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Do adult eastern bluebird, *Sialia sialis*, males recognize juvenile-specific traits?

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Juveniles of many avian species possess spotted or mottled plumage that is distinct from the plumage of adults. Such plumage has typically been assumed to aid in camouflaging vulnerable immature birds. Here, we propose that spotty plumage signals juvenile status, thereby decreasing aggression from territorial adults. We tested this hypothesis by measuring the aggressive responses of adult eastern bluebird males to different combinations of simultaneously presented taxidermic mounts. We found that territorial males attacked adult models significantly more than juvenile models, and that they attacked adult models with orange breasts (typical of adults) more frequently than they attacked adult models with spotty breasts (typical of juveniles). We found no difference in attack rates when models with white breasts (a novel trait) were presented with models possessing spotty breasts. These observations indicate that breast colour is a cue used by territorial adults when identifying conspecific intruders, but that adults do not recognize juvenile-specific plumage as such. Adults respond aggressively only to orange-breasted intruders.

A growing empirical and theoretical literature supports the hypothesis that the plumage colour and pattern of many adult birds is shaped by sexual and social selection (Hill & McGraw 2006), but relatively little research has explored how intraspecific influences may shape the appearance of juvenile birds. Functional explanations regarding the appearance of juvenile plumage have been few (Penteriani et al. 2007; Tanner & Richner 2008; Galvan et al. 2008), possibly because drab juvenile plumage is presumed to represent an ancestral appearance with no current functional significance (Maley & Winker 2007).

When the function of juvenile plumage has been considered, it has generally been assumed to aid in the concealment of vulnerable fledglings (Graber 1955); however, there is little empirical evidence to support this assumption. Another commonly held hypothesis regarding the spotted and streaked breasts and backs of juvenile sparrows (family Emberizidae) and thrushes (family Turdidae) is that these characteristics are ancestral traits that appear during development with no adaptive function. Certainly, juvenile plumage appears to be highly conserved; that is, juvenile plumage within a taxonomic group is frequently quite similar despite stark differences between adult plumages within the same group (Graber 1955). However, given the conspicuousness of some juvenile colour displays and the variation in colour expression among closely related taxa (Maley & Winker 2007), functional explanations for the colour and pattern of juvenile plumage warrant consideration.

An alternative to these hypotheses is that juvenile plumage coloration serves as an intraspecific signal. When intraspecific aggression is high, both subordinate and dominant individuals benefit from honest signals that communicate status (Parker 1974; Johnstone 1997; Dale 2006). Such signals can benefit subordinate individuals by decreasing aggression from dominant individuals, and they can also benefit dominant individuals by limiting the number of aggressive actions they must take (Rohwer 1978; Møller 1987; Hein et al. 2003). If juveniles aggregate after the breeding season while still wearing juvenile plumage, the appearance of this plumage could serve as signal of rank, mediating interactions with other juveniles. Alternatively, juvenile appearance could function as a signal of age, thereby limiting aggression during encounters with conspecific adults. Accordingly, in species with high levels of territoriality and intraspecific aggression, juveniles should benefit from traits that honestly signal age and reproductive immaturity (Ligon 2009).

One species in which juveniles would appear to benefit from a signal of immaturity is the eastern bluebird. Adult bluebirds are aggressively territorial and have extended breeding seasons in the southeastern United States (Gowaty & Plissner 1998). Protracted breeding seasons increase the likelihood that juvenile bluebirds

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from early season nests will encounter aggressive, breeding, territorial adults after fledging. Therefore, we hypothesized that juvenile-specific traits may serve as a signal of age and reproductive status to territorial adults. Recognition of juveniles as noncompetitive, sexually immature birds should benefit both adults and young birds.

To test whether the distinctive breast plumage of juveniles serves as an honest signal of age to territorial adults, we measured the aggressive responses of breeding bluebird males to dyads of taxidermic mounts. First, we needed to establish the baseline degree to which territorial adults differentiate between juvenile and adult intruders. To do this, we simultaneously presented juvenile and adult models to territorial adults. Second, we investigated whether eastern bluebirds use breast plumage to distinguish between adult and juvenile intruders by simultaneously presenting one adult model with orange (adult) breast plumage and one adult model with spotty (juvenile) breast plumage. Third, we tested whether adults recognize juvenile-specific plumage traits and avoid attacking models with juvenile plumage. We simultaneously presented adult models with spotty (juvenile) breast plumage and adult models with white (novel) breast plumage. We predicted that the novel white-breasted models would receive more aggression in these trials if, as we hypothesized, spotty plumage serves as a signal of age and reproductive immaturity. The increasing specificity of the questions addressed by our experiments enabled us to better understand the role of juvenile plumage colour and pattern in an intraspecific context.

METHODS

Study Species

The eastern bluebird is a socially monogamous and sexually dimorphic thrush (family Turdidae) that breeds throughout eastern North America (Gowaty & Plissner 1998). Adult male bluebirds have rich blue coloration on their heads, backs, rumps, tails and wings. The upper breast of an adult male is orange, and the belly is white. Adult females have blue-grey upper parts with dull blue wings and tails and pale orange breasts. Juvenile plumage is composed of both adult-like feathers and feathers that are distinct from adults in colour and pattern. Juveniles have whitish streaks on their backs and dusky brown spotting on breast and belly feathers. However, the remiges and rectrices (wing and tail feathers) of juvenile bluebirds are similar to those of adults (plumage information from Gowaty & Plissner 1998). Young bluebirds first acquire blue plumage coloration as they grow wing and tail feathers during the nestling stage.

After spending the summer in this juvenile plumage, young bluebirds undergo a partial prebasic moult (breast, back and rump feathers lost) into their first basic body plumage during the autumn (Pitts 1985). Following the breeding season, birds 2 years of age or older undergo a complete annual moult.

Although socially monogamous, extrapair copulations are frequent in some eastern bluebird populations. As a consequence of extrapair mating behaviour, eastern bluebird pairs are highly aggressive towards intraspecific intruders once they have established a territory (Gowaty & Plissner 1998).

Study Site

We studied a banded population of eastern bluebirds in Lee County, Alabama, U.S.A., between March and July 2008. Nestboxes were monitored throughout the season in order to standardize model presentation times with respect to breeding stage. Each nest was used only once per laying period. Several nestboxes were used more than once during the season, but only once per experiment and only on subsequent breeding attempts (>30 days apart).

Experimental Design

During the spring and early summer of 2008, we conducted three experiments to determine the visual cues that territorial bluebirds respond to when assessing conspecific intruders. In each experiment, dyads of taxidermic mounts were simultaneously presented to nesting bluebird pairs during the egg-laying period, when males are most likely to respond aggressively to conspecific intruders. Except for one juvenile mount, mounts were realistically posed adult male bluebird specimens. Breast plumage treatments were achieved by exposing the natural orange breast plumage of the male mounts (experiments 1 and 2) or through use of juvenile breast plumage vests (experiments 2 and 3) and white plumage vests (experiment 3). Plumage vests were attached with hidden elastic string and were interchangeable, allowing the treatment of the models to be reversed within dyads between trials. Reversing the breast coloration of the models within dyads effectively controlled for all other potential differences between models (e.g. blue plumage colour and brightness), thereby providing a more convincing test of the specific effect that intruder breast coloration has on the aggression of territorial bluebirds (Fig. 1).

We attached the models to the tops of 1 m metal posts and placed them 6 m from the nestbox of a given bluebird pair and 2 m apart (Fig. 2). At 2 m intervals between the nestbox and each model, we

Figure 1. Photographs of model dyads used for experiment 2. Breast plumage treatment was switched between members of each dyad between trials, controlling for inherent differences between models (e.g. posture, brightness of blue head and back feathers, etc).