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Plumage color as a status signal in male–male interaction in the red-flanked bushrobin, *Tarsiger cyanurus*

Abstract Recent studies have suggested that structural-based coloration is an honest signal of male genetic and/or conditional quality in sexual selection. However, whether structural coloration functions in intrasexual competition is unknown. We examined whether plumage color functions as a status signal during intrasexual interactions in the red-flanked bushrobin *Tarsiger cyanurus*; adult males have many blue plumes as structural coloration whereas yearling males and females are olive brown with few blue plumages. Blue males did not always dominate olive-brown males. The number of interactions did not differ with the colors of the two birds involved. The interactions of a blue male and an olive-brown male were less aggressive than those of two blue or of two olive-brown males. In this study, we found that structural plumage coloration may serve as a signal of aggressive intent and lower the escalation level of an aggressive interaction in a manner consistent with hypotheses regarding the evolution of delayed plumage maturation.

Key words Delayed plumage maturation · Intrasexual signaling · Male–male interaction · Status signaling · Structural coloration

Introduction

The adaptive functions of sexual dichromatism have been well studied, mainly from a sexual selection perspective (reviewed by Andersson 1994). Sexual selection models have proposed that conspicuous coloration and ornaments in bird plumage function as an honest signal of individual genetic and/or conditional quality (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Grafen 1990; Andersson 1994; Ligon 1999). Exaggerated traits of

males are associated with benefits for females – either indirect benefits, such as good genes for parasite or pathogen resistance (Hamilton and Zuk 1982; Clayton 1991), or direct benefits, such as parental quality as parental effort (e.g., Hoelzer 1989). Many studies have also suggested that avian plumage characteristics function as status signals among males (Rohwer 1977; Studd and Robertson 1985; Hansen and Rohwer 1986; Møller 1987a, b; Hill and Montgomerie 1994; Mateos and Carranza 1997; McGraw et al. 2003). Males with conspicuous plumage tend to win aggressive interactions and have high social status (e.g., Rohwer 1975, 1977; Møller 1987a, b; Senar 1999).

Recent studies suggest that different plumage colors contain different information (Owens and Hartley 1998; McGraw and Hill 2000; McGraw et al. 2002; Siefferman and Hill 2003). Plumage coloration is mainly produced from two types of pigment and from feather microstructure and is classified into three types: carotenoid-based, melanin-based, and structural-based coloration (Fox and Vevers 1960). As the types are produced by different physiological mechanisms, they may convey different information to recipients (e.g., McGraw et al. 2002). However, many studies of avian signaling systems have tended to focus on carotenoid- and melanin-based coloration (Pryke et al. 2001; reviewed in Senar 1999). Melanin-based coloration is a signal of social dominance in males of many species (reviewed in Senar 1999). Carotenoid-based coloration signals affect female choice (Hill 1999). Recent studies report that carotenoid-based coloration also affects male agonistic behavior (e.g., Pryke et al. 2001, 2002). The function of structural-based plumage coloration, however, has been studied little.

We studied the effect of structural-based coloration on male–male aggressive interaction in the red-flank bushrobin *Tarsiger cyanurus*. This species has structural-based coloration and delayed plumage maturation (DPM). DPM is a phenomenon in which male plumage matures a few years after the first potential breeding season (Rohwer et al. 1980). It is suggested that one adaptive significance of DPM is status signaling between individuals in male–male interaction (reviewed by Lyon and Montgomerie 1986).

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In the red-flank bushrobin, the plumage color of yearlings (first- and second-year males) is olive-brown whereas that of adult males (after the second year) is bright blue (Cramp 1988; G.M., personal observation). Blue is a structural-based color in birds (Fox 1976). Males frequently dispute territory boundaries early in the breeding season (G.M., personal observation). This system enables us to examine whether the presence of structural-based coloration functions as a signal in male–male competition and whether a blue adult bird behaves differently when involved in an interaction with olive-brown (subadult) males than with blue males.

In this study, we examined: (1) which male was dominant in interactions of blue versus olive-brown males (hereafter called B vs. O interaction); (2) whether the frequency of interaction differed among the three types of male pairings: blue male versus blue male (hereafter, B vs. B interaction), olive-brown male versus olive-brown male (hereafter, O vs. O interaction) and B vs. O interaction; and (3) whether the degree of escalation differed among the three types of male interaction. We predicted that blue males would be dominant in B vs. O interactions and that the frequency and intensity of B vs. O interactions would be less than that of O vs. O and B vs. B interactions.

Material and methods

Study area

We conducted the study in a subalpine forest (1,900–2,100 m above sea level) on a slope of Mt. Fuji (35°22′N; 138°46′E). The forest is composed mainly of conifers (*Abies veitchii*, *Tsuga diversifolia*, and *Larix kaempferi*) and some broad-leaved trees (*Sorbus aucuparia* and *Betula ermani*). *Cacalia adenostyloides* covers the forest floor in the summer.

Material

The red-flanked bushrobin is a small passerine with a wide distributional range throughout northeast Eurasia (The Ornithological Society of Japan 2000). This species is socially monogamous. Male bushrobins exhibit DPM (Cramp 1988). The back and head is olive-brown in subadult males (first- and second-year males) and bright blue in third-year or older males (hereafter, blue males). Olive-brown males and females resemble each other though olive-brown males have bright blue plumes in their lesser wing coverts and upper tail covert. Therefore, the amounts of structural blue feathers were greatly different between these males. The spectra of plumage including the ultraviolet (UV) region are perfectly different between each other (representative spectral measurements are shown in Fig. 1).

Bushrobins arrive at the study area in late April, with males generally arriving earlier than females. This species is
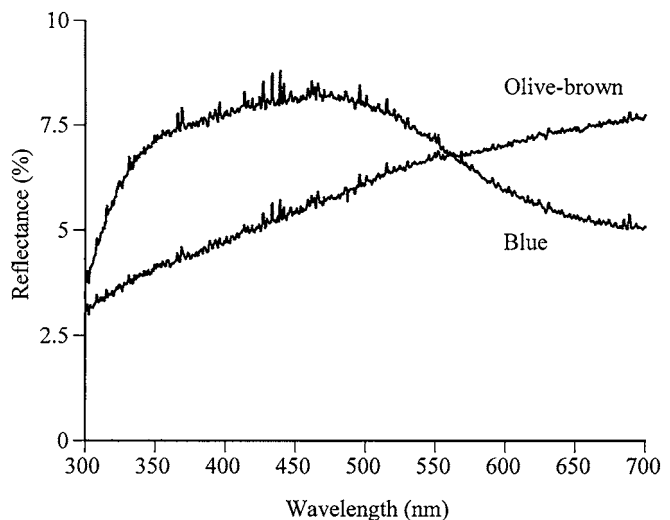

Fig. 1. Reflectance spectra of male bushrobins

territorial during breeding season, which lasts until September. The radius of the bushrobin's territory is roughly 50 m (Cramp et. al. 1988; G.M., unpublished data), and unmated territory owners sing every day until they mate (G.M., unpublished data).

Methods

We observed the birds for a total of 120 days from 25 or 27 April to 1 July 2001 and 1 July 2002. We checked for newly arriving males nearly every day early in the breeding season and tracked the process of territory establishment. We performed mapping territories and checked them every 1–3 day from sunrise to sunset throughout the study season. Territory maps were made by recording the locations of song posts. To find song posts completely, we patrolled on a winding route that covered the entire study area. In addition to the patrol, we traced the male as long as possible and tried to find other song posts when we found a singing male. The distance between the observer and a focal bird were kept about 20 m, which was enough to avoid any disturbance by the observer. We checked the number of males in the study area and positions of their territories through making territory maps. All territories were covered by the route of territory mapping. We traversed the study area and recorded breeding stages (single, pairing, egg-laying, incubating, and nestling stage) for each territory. When we found a newly arrived male, its arrival date and plumage color were recorded.

We caught males by using mist nets and marked each with a metal ring (authorized by the Japan Environment Agency) and a unique combination of three colored plastic rings for individual identification. We included data from unmarked individuals in analyses because some males were not caught before observation of male–male interactions. We were able to specify the territories of those males by tracing their return paths and were able to confirm that the territories were occupied by unmarked males for at least a month.

These unmarked males exhibited territorial behavior (singing at song posts and trying to exclude other males). Most marked males did not lose their territories during the season and unmarked males were neighbored on marked males in many cases. We could identify these interacting males in all cases. We assumed that unmarked territory owners did not change either when two unmarked males neighbored each other.

Dominance measurement

Territories adjoined to each other throughout the study area (G.M., personal observation). It allowed us to observe male–male interactions at territory boundaries. We collected male–male interaction data in parallel with territory mapping. Observational effort was allocated equally among territories. The direction and starting points on the route were changed randomly on each day. We observed male–male interactions during the early period of each breeding season. When we observed an aggressive interaction among males, we recorded the outcome. Male bushrobins usually claim their territories by song; direct territory disputes rarely occur. We observed at least one interaction for most pairs of males. We determined the winner as dominant and loser as subordinate. When we observed several interactions for a pair of males, we used the outcome of the first interaction in analyses of male dominance in order to avoid pseudoreplication. Each male was monitored only from his arrival date to the egg-laying date of his mate to avoid the possibility that birds learned the aggressive ability of a neighboring male. It mediates their interactions since they are so familiar with one another.

Aggressive interactions were categorized into B vs. B, O vs. O, and B vs. O. We defined the intensity of interaction (in increasing order of intensity): threatening, chasing, or fighting. A threatening interaction involved a male flushing his flank feathers at another male and giving a warning call (Nakamura 1995; G.M., personal observation). Fighting and chasing, direct attacks, sometimes occurred after threatening interaction, but threatening interaction never occurred concurrently with a direct attack. Fighting involved intense combat, with males grappling and poking each other. When threatening escalated to higher-intensity interactions, we recorded highest agonistic level only.

A winner and a loser were defined as follows: a winner was the bird that chased the escaping bird at the end of interaction and a loser was the escaping bird at the end of interaction. We confirmed that an interaction ended if the interacting birds returned to their territories and no warning calls were heard for 10 min. We did not determine a winner for threatening interactions. When both males edged away at the end of interaction, we called the interaction a draw.

Statistical methods

Statistical analyses were performed using R version 2.0.1 (http://www.r-project.org/). To determine which type of interaction (B vs. B, B vs. O, O vs. O) frequently occurred, we used the Cochran–Mantel–Haenszel test (Agresti 1990). We calculated expected values from the total number of pairs for each type of interaction. For example, potential number of pairs of (1) B vs. B interaction and (2) O vs. O interaction can be calculated from $_nC_2$ in which n is the number of individuals in each plumage coloration in a year. For (3) B vs. O interaction, the number of pairs was calculated from the multiplication of the number of blue individuals and the number of olive-brown individuals. We calculated expected values from the ratio of (1):(2):(3). Expected values were derived for 2 years, and the test statistics were incorporated by the Cochran–Mantel–Haenszel test. To determine whether the degree of escalation differed among the three types of interaction, we used a generalized linear mixed model (GLMM) with binomial errors and a logit link. Using GLMM, we were able to remove the effect of individual attributes (e.g., winner/loser effect or individual genetic/conditional property) from the effect of coloration in the case that individuals were contained multiple times in different dyads. The response variable was the types of interaction (fighting or other; chasing and threatening). Terms of individual identity (winner ID and loser ID) were included in the model as random factors in order to separate out individual attributes other than plumage coloration. For B vs. O interactions, we determined the color type of males that tended to win by using GLMM with binomial errors and a logit link. The response variable was interaction outcome (win or not). Random factors were blue male and olive-brown male identities. Differences in arrival order (which male arrived earlier) were included in all GLMM models to detect the effect of prior residence.

Results

We observed 150 males with territories in two breeding seasons (60 in 2001 and 90 in 2002). We recorded 122 aggressive interactions (71 in 2001 and 51 in 2002) between males. In total, we observed 96 interactions (46 in 2001, 50 in 2002) of 55 blue males (20 in 2001, 35 in 2002) and 51 olive-brown males (28 in 2001, 23 in 2002). Of these, 11 (three in 2001, eight in 2002) were excluded from analyses because they were replicate observations. Of the remaining 85 interactions, 42 were chasing, 30 were fighting, and 13 were threatening.

The number of interactions did not differ significantly among B vs. B, O vs. O, and B vs. O interactions ($df = 2$, $M^2 = 2.10$, $P = 0.351$, $n = 85$; Cochran–Mantel–Haenszel test), but the degree of escalation did (Table 1). In B vs. B and O vs. O interactions, fighting occurred more frequently than chasing in comparison with B vs. O interaction (Fig. 2).

In B vs. O interactions, plumage color did not affect the outcome (Table 2, Fig. 3). No prior residential effect was detected (Table 2).
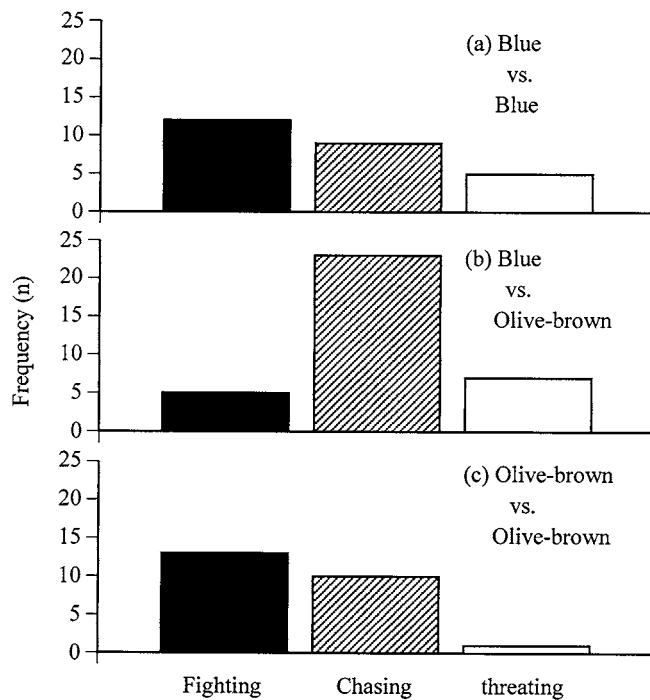
Fig. 2. Frequency of escalation level among the three types of male–male interactions: blue versus blue (B vs. B) (**a**), blue versus olive-brown (B vs. O) (**b**), and olive-brown versus olive-brown (O vs. O) (**c**). *Dark hatched bars* indicate fighting, *light hatched bars* indicate chasing, and *white bars* indicate threatening. When male plumage color was the same, the escalation level was high. When male plumage color was different, the escalation level was low
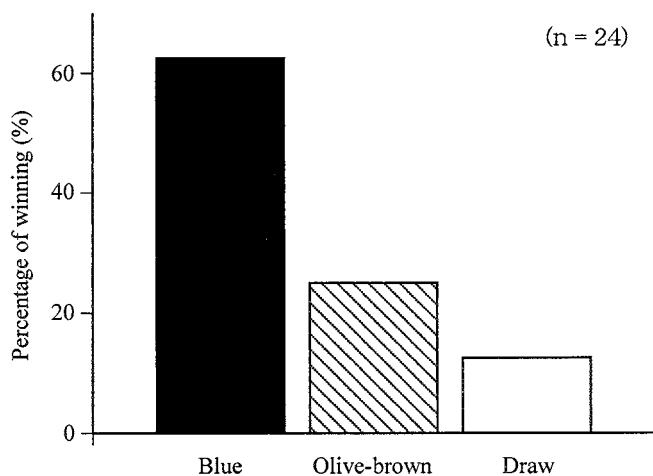

Fig. 3. Percentage of winning in blue versus olive-brown (B vs. O) interactions

Table 1. Generalized linear mixed model (GLMM) analysis of escalation in male–male interactions

	n	df	F	P
Arrival order	56	14	1.415	0.254
Male color combination	74	14	9.411	0.003

Table 2. Generalized linear mixed model (GLMM) analysis in blue versus olive-brown (B vs. O) interactions. Arrival order and male coloration did not affect the outcome

	n	df	SS	F	P
Prior resident effect	14	12	7.41	1.21	0.29
Coloration	22	12	6.57	2.68	0.13

Discussion

Blue plumage in the red-flanked bushrobin functioned as a signal in male–male territorial interactions observed in the breeding season. The degree of escalation differed significantly among three types of male–male interaction. As we predicted, B vs. O interactions were less intense than the others. This is the evidence that structural-based coloration can be a signal in male–male interaction in birds.

However, blue males did not always dominate the olive-brown ones. This seems to be contrary to the results of previous studies of pigmentation-based coloration, which have reported that conspicuous individuals are usually dominant in male–male interactions (e.g., carotenoid-based coloration: Mateos and Carranza 1997; Pryke et al. 2001, 2002; melanin-based coloration: Rohwer 1975; Møller 1987a; McGraw et al. 2003; reviewed in Senar 1999). There are a few studies of structural-based coloration. Those described that bright males were socially dominant or kept large territory [aggressive behavior: satin bowerbirds *Ptilonorhynchus violaceus* (Collis and Borgia 1992, 1993); lazuli bunting *Passerina amoeea*) (Greene et al. 2000); blue tit *Parus caeruleus* (Alonso-Alvarez et al. 2004); eastern bluebird *Sialia sialis* (Siefferman and Hill 2005); keep large territories: blue grosbeak *Guiraca caerulea* (Keyser and Hill 2000)]. These studies suggested that structural-based color has a similar function to that of pigment-based coloration in male–male interaction. Given that blue plumage in the red-flanked bushrobin also exhibits high social status, our results would imply that blue males allow some neighboring olive-brown ones to hold territories for extra-pair copulating with females, which paired with olive-brown ones. Conspicuous and dominant lazuli bunting males gain high extra-copulation success from females mated with neighboring dull males (Greene et al. 2000). In contrast to B vs. O interactions, B vs. B interactions tended to escalate, probably because neighboring blue males are potential cuckolders. This is interesting for the reason that it means males are probably making some sort of assessment about other males based on color.

Alternatively, our results did not support previous studies because we focused on territorial behavior. For the breeding males of red-flanked bushrobins, losing interactions means losing a territory and breeding opportunities. Therefore, olive-brown males may be highly motivated. In addition, some territory-holding olive-brown males may be conditionally and/or genetically high-quality males that will survive to become blue males. Whether the olive-brown territory holders have greater lifetime reproductive success

compared with other (floating) olive-brown males has yet to be determined.

For data analysis, we used GLMMs that considered the individual attributes other than plumage color (e.g., conditional/genetic value, winner–loser effect, bystander effect; Dugatkin 1997, 2001) as random effects. The prior resident effect was included in models as a dependent variable. When we eliminated the random effects, male age/color affected the results of male–male interactions (in other words, age/color factor is changed to significance). Therefore, we believe our results to be accurate. Since our purpose was to reveal the function of structural-based coloration in the DPM system, the complete confounding between age and color is not a problem.

The frequency of aggressive interactions did not differ among the three types of interactions. This suggests that plumage color does not affect the likelihood of occurrence of an interaction. Collis and Borgia (1993) reported that adults of male satin bowerbirds (with blue plumage as structural color) interacted with each other more often than with dull subadult males, and interactions between an adult male and a subadult male did not escalate as much as interactions between adult males. In the lazuli bunting, the aggressiveness of adult males with blue coloration was greatest against a bright adult male model and less against a dull male model followed by a female model (Muehter et al. 1997). In the eastern bluebird, brighter males are dominants in access to resources (nest boxes; Siefferman and Hill 2005). Our findings regarding the intensity of interactions in the Red-flanked Bushrobin are consistent with the results found for these other species. However, our results for interaction frequency differed. In the breeding bushrobins, subordinate males perhaps cannot avoid interactions if the opponent's territory is adjacent because they have to retain their territory. Moreover, male bushrobins may not be able to see the plumage coloration of opponents just before an interaction because, in our study area, they interacted inside the crowns of dense trees. Alternatively, aggressive olive-brown males may be conditionally and/or genetically high-quality males.

Some problems remained on this study. Since we did not control for age, it remains a possibility that the effects we found from plumage color on levels of escalation are dependent on difference of color as relative age. Furthermore, our finding that color did not predict the outcome of interaction does not account for variation of blueness between blue males. One possible follow-up study would be to determine the winner of interactions between males of the same age but that differ in plumage color, thus allowing us to control for both age and variation in color. Nevertheless, our study suggests that first-year males benefit by being brown since they receive less aggressive responses from blue males, which may allow some subadult males to establish and maintain territories in their first breeding season. This result is consistent with the status-signaling hypothesis for the evolution of delayed plumage maturation in male–male interaction (Lyon and Montgomerie 1986).

We conclude that structural-based coloration functions as a status signal in male red-flanked bushrobins. The structural blue signal lowers the escalation level of aggressive interaction. However, plumage coloration does not always determine the winner of male–male interactions in territorial disputes. This is because blue adult males behave differently toward birds within different color/age classes.

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