Animal Behaviour 77 (2009) 1267–1272

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

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

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ARTICLE INFO

Article history:
Received 17 October 2008
Initial acceptance 8 December 2008
Final acceptance 22 January 2009
Published online 12 March 2009
MS. number: A08-00671

Keywords:
aggression
eastern bluebird
honest signal
juvenile
juvenile plumage
Sialia sialis
territoriality

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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0003-3472/$38.00
doi:10.1016/j.anbehav.2009.01.031

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).

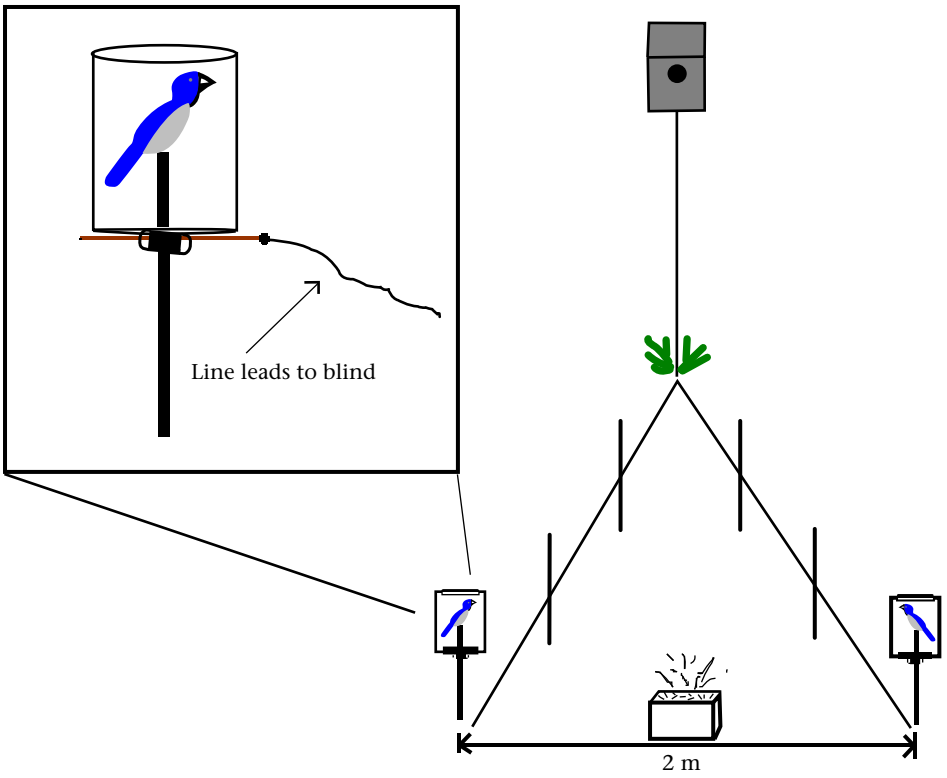

Figure 2. Representation of basic experimental set-up. Models were placed 6 m from the nestbox of the pair being examined and 2 m apart. Between models, we placed a speaker playing eastern bluebird calls and song. Vertical metal posts were placed in 2 m increments between the nestbox and the models in order to provide perches for territorial adults, enabling us to quantify the nearest approach of adult males in discrete units. Models were temporarily shielded from view by PVC pipes, then simultaneously exposed. The side on which models were presented was randomized, and the order of presentation (spotty versus non-spotty) was alternated. During trials, both models faced the focal nestbox, but for illustrative purposes, the models are represented in profile.

placed vertical metal posts to serve as perches for the bluebirds and enable us to quantify the nearest approach of adult males into discrete units. To attract territorial adults and increase their frequency of response, we placed a small speaker directly between the models, which played a 15 s loop of eastern bluebird calls and song. Learning plays little role in the development of bluebird calls, and individuals in juvenile plumage are able to sing (Pinkowski 1971; Gowaty & Plissner 1998). The similarity in vocalizations between adults and juveniles gives us confidence that the aggressive responses we observed were directed relative only to the appearance of models and that our results were not confounded by the use of playback.

After setting the models atop the metal posts, we placed PVC cylinders over the models to shield them from view. By temporarily concealing the models, we were able to complete trial set-up without exposing the nesting pair to the visual stimuli of the models. Once the models, posts, PVC cylinders and speaker were set for a given trial, we retreated to a camouflage blind 20–30 m away. The PVC cylinders concealing the models rested atop metal pins connected to monofilament lines, and by pulling these pins from the blind, we were able to present both models simultaneously and begin the trial. Models were presented for 12 min unless one of the resident bluebirds alighted upon a model and began to destroy it by tearing or pecking. In these cases, the trial was immediately stopped. We recorded all trials ($N = 110$) with a video camera (Sony Hi8) from our position in the blind. Trials were later analysed by an observer blind to model treatments.

Experiments 1, 2 and 3

First, we measured the baseline degree to which adult males differentiated between juvenile and adult intruders by presenting a juvenile bluebird mount paired with one of four different adult bluebird mounts (number of trials = 13). Using a single juvenile model increased the chances that behavioural responses of adults were influenced by idiosyncrasies of the mount used, rather than general juvenile qualities. These effects were minimized, however, by presenting this model to multiple males and by pairing this model with multiple adult mounts. Ultimately, we would have preferred to use multiple juvenile mounts but did not feel justified in collecting additional juvenile specimens for this purpose.

Second, we examined whether bluebirds use breast plumage to distinguish between adult and juvenile intruders by presenting four different dyads of adult mounts (to reduce the effects of pseudoreplication) in a sequential manner. In each of these trials ($N = 33$), one member of the dyad displayed the orange breast plumage typical of adult males and the other member displayed the spotty breast plumage typical of juveniles.

Third, we tested whether adult males could recognize juvenile-specific plumage using the same four dyads of adult mounts. During these trials ($N = 64$), one member of each dyad displayed spotty breast plumage while the other member displayed plain white breast plumage. Plain white breast plumage represents a novel trait for bluebirds.

Female Aggression

Females periodically responded aggressively towards model intruders. However, we chose not to focus on female aggression towards models because (1) quantifiable aggressive actions by females were infrequent and sample sizes were small and (2) female responses were frequently correlated with the responses of

their mates. From the outset, the focus of this study was the response of territorial males to intruders with different plumage patterns. Therefore, we present only the behavioural responses of males in our results.

Aggression Scoring and Analyses

For each trial, we used the highest level of aggression displayed by the adult male to determine his primary target. This enabled us to label one model the winner (receiving more intense aggression). Aggressive behaviours fell into one of six categories, although only the highest level of aggression displayed was used to determine the winner of each trial. When there was a tie between models for the highest category of aggression, the next highest category was used to determine the winner and loser (Table 1). If an adult male returned to his nestbox during the trial, but never performed any measurable aggressive behaviour, the trial was scored as a draw and excluded from subsequent analyses. Because variation between individual males was high with respect to aggression displayed towards models, and because we wanted to compare only the relative levels of aggression directed at each type of model intruder, we used nonparametric sign tests to compare the responses of adult males to the different model types. One-tailed tests were used because we had specific, a priori predictions regarding the effects of juvenile-specific traits on adult aggression.

In addition to recording the highest level of aggression displayed by each adult male, we also recorded the target model of each male's initial aggression. Despite our attempts to place models equidistant from nearby shrubs, trees and perches, such placement was not possible at all nestbox sites. Because the direction from which males approached might influence their initial target, but not necessarily their final target, we examined instances where these two categories differed (i.e. where initial aggression was directed towards one model, but the highest level of aggression was directed towards the other model). In instances where males 'switched', we predicted that switches from spotty-breasted models (juveniles in experiment 1, adults with juvenile breast plumage in experiments 2 and 3) towards non-spotty-breasted models (adults in experiments 1 and 2 and adults with white breast plumage in experiment 3) would be more common than the reverse (i.e. spotty to orange > orange to spotty).

Ethical Note

This study was approved by the Auburn University Internal Animal Care and Use Committee (IACUC project registration no. 2008-1341) and conducted under Alabama State and U.S. Fish and Wildlife permits. Aggression trials were conducted during the egg-laying period of nesting and no abandonment of nests was recorded during the 2 days following trials. Early season observations also indicated that adult bluebirds resumed normal singing and foraging behaviours soon after the models were removed.

Table 1
Ranks of aggressive behaviours displayed by eastern bluebirds towards models in descending order of intensity

Aggressive behaviour	Category
Perching attack (pecking and tearing at model while perched on it)	6
Physical contact (brief physical contact with model, no perching)	5
Number of physical contacts	4
Number of dive bombs (swooping attacks without physical contact)	3
Nearest approach (4 m, 2 m, <2 m)	2
Time spent at nearest approach distance	1

The highest level of aggression displayed by a male in each trial was used to determine the primary target of aggression (winner).

RESULTS

Experiment 1: Adult Models versus Juvenile Models

In 10 of 11 trials where an aggressive response was recorded, males displayed their highest level of aggression towards the adult model (sign test: $m = 4.5$, $P < 0.01$; Fig. 3). In the only trial where a male showed more aggression towards the juvenile model, it was in the form of a nearer approach.

In only one trial did an adult male direct his initial aggression towards one model, then switch and display his highest level of aggression towards the other model. In this instance, the adult first approached the juvenile model, but displayed higher aggression towards the adult model (Fig. 4).

Experiment 2: Adult Models (Juvenile Breasts) versus Adult Models (Adult Breasts)

In 23 of 28 trials with measurable aggression from territorial males, adult males were most aggressive to models with orange breasts (sign test: $m = 9.0$, $P < 0.001$; Fig. 3).

In 10 trials, the territorial male first directed his aggression towards one model, then switched targets and displayed his highest level of aggression to the other model. In nine of these 10 instances, the male switched from the spotty-breasted model to the orange-breasted model (sign test: $m = 4.0$, $P < 0.02$; Fig. 4).

Experiment 3: Adult Models (Juvenile Breasts) versus Adult Models (White Breasts)

In 26 of 53 trials where an aggressive response was directed at one of the models, the highest level of aggression was directed

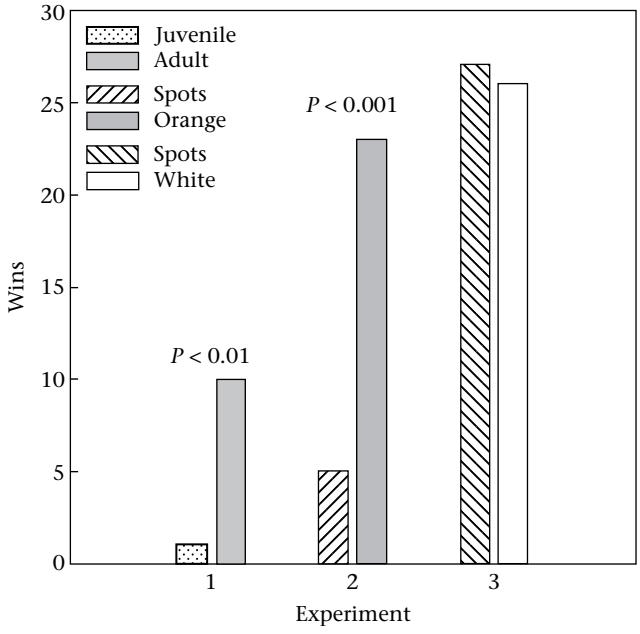

Figure 3. Intruders targeted by male eastern bluebird adults. Different pairs of model intruders were simultaneously presented to adult males and the number of 'wins' for each model type was recorded (wins = instances when a model received greater aggression in a given trial). In experiment 1, adult models were paired with juvenile models. In experiment 2, adult models with spotty (juvenile) breast plumage were paired with adult models with orange (normal) breast plumage. In experiment 3, adult models with spotty (juvenile) breast plumage were paired with adult models with white (novel) breast plumage.

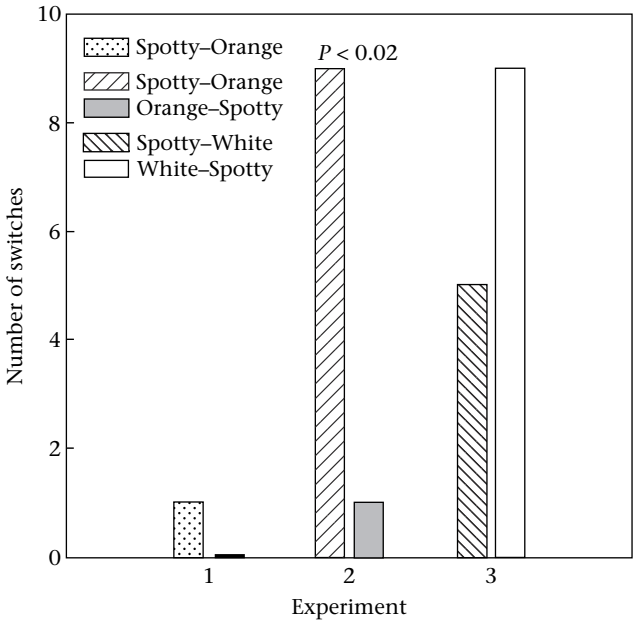

Figure 4. Instances of aggression switching by territorial males. The original model to which an adult displayed aggression is listed first, followed by the model to which he switched and displayed his highest level of aggression (e.g. Spotty–Orange indicates males that first behaved aggressively towards spotty-breasted models, then behaved most aggressively towards orange-breasted models).

towards the model with white breast plumage (sign test: $m = -0.5$, $P = 0.5$; Fig. 3).

In 14 of the 53 trials, the territorial male first directed his aggression towards one model, then switched targets and displayed his highest level of aggression to the other model. In five of these 14 instances, the male switched from the spotty-breasted model to the white-breasted model (sign test: $m = 2.0$, $P = 0.21$; Fig. 4).

DISCUSSION

When a male bluebird encounters an avian intruder on its territory, it must assess the bird quickly to determine whether the trespasser poses a threat to itself or its mate. Bluebirds rely on a suite of visual and auditory cues to assess intruders and, through a series of experiments, we demonstrated that the colour and pattern of the intruder's breast plumage is one such cue. When orange-breasted models were presented in our trials, they were targeted significantly more often than their simultaneously presented counterparts. When no orange stimulus was provided, aggression was meted out equally to both model types.

Contrary to our hypothesis that the spotted pattern of juvenile breast plumage serves as a signal of immaturity to territorial adults, adult males did not recognize spotty breast plumage as a signal of juvenile status, and spots did not deter territorial aggression. In our population, adult males appear to have a simple strategy wherein they direct their aggression towards intruders with orange breasts. Rather than responding to two different signals, one triggering aggression (orange) and one preventing aggression (spots), adults responded with directed aggression only to orange-breasted intruders. All non-orange-breasted intruders were treated in a similar fashion whether they were juveniles or members of another species. This strategy reduces the likelihood of inappropriately directing aggression to a bird that is not a rival male bluebird.

It has recently been proposed that juvenile thrushes that fledge into environments amid breeding and territorial adults should benefit from honestly signalling their age and reproductive immaturity (Ligon 2009). Longer breeding seasons in the tropics, coupled with an increased likelihood of year-round territoriality, are thought to have contributed to the evolution and maintenance of distinct juvenile plumage in tropical thrush species. Although eastern bluebirds are temperate, they produce multiple broods per breeding season in the southeast United States. In these populations, young from early season broods will probably encounter breeding and territorial adults, thus facing intraspecific pressures similar to those proposed for tropical thrushes. While adult eastern bluebirds do not recognize the specific patterns of juvenile breast plumage, we have shown that they direct significantly less aggression towards this pattern when it is presented simultaneously with an adult pattern. Because plumage distinctiveness, rather than any specific pattern or colour, is proposed to serve as the signal of age, our findings agree with the predictions of Ligon (2009).

In addition to the proposed intraspecific pressures responsible for the appearance of juveniles, spotty and mottled juvenile plumage may also serve to provide camouflage from visual predators. Because spots, streaks and stripes are widespread among the juveniles of many species, this possibility needs empirical testing. Another alternative is that mottled breast plumage is widespread in juvenile thrushes because it represents an ancestral appearance. Insufficient selection pressure against this trait could also result in the observed prevalence of spotty juvenile thrushes. However, none of the proposed benefits or explanations for spotty plumage is mutually exclusive.

Regardless of whether there are benefits of crypsis or whether breast spottiness reflects the expression of an ancestral trait, our experiments suggest that a current benefit of spotty breast plumage for juveniles lies in being distinct from adults. The spotty and brown plumage of juvenile eastern bluebirds is distinctive in both colour and pattern from the orange breast plumage of adults, making juveniles readily recognizable as 'different'. Quick recognition of juvenile intruders as nonthreats is a requirement for the proposed benefits to adults and juveniles because this recognition enables both to avoid costly physical interactions. It seems likely that many of the distinctive juvenile plumages, as was well as juvenile bill, leg and eye coloration, seen across an array of avian taxa serve as similar signals of sexual immaturity.

Acknowledgments

We thank J. D. Ligon, M. Scott, two anonymous referees, and members of the Hill lab for constructive comments on this manuscript. Additionally, we would like to thank J. Hill and M. Buschow for assistance monitoring bluebird nests and A. Hitch for assistance in preparing taxidermic models. This research was supported by a grant from the National Institute of Allergy and Infectious Diseases, Project no. R01AI049724 to G.E.H. and by grants from the Birmingham Audubon Society, Sigma Xi and the American Ornithologists' Union to R.A.L.

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