & SAETRE 1992, HUHTA & ALATALO 1993 for pied flycatchers, STUTCHBURY 1992 for purple martins). However, the fact that young males generally responded more aggressively to intruders than to adults is a bit confusing because most young males tested in 1991, as in preceding years (LANDMANN & KOLLINSKY 1995), held territories in low-quality habitat and, according to our data, were unable to attract a mate. One might thus wonder about the benefits to young males of responding with the observed and potentially costly intensity and we are not able to offer a fully satisfactory explanation for the observed behaviour. Nevertheless, data of our long-term population study (LANDMANN & KOLLINSKY 1995; LANDMANN unpubl. data) show that some young males which remained unpaired in suboptimal territories over longer periods

were able to attract a mate and to successfully rear a brood late in the season, and thus suggest that it could be advantageous to defend a territory for such lucky opportunities.

Overall the amount of aggressive response to intruders was more significantly influenced by individual aggression levels of the owners than by the plumage (age) of the intruder or owner. We found no external parameters which could satisfactorily explain the individual differences in the level of aggressiveness within age classes. In adult males, for instance, neither territory character, nor subsequent mating status or reproductive success seemed to have a clear directional influence on the intensity of response, and young males which occupied peripheral territories responded as aggressively to dummies as did the few males that settled in village parts which are generally preferred by the species (LANDMANN & KOLLINSKY 1995).

The observed individual differences in aggressive motivation may thus reflect individual variation in hormonal level, even within age classes. Aggressiveness might therefore be an inherited trait which does not necessarily guarantee success in terms of territory or mate acquisition and reproductive success.

More data and additional experiments are needed to clarify which factors influence the territorial behaviour and aggressive motivation of male black redstarts. However, at the present stage of our investigations, it seems that in this species none of the breeding season communication hypotheses is satisfactory to explain the evolution and function of delayed plumage maturation (DPM). This fits the results of other studies which recently have evoked doubts that DPM is beneficial for subadult males and is the result of direct selection (STUTCHBURY 1991; ENSTROM 1993; HUHTA & ALATALO 1993).

Acknowledgements

We thank J. SUNDBERG and G.-P. SAETRE for comments on a previous version of this manuscript.

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Received: January 30, 1995

Accepted: April 13, 1995 (W. Wickler)