INTRASPECIFIC SIGNALING FUNCTIONS OF JUVENAL PLUMAGE

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INTRASPECIFIC SIGNALING FUNCTIONS OF JUVENAL PLUMAGE

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INTRASPECIFIC SIGNALING FUNCTIONS OF JUVENAL PLUMAGE

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Russell Andrew Ligon, son of James David Ligon and Sandra Husar Ligon, was born on March 18, 1984 in Albuquerque, New Mexico. He graduated from Manzano High School in 2002 ranked third in his graduating class of 430. Russell attended Pomona College in Claremont, California for four years, graduating in May of 2006. While at Pomona, he became enthralled with the field of animal behavior, devoting two summers to biological field research as an undergrad. Additionally, Russell designed and conducted his first independent research project while at Pomona, a senior thesis focused on the acorn-caching behavior of acorn woodpeckers. In addition to realizing his love for behavioral ecology while at Pomona, Russell also started on the varsity football team for four seasons, competed as a hurdler on the varsity track and field team for one year, and played two seasons of rugby for the Claremont Colleges Rugby Football Club, a perennial powerhouse. After Pomona, Russell joined the Hill lab at Auburn University in the fall of 2006 to pursue research related to the behavioral ecology of birds.

THESIS ABSTRACT

INTRASPECIFIC SIGNALING FUNCTIONS OF JUVENAL PLUMAGE

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The function and evolution of avian plumage coloration has been the subject of many studies over the past decade, but virtually all of this research has focused on the plumages of sexually mature individuals. The color and pattern of juvenal plumage, which is worn only for the first few months of life by altricial songbirds, remains essentially unstudied. To examine how juvenal plumage functions in intraspecific contexts, we developed a three-pronged approach designed to uncover the evolutionary origins and current adaptive functions of several juvenal plumage traits.

First, we developed the idea that distinctive juvenile appearance may be a signal of sexual immaturity, serving to reduce aggression from conspecific adults. We used a comparative approach to test this hypothesis in the thrushes (Family Turdidae) and found that distinctive juvenile appearance was significantly correlated with increased risk of conspecific aggression. The observed associations are consistent with our hypothesis that the benefits of signaling sexual immaturity have driven the evolution of distinctive juvenal plumage. Second, we tested the applicability of the comparative study results by employing a field study of eastern bluebirds, *Sialia sialis*. We tested the hypothesis that spotty plumage of eastern bluebird juveniles' signals age, thereby decreasing aggression from territorial adults, by measuring the aggressive responses of adult bluebird males to different combinations of simultaneously presented taxidermic mounts. We found that territorial males do not recognize juvenile-specific plumage, but avoid attacking intruders that lack adult plumage characters. Third, we tested the idea that plumage color may serve as a signal of quality in fledgling eastern bluebirds and that parental feeding decisions are influenced by differences between offspring with respect to plumage color. Fledglings were presented in pairs and parental investment was scored as a percentage of feeding attempts to each individual. Our results support the hypothesis that feather coloration of male bluebird fledglings affects the care they receive from parents. Eastern bluebird parents appear to use juvenal plumage coloration as a signal to assess the relative quality of offspring after fledging and to adjust parental investment in a manner that maximizes their reproductive success.

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THE JUVENAL PLUMAGE OF ALTRICIAL SONGBIRDS AS AN HONEST SIGNAL OF STRATEGY: COMPARATIVE PHYLOGENETIC EVIDENCE FROM THE TURDIDAE

ABSTRACT

The function and evolution of avian plumage coloration has been the subject of many studies over the past decade, but virtually all of this research has focused on the plumages of sexually mature individuals. The color and pattern of juvenal plumage, which is worn only for the first few months of life by altricial songbirds, remains essentially unstudied. We develop the idea that distinctive juvenile appearance may be a signal of sexual immaturity, serving to reduce aggression from conspecific adults. We use a comparative approach to test this hypothesis in the thrushes (Family Turdidae). Honest signals of reproductive immaturity should be more valuable when juveniles fledge into environments with aggressive adult conspecifics. Therefore, we predicted that distinctive juvenile appearance would be more likely to evolve in species with extended breeding seasons and high levels of territoriality. We used breeding latitude as a proxy for these variables. As predicted, distinctive juvenile appearance was significantly correlated with occupancy of tropical latitudes. The observed associations are consistent with our hypothesis that the benefits of signaling sexual immaturity have driven the evolution of distinctive juvenal plumage.

INTRODUCTION

The external coloration of diurnal animals is likely to be shaped by two distinctly different forms of selection: risk of capture by visual predators and the benefits of communication with conspecifics (Darwin 1859; Wallace 1889; Williams 1996). From the time of Darwin and Wallace, these two forms of selection have been recognized as often opposing influences, with predation selecting for crypsis and disruptive patterns and intraspecific interactions promoting bold and brilliant coloration. Numerous studies have confirmed that both influences shape the coloration of birds (reviewed in Hill and McGraw 2006). This well-supported theory on the function and evolution of plumage coloration, however, has focused almost entirely on the basic and alternate plumages (i.e., "adult plumage") of birds. Juvenal plumage has been left out of the discussion.

Before attaining a first basic (adult) plumage, young birds possess a juvenal plumage that they retain, at least in part, for a period lasting from a few weeks to a year (Pyle et al. 1987; Humphrey and Parkes 1959; Eisenmann 1965). Birds wear this juvenal plumage when they are not yet reproductive, when they are least competitive in intraspecific contests for resources, and when they are subject to their highest mortality rates as free-flying individuals (Bonnevie 2007). Although the color and pattern of juvenal plumage could play a central role in survival during this critical period, juvenal plumage color and pattern have received little attention by researchers. In a comprehensive review of juvenile coloration in birds, Kilner (2006) cited no studies that offered insight into the adaptive significance of any plumage color or pattern of juvenal plumage in altricial species. While a number of papers have proposed one benefit or another for the colors of downy and juvenal plumage in precocial birds (Chaniot 1970;

Dorward & Ashmole 1963; Buckley & Buckley 1972; Stoutejesdijk 2002), the possible function of the coloration of juvenal plumage in altricial species remains essentially unstudied.

Juvenal plumage is likely subject to different selection pressures than those that shape definitive plumages because inexperienced juvenile birds are faced with a variety of dangers. In addition to increased susceptibility to predation (Krams 2002), juveniles are likely to lose agonistic encounters with experienced adults of the same species (Sol et al. 1998). Because juvenile birds are also less effective than adults at foraging (Marchetti & Price 1989; Wunderle 1991; Sol et al. 1998), time spent in altercations is probably more costly for juveniles than for adults.

Aggressive interactions with older, more-experienced adults remain dangerous for yearling birds throughout their first winter and first breeding season. Consequently, the benefit of signaling subordinance is currently interpreted as a driving force in the maintenance of dull or female-like plumages by the first-year males of many North American passerine birds (Rohwer et al. 1980; Senar 2006). Explanations of delayed plumage maturation have focused primarily on reproductively mature individuals in their first potential breeding season (Rohwer et al. 1980), yet even when the functions of first basic (winter) plumage are considered (Rohwer and Butcher 1988; Berggren et al. 2004), both young and old birds are pursuing similar non-breeding strategies. In contrast, young birds in juvenal plumage are at a distinctly different life-stage than the actively breeding adults they encounter upon fledging. The delayed attainment of full adult plumage is a response to different evolutionary pressures than those that shape specific juvenile appearances. While we may draw insights from studies of subadult plumages, juvenal plumage remains a distinct display of feather coloration that requires its own explanation.

In many species of birds with extended breeding seasons, juveniles from early-season broods are independent and mobile while adults are still breeding and aggressively defending nearby territories. When aggressive territorial adults encounter juveniles, both should benefit from a signal indicating the non-reproductive status of the juvenile. Juveniles would obviously benefit by avoiding the directed attacks of territorial adults, but adults would also benefit. Territorial males normally defend their territories and mates from incursions by other reproductive adults. Time spent chasing an individual that poses no reproductive threat could give extra-pair competitors opportunities to mate with the paired female.

We propose that juvenal plumages that are distinct from adult plumage in color or pattern serve as honest signals of age and reproductive immaturity (Dale 2006) and that deflection of conspecific aggression is a primary benefit of distinctive juvenal plumage. Such a signal should be clear and unambiguous because the principal benefit, both to the signaling juvenile and the responding adult, would be in the immediate recognition of non-reproductive status. The present study investigates this hypothesis in the thrush family (Turdidae) using a phylogenetically controlled comparative analysis.

When they fledge, juveniles of a majority of thrush species have the wing and tail feathers that they will keep through their first breeding season (Pyle et al. 1987), and they are typically recognizable as members of their species at the time they leave the nest (Collar 2005). Those plumage characteristics that enable juvenile thrushes to be recognized as members of their own species may also increase the risk of aggression from conspecifics. Two circumstances in particular likely increase juvenile risk of aggression from adults: 1) when conspecific adult males are territorial and attack intruding conspecifics, and 2) when breeding seasons are prolonged so that adult males are still breeding and aggressive when juveniles from early nests have left their natal areas. Therefore, honest signals of age may be more likely to evolve in species with high levels of territoriality and extended breeding seasons.

For most thrush species there is no detailed information published on territoriality or the length of breeding season, but reasonable proxies for these reproductive parameters exist. The breeding seasons of birds from many different families are, on average, two to three times longer in tropical regions than are the breeding seasons of closely related taxa in the temperate zone (Stutchbury & Morton 2001; Baker 1938; Skutch 1950; Ricklefs 1966; Wyndham 1986). Such protracted breeding seasons increase the likelihood that young birds hatched early in the breeding season will encounter aggressive territorial adults after fledging. Additionally, year-round territoriality is common in tropical birds (Stuchbury & Morton 2001) and territorial aggression may even be higher during the non-breeding season for some tropical species (Fedy and Stutchbury 2005). Although there are relatively few studies investigating year-round territory defense, available evidence suggests that it occurs in at least 60% of Panamanian passerine species (Stutchbury & Morton 2001). The combination of lengthy breeding seasons and the prevalence of year-round territoriality amplifies the risk that juvenile thrushes will encounter aggression from conspecific adults in the tropics, thus increasing the value of signals that indicate non-threatening juvenile status. This argument leads to the prediction that intraspecific plumage differences between juveniles and adults are more likely to exist in tropical than in temperate thrush species. We tested this prediction by tracing changes in plumage distinctiveness and changes in temperate versus tropical breeding range across a phylogeny of thrushes, and looking for congruence in changes of these traits. A correlation between breeding latitude and plumage distinctiveness in thrushes would suggest an evolutionary process linking the two features (Maddison 2000).

Methods

***Terminology*.-** Despite repeated attempts to create a standard plumage nomenclature (Humphrey and Parkes 1959; Howell et al. 2003), plumage descriptions often vary between authors. Inconsistent terminology for different stages of bird plumage has undoubtedly complicated studies of the function and evolution of sub-definitive plumages (Lawton and Lawton 1986). We define juvenal plumage as a bird's first covering of contour feathers (Humphrey and Parkes 1959). Additionally, the terms 'juvenile' and 'immature' have been used to describe first-year breeding birds, but we find such terminology misleading. In this paper, juveniles are individuals that have not reached sexual maturity.

***Phylogeny Reconstruction*.-** We created a composite phylogeny for thrushes in the family Turdidae (including genera: *Turdus, Zoothera, Catharus, Cochoa, Endomodestes, Hylocichla, Ridgwayia, Ixoreus, Platycichla, Cichlherminia, Psophocichla, Chlamydochaera, Cataponera, Geomalia, Nesocichla, Cichlopsis, Myadestes, and Sialia*; Collar 2005) by joining several recently published phylogenies.

We used the general relationships of genera from Klicka et al. (2005) to create our phylogenetic 'backbone,' onto which we grafted species specific relationships from four other studies. The placement of species within the genus *Catharus* was obtained from Winker and Pruett (2006), with the exception of *C. bicknelli*, which was placed with relation to *C. minimus* and *C. fuscescens* from data in Outlaw et al. (2003). The placement of species within *Myadestes* was obtained from Miller et al. (2007), and that of species within the genera *Turdus, Cichlherminia, Nesocichla,* and *Platychichla* from Voelker et al. (2007). In addition to providing the backbone of our composite tree, Klicka et al. (2005) provided specific relationships within the genera *Zoothera*, *Hylocichla*, *Ridgwayia*, *Entomodestes*, *Cochoa*, *Chlamydochaera, Cichlopsis Psophocichia, Sialia*, and *Ixoreus.*

Equal branch lengths were used because of the difficulty associated with combining branch lengths from several different studies, each using different molecular markers. In previous studies (e.g., Garamszegi et al. 2007), the use of equal branch lengths has produced results similar to those obtained from other techniques.

Characters.-We utilized discrete binary characters, as required for the comparative methods we followed (Pagel 1994; Pagel and Meade 2006; Rubenstein and Lovette 2007). Species were characterized as either tropical or non-tropical and distinct or not distinct (see descriptions below). These characterizations allowed us to use more powerful comparative algorithms, but also eliminated variation in trait expression.

Species were characterized as "tropical" if the majority of their year-round range occurred between the tropics of Capricorn and Cancer. Species were characterized as “non-tropical” if the majority of their year-round range occurred outside of the tropics, or if they migrated out of the tropics during the breeding season. Distribution and range maps were obtained from published accounts (Clement & Hathway 2000; Collar 2005). Scoring of geographic distribution was done by RAL.

Differences between adults and juveniles, with respect to plumage, were characterized for each species. We characterized a species as “distinct” if strong dissimilarity existed between adults and juveniles with respect to 1) overall plumage coloration or 2) plumage pattern (Fig. 1). If adults and juveniles of a species were determined not to exhibit strong differences with respect to plumage 1) color or 2) pattern, then that species was categorized as “not distinct.” For the 20 sexually dichromatic species in our analysis we compared juvenile appearance to both adult males and females, such that “distinct” juveniles were readily distinguishable from adults of either sex. Because available evidence suggests that some tropical and territorial species do not differentiate between conspecific male and female intruders (Busch et al. 2004), juvenile appearance similar to either adult males or adult females resulted in a classification of “indistinct.”

Information regarding plumage traits was obtained from published color plates (Clement & Hathway 2000). Plumage character assignments were made by five volunteers unfamiliar with the species in question and blindly with respect to geographic range. Specifically, each species was assigned to a plumage category by scorers presented only with color plates of adults and juveniles, without any additional information (including range maps or species names). When plumage assignments were not unanimous, the category was assigned according to the majority designation.

***Ancestral State Reconstruction*.-**Ancestral state reconstructions of plumage distinctiveness and breeding latitude were performed in Mesquite 2.0 (Maddison & Maddison 2006) using the composite Turdidae phylogeny described above. Only those species for which we possessed plumage data and which were represented in the phylogeny were used in our reconstruction. Plumage distinctiveness was treated as a reversible, discrete, and unordered character.

***Correlated Character Evolution*.-**To examine the relationship between current distribution (year-round tropical vs. temperate/migrant) and the incidence of plumage difference between adults and juveniles, we used Pagel's discrete algorithms (Pagel 1994) in the program Mesquite v2.0 (Maddison & Maddison 2006). This analysis allows for tests of correlated evolution, as well as the order and direction of evolution for binary traits, using a continuous-time Markov model (Pagel 1994; Pagel & Meade 2006). The evolution models are fitted to the data and phylogeny with maximum likelihood and described by the log likelihood of the models. Correlated evolution is detected by comparing the likelihood of a model in which the rates of change for each character are independent of the other character and a model in which the rates of change depend on the state of the other character (Midford and Maddison 2006).

In addition to using Pagel's algorithms (Pagel 1994), we used a pairwise comparison (Maddison 2006) to test for correlation between plumage distinctiveness and latitude on our composite phylogeny in the program Mesquite v2.0 (Maddison & Maddison 2006). This method relies on relatively few assumptions and controls for the effects of phylogeny (Møller and Birkhead 1992). Because some authors (e.g. Read & Nee 1995) have suggested that the pairs of taxa selected for comparisons of two binary characters must differ in both characters to be meaningful, we analyzed only such contrasting pairs. Comparisons of these pairings allowed us to ask if species that contrast in latitude also contrast in a predictable manner with respect to plumage distinctiveness.

Results

***Ancestral State Reconstruction*.-**Distinctive juvenile appearance appears to have evolved independently 6 to 14 times among the species we analyzed, and indistinct juvenile appearance arose independently 9 to15 times.

***Correlated Character Evolution*.-**Using Pagel's (1994) test of correlated character evolution, we found a significant association between geographic distribution and distinct juvenal plumage relative to adult plumage (p = 0.006, 1000 simulations) (Fig. 2).

The results of the pairwise comparisons agree with those obtained from Pagel's test for correlated character evolution (Pagel 1994). 50,000 pairings in which both character states of pair members differed showed that latitude and plumage distinctiveness are significantly related (best tail p = 0.046, range 0.005 - 0.291).

In 45 of the 58 (78%) tropical species examined there were strong differences in plumage between adults and juveniles, but this was true of only 15 of the 33 (45%) of the temperate/migratory species that we examined (Fig. 3). For a summary of the interspecific differences in location and distinctiveness, organized by clade, see table 1.

Discussion

Dale (2006) summarized the key parameters predicted for different types of visual signals including cost of production, signal variability, and interclass overlap in expression. Our hypothesis that juvenile color and pattern serve as a signal of age and sexual immaturity places juvenile coloration into the category of a “Status-Related Strategy Signal” within Dale’s classification system. General features of juvenal plumage coloration are consistent with the predicted qualities of such a signal—plumage coloration exhibits high variability between strategies (i.e., between adults and juveniles) with a bimodal distribution of variability (with adults representing one peak and juveniles another); adult and juvenile appearances are discrete (rather than continuous); and interclass variability exists only between members of different age groups. Thus, the juvenile plumage of some altricial species of birds meets key predictions for a signal of strategy.

In our comparative analysis we made a simple prediction: honest signals of immaturity should evolve when the negative consequences of being misidentified as an adult are high. In such situations, there are potentially large benefits to revealing juvenile status. The correlation that we found between latitude and plumage distinctiveness supports the prediction that juvenile thrushes have a plumage pattern distinct from adults when they fledge into an environment where they are likely to encounter aggressive territorial adults and potentially costly physical challenges if they are perceived as reproductive competitors.

To our knowledge, this is the first proposal that distinctive juvenal plumage evolved or is maintained as an honest signal of age and sexual immaturity, but other studies have proposed that young birds benefit from signals of youth. Hardy (1974) proposed that the distinctive juvenile eye and bill color of some birds species, and particularly tropical jays (Family Corvidae), serve as a signal of age. He performed experiments altering the bill coloration of a single Purplish-backed Jay *Cyanocorax beecheii* to test this assertion. In this species, juveniles have yellow bills and adults have dark bills. Hardy (1974) painted the bill of an adult jay yellow, to make it juvenile-like in appearance. He observed that the aggressive actions of a second adult Purplish-backed Jay ceased immediately once the intruder's bill resembled that of a juvenile. The distinctive appearance of young birds, in this case achieved through age-specific coloration of eyes and soft-parts, has thus been proposed to aid in maintaining complex social organization by reducing within-group aggression (Hardy 1974; Lawton and Lawton 1986). Generally, decreasing aggression from full adults seems to be a primary benefit to individuals that have a distinct appearance when they are young and inexperienced (Senar 2006), despite the fact that individuals bearing such an appearance often have fully formed sex organs (Lawton and Lawton 1986 and references therein).

Possible signal functions of juvenile plumage color and pattern have been largely overlooked in many species with elaborately ornamented adults, possibly because drab juvenal plumage is presumed to represent an ancestral appearance with no functional explanation needed (Maley and Winker 2007). When a functional explanation has been applied to juvenal plumage coloration, it is usually that such plumage coloration aids in camouflaging young birds. Few studies, however, have demonstrated that any aspect of juvenal plumage color or pattern functions in crypsis (but see Chaniot 1970; Dorward and Ashmole 1963), and no studies have shown that a specific plumage pattern unique to juveniles makes the juveniles of altricial birds less conspicuous to predators. Nevertheless, avoiding detection by visual predators is important for naive young birds and these young birds are undoubtedly under greater threat from predators than adults because of their inexperience and incompletely developed neuromuscular systems. Therefore, crypsis may be an important adaptation that increases the survival of juvenile altricial birds during the first few days post-fledging.

The numerous differences between temperate and tropical ecosystems, including different predator communities, could explain the patterns that we found in our study. Distinctive juvenile appearance could be more prevalent in tropical juveniles simply in response to increased predation risk. Crypsis and the proposed honest signal of immaturity are not mutually exclusive hypotheses, but further studies will be required to determine the relative importance of these pressures in shaping the significant relationship between breeding latitude and distinctiveness of juvenile appearance.

Predation risks can vary not only across regions and habitats, but also between different light environments. Spectrophotometric analysis of different light environments and the plumage of species that inhabit those environments might help us understand how changes in appearance affect detectability. Such analysis might enable us to compare relative levels of conspicuousness in tropical and temperate habitats, which could useful in assessing the relative importance of intra and interspecific factors affecting plumage appearance. However, in this study, we assessed plumage pattern, not color quality, and spectrophotometric data would not contribute to interpretation of our results.

Our hypothesis correctly predicted the distinctiveness of juvenile appearance 69% of the time, but even some of the exceptions (misclassifications) strengthen our assertions. Incomplete information about breeding season length and territoriality of the thrush species forced us to use tropical breeding latitude as a proxy for both duration of breeding season and the likelihood of juveniles encountering territorial adults after fledging. There are, of course, thrush species that breed in the temperate zone and produce multiple broods every season. In the southeastern United States, for example, Eastern Bluebirds *Sialia sialis* often raise two or three broods in one season. While Eastern Bluebird fledglings have the blue wing and tail feathers that they will keep throughout their first breeding season, they also possess spotty breast and back plumage that visually distinguishes them from adults (Gowaty and Plissner 1998). Because Eastern Bluebirds were categorized as temperate breeders in our study and possess distinct juvenal plumage, they did not fit our hypothesized relationship between plumage characters and latitude. However, the Eastern Bluebird is one of the few thrush species for which we have detailed information on breeding duration and territoriality, and we know that juvenile Eastern Bluebirds should benefit from an honest signal of age and sexual immaturity.

Disentangling the relative importance of selection pressures acting upon a given trait is always difficult, particularly when basic ecological and life-history information are lacking. Though predation undoubtedly selects for crypsis in juvenile birds, we provide evidence that significant intraspecific interactions within tropical thrush species may also influence juvenal plumage. The relative importance of the different selection pressures on juvenal plumage remains to be investigated and more studies are required to fully understand the function of juvenal plumage in thrushes, as well as in other avian groups.

Table 1. Turdidae traits (distinct vs. not distinct, tropical vs. temperate) broken down by clade. Clade numbers refer to Figure 2.

	Clade	Tropical/ Distinct	Tropical/ Not Distinct	Temperate/ Distinct	Temperate/ Not Distinct	**Total**
Austral-Asian Zoothera	I	1	2	0	3	6
Catharus and Allies	II	6	3	0	5	14
Afro-Asian Zoothera	III	3	1	0	1	5
Turdus and Allies	IV	26	7	11	9	53
Myadestes and Sialia	V	9	0	4	0	13
Total		45	13	15	18	91

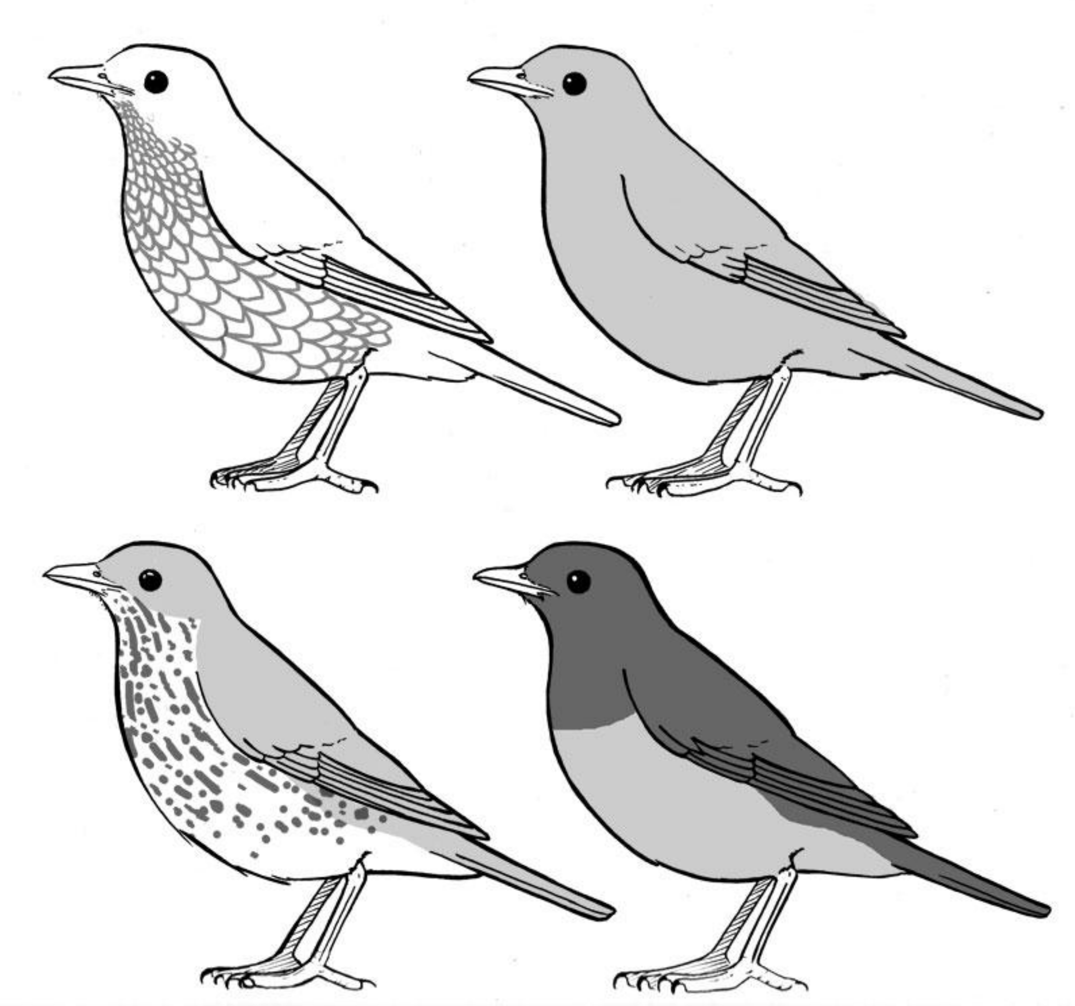

Figure 1. General plumage patterns common throughout the Turdidae. Each plumage pattern represented would be classified as "distinct" from every other plumage pattern with respect to coloration, pattern, or both.

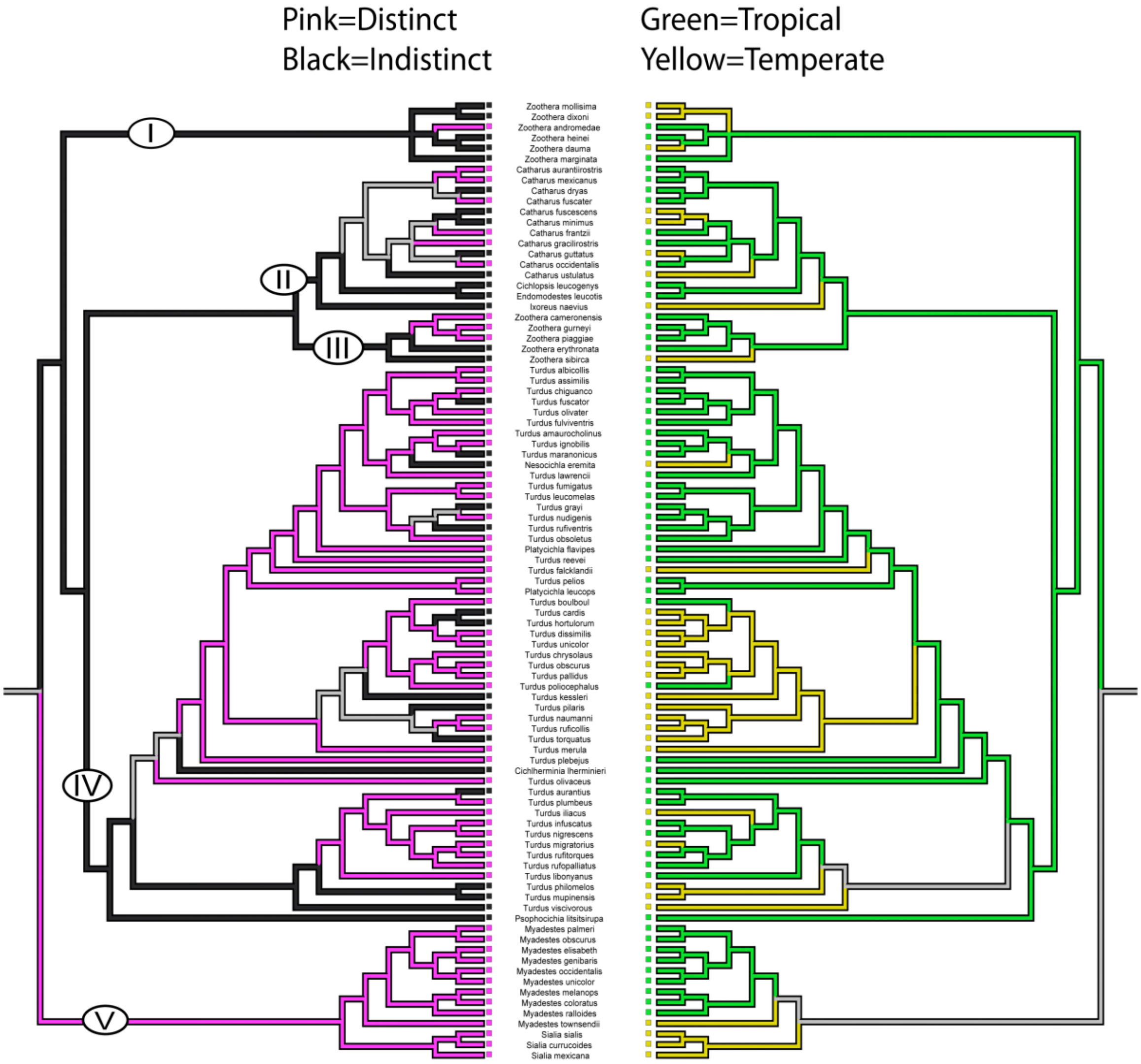

Figure 2. Composite molecular phylogeny of the Turdidae. The plumage differences and range characteristics used in the comparative analysis are indicated at the end of each terminal branch. Plumage (left side of the tree) was characterized as: **distinct** between adults and juveniles (pink) or **indistinct** between adults and juveniles (black). Range (right side of the tree) was characterized as **tropical** (green) or **temperate** (yellow). All characters are discrete and binary. Roman numerals refer to clades in Table 1.

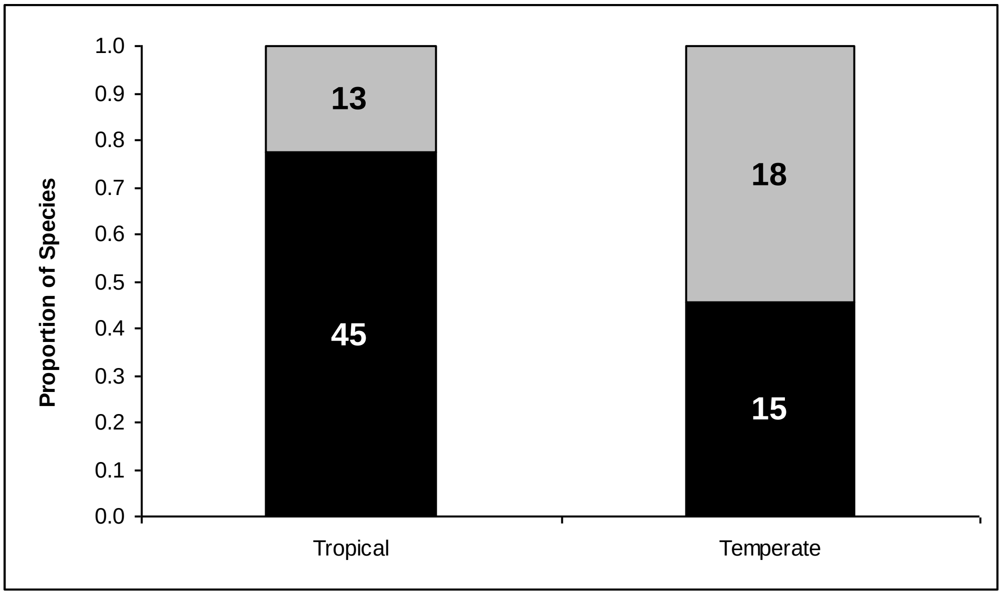

Figure 3. Differences in Plumage Distinctiveness between Tropical and Temperate Thrushes. The proportion of species exhibiting distinctive plumage within each group is shown in black, the proportion of species exhibiting indistinct plumage is shown in grey. Numbers shown are total number of species exhibiting the different plumage characteristics.

DO ADULT EASTERN BLUEBIRD, *SIALIA SIALIS*, MALES RECOGNIZE JUVENILE-SPECIFIC TRAITS?

ABSTRACT

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 color 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.

INTRODUCTION

A growing empirical and theoretical literature supports the hypothesis that the plumage color 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 juvenal plumage have been few (Penteriani et al. 2007; Tanner & Richner 2008; Galvan et al. 2008), possibly because drab juvenal plumage is presumed to represent an ancestral appearance with no current functional significance (Maley & Winker 2007).

When the function of juvenal 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, juvenal plumage appears to be highly conserved; that is, juvenal 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 color displays and the variation in color expression among closely related taxa (Maley & Winker 2007), functional explanations for the color and pattern of juvenal plumage warrant consideration.

An alternative to these hypotheses is that juvenal 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 juvenal 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 (Chapter 1).

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 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 juvenal 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 juvenal plumage color 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. Juvenal plumage is composed of both adult-like feathers and feathers that are distinct from adults in color 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 juvenal 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 molt.

Although socially monogamous, extrapair copulations are frequent in some Eastern Bluebird populations. As a consequence of extrapair mating behavior, 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 color 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 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 juvenal 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 analyzed 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 behavioral 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 behavioral 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 behaviors 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 behavior, 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 behaviors soon after the models were removed.

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 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 color 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 juvenal 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.

We recently proposed that juvenile thrushes that fledge into environments amid breeding and territorial adults should benefit from honestly signaling their age and reproductive immaturity (Chapter 1). 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 juvenal 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 juvenal 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 results from the comparative study described in Chapter 1.

In addition to the proposed intraspecific pressures responsible for the appearance of juveniles, spotty and mottled juvenal 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 juvenal 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.

Table 1

Ranks of aggressive behaviors 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).

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).

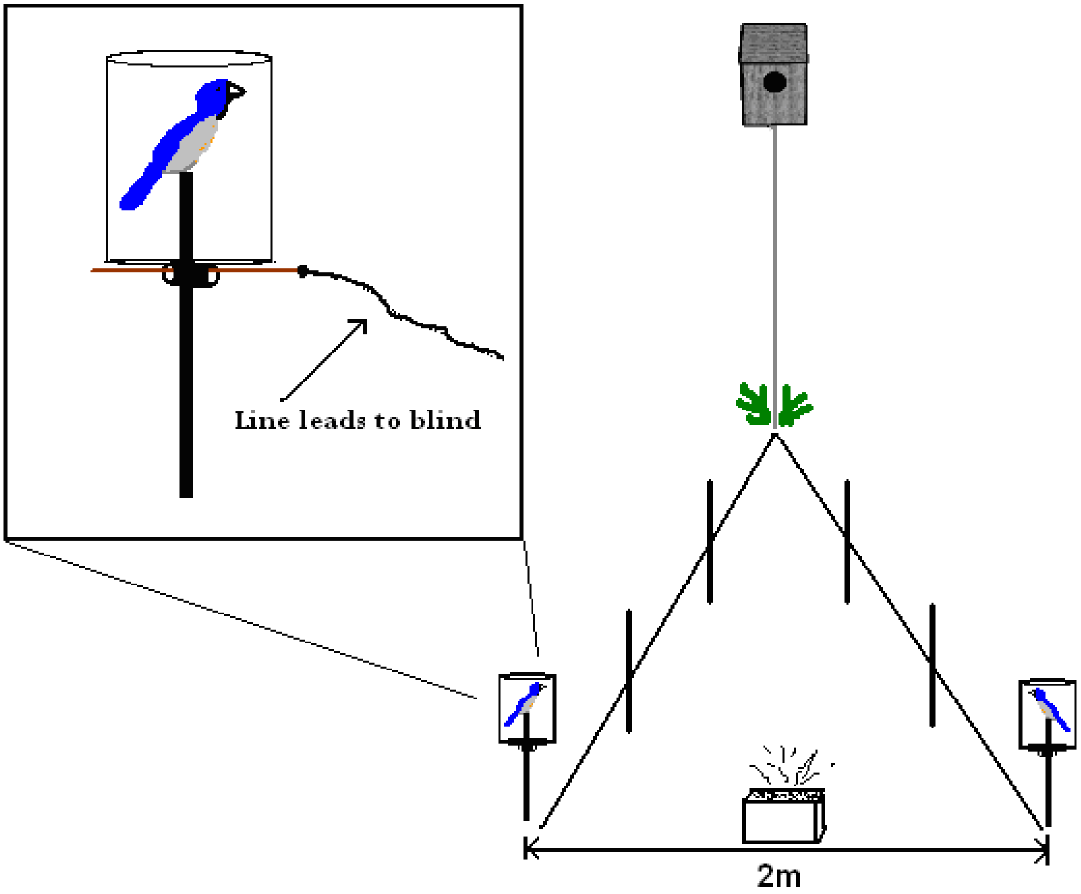

Figure 2. Representation of basic experimental set-up. Models were placed 6 m from the nestbox of the pair being examined and 2 m apart. Between models, we placed a speaker playing Eastern Bluebird calls and song. Vertical metal posts were placed in 2 m increments between the nestbox and the models in 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.

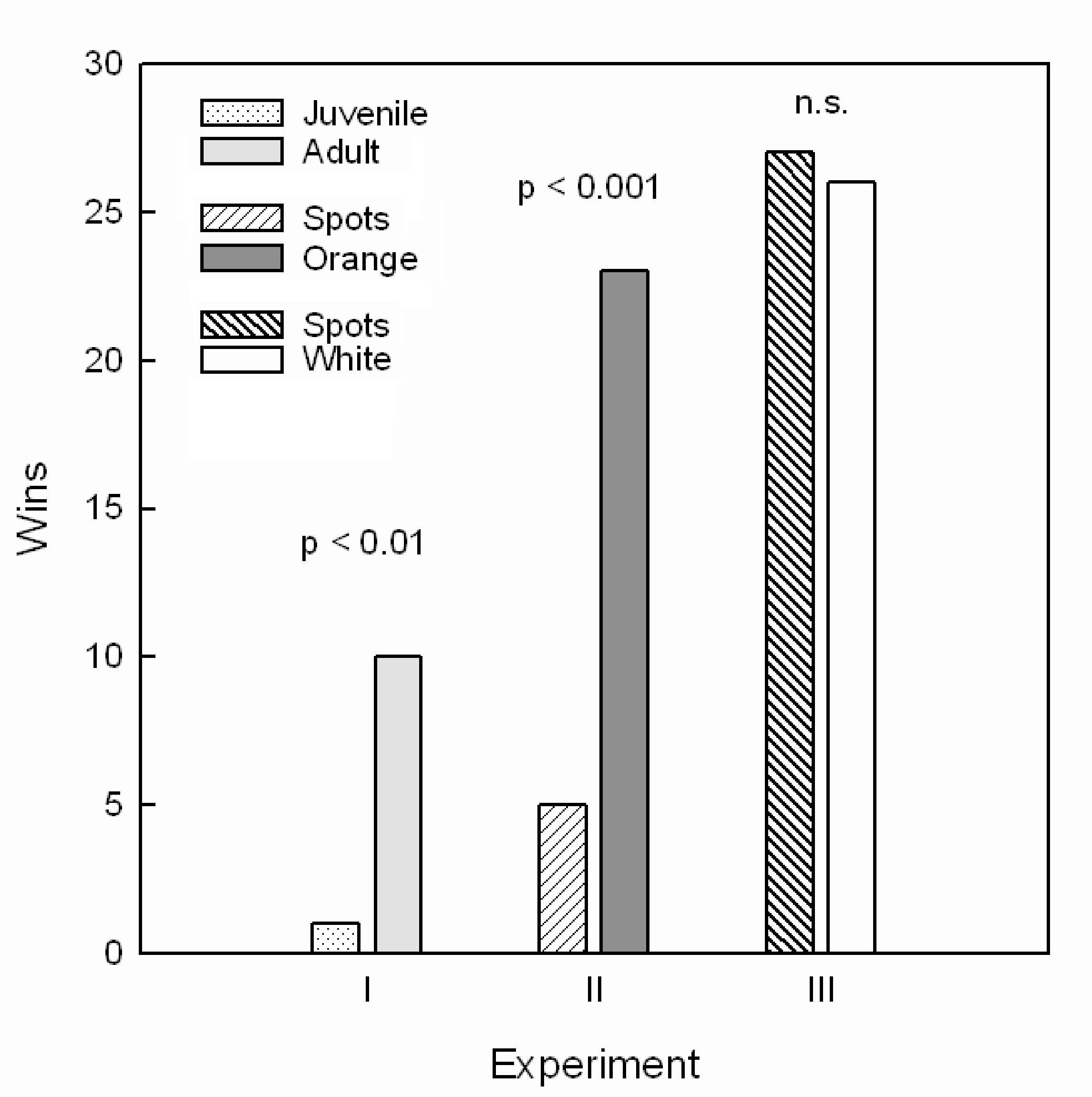

Figure 3. Intruders targeted by male Eastern Bluebird adults. Different pairs of model intruders were simultaneously presented to adult males and the number of 'wins' for each model type was recorded (wins = instances when a model received greater aggression in a given trial). In experiment 1, adult 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.

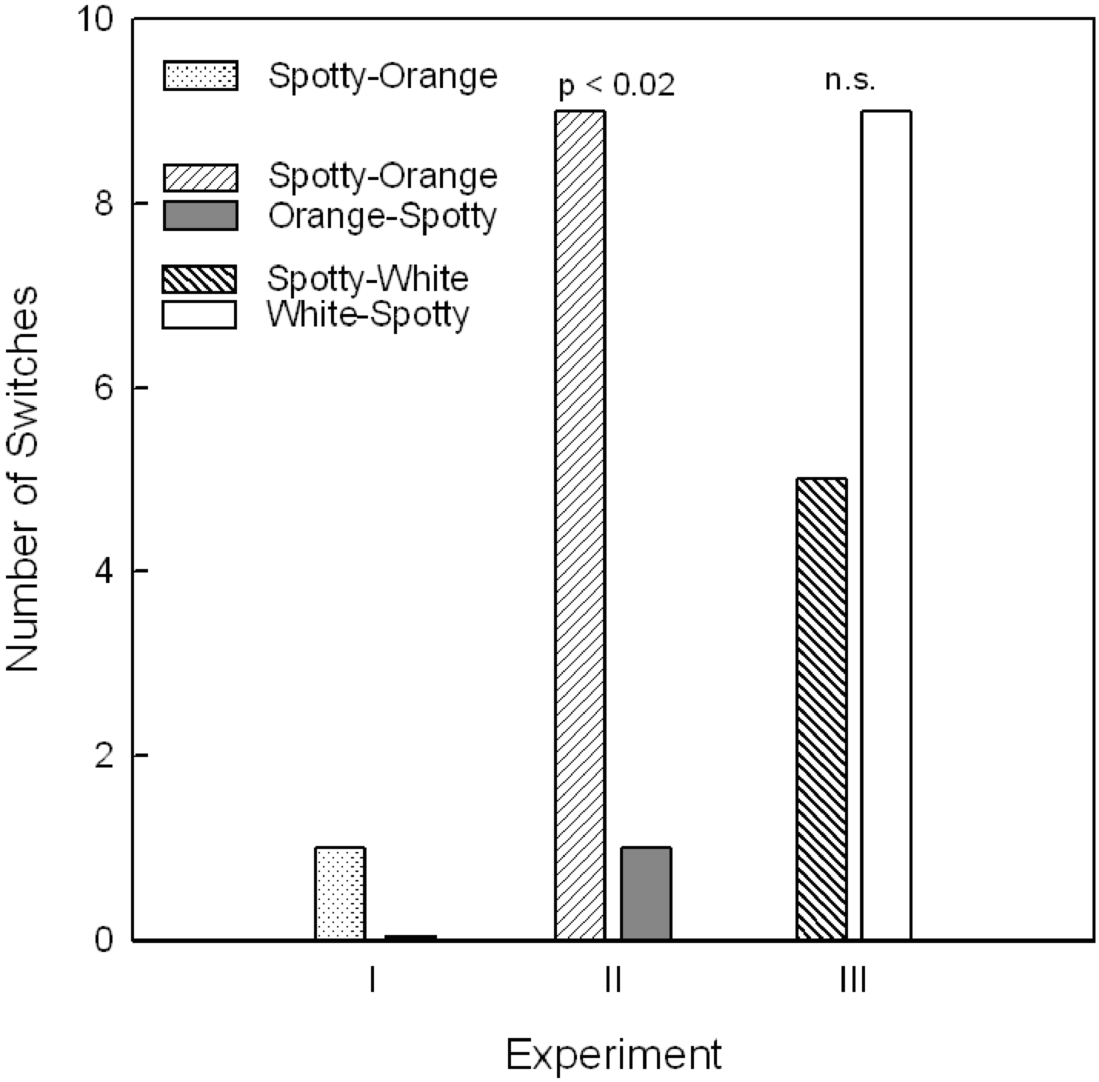

Figure 4. Instances of aggression switching by territorial males. The original model to which an adult displayed aggression is listed first, followed by the model to which he switched and displayed his highest level of aggression (e.g. Spotty–Orange indicates males that first behaved aggressively towards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

OFFSPRING PLUMAGE COLOR INFLUENCES PARENTAL FEEDING DECISIONS IN THE EASTERN BLUEBIRD

ABSTRACT

The amount of resources that avian parents provide to individual offspring within a brood represents a strategy that can have profound effects on reproductive success. We propose that parental feeding decisions of Eastern Bluebirds (*Sialia sialis*) are influenced by offspring plumage color, which serves as a signal of quality in fledglings. Because feeding decisions based on offspring quality likely differ with resource availability, we also predicted that parental responses would differ in high and low quality habitats. We tested these ideas by manipulating the plumage color of fledglings and measuring parental responses in feeding behavior. Fledglings were presented in pairs, and parental investment was scored as a percentage of feeding attempts to each individual. As predicted, experimentally increasing juvenal plumage brightness resulted in increased maternal feeding attempts in low quality habitats. No such relationship was found in high quality habitats. Paternal feeding rates were positively correlated with increases in juvenal plumage brightness across all habitat types. These results indicate that feather coloration of Eastern Bluebird fledglings affects the care they receive from parents. Our findings suggest that parents use plumage as a signal to assess the relative quality of fledglings and adjust investment in a manner that maximizes reproductive success.

INTRODUCTION

In bird species with altricial young, parents provide all of the food resources for their offspring, both while they are contained within a nest (nestlings) and for a period after they have left the nest (fledglings) (Skutch 1976). How parents distribute food among offspring can have profound effects on their reproductive success. When food is abundant, parents are expected to distribute food equally among all offspring (Davis et al. 1999). When food is limited, however, parents typically benefit by allocating more resources to the offspring in the best condition (Davis et al. 1999).

If parents are to distribute food based on the future reproductive value of their offspring (Clutton-Brock 1991) they need to be able to accurately assess the condition of these offspring. Accurate assessment of nestling quality by parents may depend on multiple signals (Johnstone 1995; Johnstone 1996) and there are a number of cues potentially available to parents when assessing the condition of their young. During the nestling period, offspring are tightly clustered in a common nest environment which allows direct comparisons of mouth color, begging intensity, and size. After young have left the nest and spread out in the environment, such comparisons may become more difficult. Fledged siblings are no longer grouped tightly together and many of the signals used by parents to make feeding decisions during the nestling stage are likely less useful. Between the nestling and fledgling stages, however, altricial young grow most of their juvenal plumage and differences in plumage coloration might allow parents to accurately assess offspring quality outside of the nest. The possibility that plumage of juvenile birds may serve as a signal of quality to parents has only recently been considered.

The function of ornamental plumage coloration has typically been examined in the context of sexual selection. It follows that signals similar to those used in assessing mate quality during sexual selection could be used by parents attempting to assess the fitness of their offspring outside the nest because such traits may provide an honest signal of genetic or phenotypic quality (Zahavi 1975; Grafen 1990). Although many studies have shown the condition-dependent nature of pigment-based coloration in birds (reviewed in Hill 2006a), the honesty of structural coloration is less well-established. Correlations between structural plumage color and individual condition have been reported in a few taxa [e.g., blue grosbeaks *Guiraca caerulea* (Keyser and Hill 2000), blue tits *Parus caeruleus* (Johnsen et al. 2003) and blue-black grassquits *Volatinia jacarina* (Doucet 2002)], and manipulative studies have shown that structural coloration is condition-dependent in adult wild turkeys *Meleagris gallopavo* (Hill et al. 2005), brown-headed cowbirds *Molothrus ater* (McGraw et al. 2002), and Eastern Bluebirds *Sialia sialis* (Siefferman and Hill 2005). Although less well-studied, the structural plumage color of juveniles also seems to be condition-dependent in blue tits *Parus caeruleus* (Jacot and Kempenaers 2007) and Eastern Bluebirds *Sialia sialis* (Siefferman and Hill 2007).

Despite the apparent honesty of different plumage colorants and the ability of plumage characteristics to accurately convey information about individual condition or quality, experimental evidence for parental investment based on plumage ornamentation is currently limited. Two recent studies have shown that parents feed control offspring at higher rates than their experimentally ultraviolet (UV) blocked siblings in the great tit *Parus major* (Tanner & Richner 2008; Galván et al. 2008). However, the impact of habitat quality (specifically, resource availability) on provisioning decisions with respect to juvenal plumage ornamentation has not been explored in any species. A model presented by Davis et al. (1999), using western bluebirds *Sialia mexicana* as the focal species, predicts that parents should allocate more resources to "better" (i.e., bigger) chicks when resources are scarce and more evenly distribute food when resources are plentiful. Indeed, resource availability influences parental feeding decisions in alpine swifts *Apus melba* and European starlings *Sturnus vulgaris* (Bize et al. 2006). In both species, UV skin coloration of nestlings is correlated with nestling mass and skeletal size (Bize et al. 2006) and is used by parents to make provisioning decisions. As predicted by Davis et al. (1999), parents attempted to 'catch-up' their inferior offspring (no UV reflectance) when there was abundant food but invested maximally in their best offspring (normal UV reflectance) when resources were limited.

Nesting conditions affect the brightness of plumage in juvenile male (but not female) bluebirds (Siefferman and Hill 2007), potentially enabling parents to evaluate the relative condition of their sons by assessing their plumage. Building on recent studies exploring the function of ornamental plumage in juveniles, we tested whether the blue structural plumage of juvenile Eastern Bluebird males influences feeding decisions made by parents. We also compared the effects of habitat quality on parental provisioning decisions because resource allocation decisions are likely to be influenced by food availability. In this experiment, we manipulated the plumage coloration of fledgling juvenile bluebirds within the range of natural variation to create both relatively brighter and darker individuals and then recorded changes in parental provisioning behavior.

METHODS

Study Site

This study was conducted using a banded population of Eastern Bluebirds in Lee County, Alabama (32°35’N, 82°28’W) between March, 2008 and August, 2008. Approximately 150 nestboxes were monitored throughout the breeding season and the date of the first egg laid in each nest, as well as the date of hatching, was recorded.

Experimental Protocol

When nestlings were between 15 and 18 days of age we determined the sex of all brood members in the field and selected two male nestlings from each nest containing two or more male nestlings. We determined the sex of nestlings by examining the amount of blue in emerging flight feathers (Pinkowski 1974), and blood samples taken from each nestling when offspring were 8 days old enabled us to double-check the accuracy of our sex-assignments in the field (148/150 accurately sexed, remainder excluded from analyses). Eastern Bluebird nestlings typically fledge 15-18 days after hatching, and we chose specific trial dates on a brood-by-brood basis depending on the development of nestlings in each nest: Nests containing more developed (e.g., greater feather development) juveniles were tested earlier than nests containing less developed juveniles. When broods contained more than two male nestlings, the two individuals closest to one another with respect to mass were tested, and in cases where there were multiple possible pairings we always tested the heaviest pair (average mass of heavier male 26.51g ± Standard Deviation 1.58, average mass of lighter male 25.60g ± 1.56, average difference 0.90g ± 0.74).

On the day of the trial, we gathered all nestlings from a given box to measure mass. To minimize the effects that different hunger levels might have on fledgling begging rate and intensity, as well as the effects that such differences might have on parental provisioning patterns, we fed each nestling one mealworm before all members of the brood were returned to the natal nestbox. At this point, we sealed the entrance to the nestbox to prevent any feeding by parents and any premature fledging attempts. We then left the immediate area for 30 minutes to allow the nestlings to digest the recently consumed mealworm. After the 30 minute pre-trial period, we returned to the nestbox, selected the pre-determined males, and placed them separately in a divided wire cage near the natal nestbox. A solid partition prevented any physical or visual contact between siblings in the wire cage (Fig 1) and, to create a location from which bluebird parents could assess their offspring, we placed a 50 cm tall perch one meter away from the front of the cage. We kept all remaining nestlings in a cloth box and fed them mealworms throughout the duration of the trial.

Parent bluebirds quickly adjusted to the experimental setup and began to feed their offspring through the wire mesh of the cage in as little as 45 seconds. A tripod mounted video camera (Sony Hi-8) was used to record parent and chick interactions during a control period, after which we returned to the area and manipulated the plumage of both juveniles (see *Color Manipulation* below). After manipulating the plumage of the chicks, we resumed recording parent/chick interactions for two hours. Initially, we used a control period of 30 minutes (± 5 minutes) but, after briefly investigating several of these trials, we discovered that this duration was not long enough to consistently observe a sufficient number of feeding attempts from parent bluebirds. Subsequently, we used one hour (± 5 minutes) control periods. After each trial, fledglings were removed from the cage and returned to their nestbox along with their siblings.

To compare feeding rates between control and experimental periods, we analyzed the percentage of feeding attempts by male and female parents to each offspring. Because percentage values were potentially biased when a low number of feeding attempts occurred, we only used trials wherein parents completed at least 10 feeding attempts per period (10 per control period, 10 per experimental period). This reduced our sample size (n = 86 trials, number of 10+ maternal feeding attempts = 45, number of 10+ paternal feeding attempts = 30). However, we were unable to obtain habitat quality data for all of these nests (see below) so our final sample sizes were further reduced (36 maternal trials, 26 paternal trials).

Parental investment was quantified from video-tapes by observers blind to color differences, experimental treatments, and habitat quality. Unfortunately, we could not reliably assess the size of food items brought to fledglings during the trial. However, previous research indicates that prey size does not vary with feeding rate in this population (Siefferman & Hill 2007). Food handling and transfer difficulties between parents and offspring, exacerbated by the wire mesh separating them, often caused parents to temporarily abandon feeding one fledgling and begin attempting to feed the other fledgling. Due to the inconsistency of food transfer, we used long-distance parental approaches to juveniles as a proximate measure of investment. Every time an adult directly approached one of the juveniles from outside the frame of the video screen, or from the perch one meter in front of the cage, we scored the event as a feeding attempt. Instances in which adults approached one juvenile, failed to deliver the food item, and immediately (and without retreat) approached the second juvenile with the food item were scored only as an approach for the first offspring. We feel that this scoring method, while less than perfect, best captures the choices that parents make when delivering food and minimizes the effects that delivery complications and additional offspring signals (e.g., close-range begging) had on parental feeding decisions.

Although we attempted to control for differences in hunger and begging between juveniles within trials, we also evaluated the effect that juvenile begging behavior had on parental feeding decisions. In a subset (n = 6) of trials we recorded the instances in which feeding attempts by parents were preceded by begging attempts in the ten seconds before the parental approach.

Color Manipulation

In every trial, the plumage of one fledgling (alternating between the heavier and the lighter bird between trials) was treated with a violet permanent marker (Prismacolor® PM-60: violet mist) while the plumage of the second juvenile was treated with a nontoxic black permanent marker (Sharpie® permanent marker: black). We attempted to apply marker ink to all of the blue feathers of each juvenile bluebird we manipulated (these feathers are limited to the wings and tail). Because the blue coloration of bluebirds results from microstructure rather than pigments, feathers colored with these markers still looked blue to a human observer and the reflectance from such feathers still had the spectral shape characteristic of blue (ink from the pens absorb a percentage of light reaching the microstructures, uniformly reducing the brightness of coloration; Liu et al. 2007).

In contrast to the results of previously published work that relied on violet markers to increase the brightness of adult bluebird contour feathers (Liu et al. 2007), we found that these markers actually reduced the mean total brightness of the blue juvenile feathers in our experiments (Fig. 2). However, treatment with black markers reduced mean total brightness to an even greater degree. Because we compared only the relative values of each color variable (see below), these treatments still produced the desired color changes between siblings.

Color Measurements

In order to examine whether the pre-manipulation color of juveniles played a role in parental provisioning during the control period, we obtained measurements of juvenal plumage color following the procedures described in Siefferman and Hill (2007). Briefly, we collected ~2cm of the fifth primary from all juveniles. One researcher (RL) then used an S-2000 spectroradiometer with a deuterium-halogen lamp (Ocean Optics, Dunedin, Florida, USA) and a micron fiber-optic probe at a 90° angle to the feather surface. The spectral processing program (ColouR v1.7, Queens, Ontario), was then used to quantify two standard descriptors of reflectance data for each individual: Mean brightness and UV chroma. Mean brightness is the average reflectance (R_{av}) in the 300-700-nm interval and UV chroma is the proportion of total reflectance that is in the UV range ($R_{300-400}/R_{300-700}$). Hue, defined as the wavelength of peak reflectance, was not used because the flattened shape of the reflectance curve in the UV-blue region (Fig. 2) meant that wide variation in hue values was possible with minimal differences in the actual shape of the reflectance curve. In addition to measuring the natural color of juvenile feathers, we also measured the color of feathers after they were manipulated.

Because relative differences in trait expression between offspring likely provide the most informative cues to parents when assessing their current brood, we used relative measures of color in all analyses. For each trial, the color values of the violet-treated fledgling served as the baseline value from which the color values of his brother were subtracted. When the violet-treated individual was brighter than his brother, this method resulted in positive brightness values. When the violet-treated individual was not as bright as his brother, negative values were obtained from the calculation. After analyzing the effects of natural color differences between brothers (relative color) on parental feeding rates, we isolated the effects of color manipulation on parental feeding decisions by examining the changes in relative color between control and experimental periods.

To ensure that our color manipulations did not influence the perceived sex of the fledglings in our experiment (i.e. sons not perceived as daughters by parents) we compared plumage color variables between darkened sons and unmanipulated daughters. We found that the plumage of daughters had significantly less UV-chroma than that of darkened males (t-test $T_{164} = 21.64$, $p < 0.0001$), significantly less reflectance in the UV (t-test $T_{164} = 4.79$, $p < 0.0001$), but did not differ in mean brightness (t-test $T_{164} = -0.50$, $p = 0.62$). The spectral shape of the female plumage was flatter (more achromatic) than that of darkened males, with higher reflectance at longer wavelengths (Fig. 3), therefore we feel confident that parents could accurately distinguish between darkened males and females.

Habitat Quality Measures

Breeding birds in low quality habitats exhaust food resources near their nestboxes more quickly than birds in high quality habitats and are therefore subsequently forced to travel greater distances to obtain food (Tremblay et al. 2005). The increased travel time results in lower provisioning rates for birds occupying areas with less abundant food resources. Because parental provisioning rates to offspring are correlated to habitat quality (Luck 2002; Tremblay et al. 2005), and because habitat quality is expected to influence parental feeding decisions (Davis et al. 1999), we measured the feeding rate of parents to nestlings several days prior to fledging and used this rate as a proximate measure of habitat quality.

Parental feeding rates were obtained by recording visits to nestboxes with a Hi-8 video camera for approximately 2 hours (beginning between 0600 and 0730 hours) on nestling days 10 (nests recorded = 5), 11 (n = 29), 12 (n = 6), or 13 (n = 2). Within this range, mean feeding rates did not differ by age (One-way ANOVA, $F_{3, 42} = 1.31$, p = 0.28). Recordings in which neither parent returned to the box for an extended period of time (>45 minutes) were excluded from analysis. To control for any differences between parents with respect to human-induced changes in behavior, the first 20 minutes of each tape were not scored. The total feeding rate (maternal rate plus paternal rate) was used to calculate habitat quality. In a study utilizing 12 hours of radio-transponder data to determine feeding rates of blue tits, Johnsen et al. (2005) found no difference between their observations and those obtained from one hour direct feeding observations. Additionally, previous research on this population of bluebirds found no difference in feeding rates between four-hour recordings and two-hour recordings (L. Siefferman, personal communication). Therefore, we feel confident that the length of our observation periods accurately captured the relevant information regarding relative parental feeding rates between nests.

In order to maximize our ability to detect different parental responses to nestling color in different quality habitats, we chose to split our territories into high and low quality habitats (upper half vs. lower half). When significant or near significant relationships were uncovered, we also compared changes in feeding rates in adjacent groups comprised of ten nests each.

For example, we compared parental responses in the ten lowest quality habitats (rank 1-10) to parental responses in the next ten habitats (rank 11-20). We performed these comparisons for all available sets of 10 (i.e. for females, 1-10 vs. 11-20, 2-11 vs. 12-21…17-26 vs. 27-36). Using this method, we were able to compare slope values in high and low quality habitats, which gave us an additional method to evaluate differences in parental responses between habitat qualities. These results agreed with those found using the larger (and more statistically robust) groups generated from splitting habitats into high and low groups.

Analyses

Because we predicted a causal effect of plumage color on parental feeding attempts we performed linear regressions between relative color and the percentage of feeding attempts each parent delivered to the violet-treated offspring (mothers and fathers analyzed separately). We analyzed nests irrespective of habitat quality and again after separating nests into high and low quality habitats. Identical tests were used to determine the effects of UV chroma on parental feeding during the control period.

The one hour control period established a baseline percentage of feeding attempts to each juvenile in a given trial and controlled for any pre-existing differences in parental preferences between offspring. We analyzed the effects of plumage manipulations on feeding decisions by comparing changes in relative color between control and experimental periods to changes in the percentage of feeding attempts (linear regression). By analyzing only the *changes* in the percentage of feeding attempts after color manipulations, we were able to more effectively isolate the effects of plumage manipulation on parental feeding decisions.

RESULTS

Control Period

Maternal feeding attempts during the control period were positively correlated with natural differences in brightness between sons ($R^2 = 0.11$, $F_{1, 45} = 5.32$, $p = 0.03$; Fig. 4). However, there was no significant correlation between relative brightness and maternal feeding percentage when analyzing habitat qualities separately nor was there any significant correlation between feeding rate and the relative UV chroma of sons.

During the control period, there was no significant relationship between paternal feeding rates and differences in either brightness or UV chroma.

Experimental Period

There was a tendency for mothers in low quality habitats to increase feeding attempts to sons as they became brighter relative to their brothers ($R^2 = 0.20$, $F_{1, 18} = 3.9$, $p = 0.067$; Figure 5) but there was no significant correlation between brightness changes and feeding attempts in high quality habitats ($R^2 = 0.00$, $F_{1, 18} = 0.0$, $p = 0.98$). When trials were analyzed irrespective of habitat quality, the effects of brightness on feeding attempts approached significance ($R^2 = 0.08$, $F_{1, 45} = 3.8$, $p = 0.06$). Changes in relative UV chroma did not influence maternal feeding attempts in any habitat.

Fathers in low quality ($R^2 = 0.38$, $F_{1, 13} = 6.84$, $p = 0.02$), high quality ($R^2 = 0.34$, $F_{1, 13} = 5.68$, $p = 0.04$), and all combined habitats ($R^2 = 0.29$, $F_{1, 30} = 11.67$, $p < 0.005$) increased feeding attempts to sons as they became relatively brighter (Fig. 6). However, changes in relative UV chroma were not related to changes in paternal feeding attempts in any habitat during the experimental period.

Influence of begging behavior on parental feeding attempts

Analysis of six trials in which we recorded whether begging occurred in the 10 seconds prior to parental approaches revealed that begging had little impact on parental feeding decisions. Only twice in the 366 feeding attempts recorded during these six trials did a juvenile beg before its parent landed near it.

DISCUSSION

We found a large effect of fledgling feather coloration on the rate at which offspring were provisioned by their parents. In our population, female bluebirds fed naturally brighter sons more than naturally darker sons. Natural differences in plumage color did not appear to influence male provisioning rates, but experimental changes in the relative brightness of juveniles caused males to increase feeding rates to relatively brighter juveniles in habitats of all qualities. In contrast, only females in low quality habitats increased the percentage of feeding attempts to sons as they got brighter relative to their brothers.

Feather brightness makes sense as a cue for assessing offspring quality because the brightness of blue primary feathers is a condition-dependent trait in juvenile bluebirds. Young male bluebirds raised in less-crowded nests with access to more food grow brighter feathers (Siefferman and Hill 2007). Prior studies with other bird species have also found that juvenal plumage coloration can be a signal of quality that alters the amount of food provided by parents. Direct (Tanner & Richner 2008) and indirect (Galván et al. 2008) measures of parental investment indicate that UV plumage coloration of great tit *Parus major* offspring influences the feeding decisions of parents. Tanner & Richner (2008) found that female great tits preferentially fed fledglings with normal plumage over fledglings with UV blocked plumage. No difference in feeding rate was observed for males. Galván et al. (2008) manipulated great tit plumage color in a similar manner, but only during the nestling period. These authors found a decrease in tarsus length in juveniles with UV-blocked plumage, indicating that parents reduced provisioning to these offspring. Both studies interpret parental preferences for juveniles with normal plumage as evidence that juvenal plumage is used as a signal of quality by great tit parents, contrary to the results found by Tschirren et al. (2005). These authors examined carotenoid-based breast plumage in juvenile great tits but detected no relationship between nestling plumage color and parental investment. This apparent disagreement in results may have arisen from differences in the plumage manipulation techniques used by the different authors. Tschirren et al. (2005) manipulated nestling color by increasing carotenoid ingestion to nestlings which likely resulted in color changes within the natural range of variation. In contrast to this dietary manipulation, both Tanner & Richner (2008) and Galván et al. (2008) used UV blocking techniques that reduced UV reflectance outside the range of natural variation. While these studies provide important preliminary analyses of the signaling function of juvenal plumage, they provide little information about how parents respond to natural variation in a trait (Hill 2006b).

In this study, we found that habitat quality influenced the relationship between parental feeding decisions and fledgling plumage color. Females increased feeding attempts to sons with relatively brightened feathers in low quality habitats, where food is presumed to be limiting, but not in high quality habitats, where food is presumed to be abundant. These observations are consistent with the theory that predicts that when food resources are limited, as in low quality habitats, parents will benefit if they invest more in their "best" offspring (Davis et al. 1999). Conversely, parents in high quality habitats might benefit by distributing food equally among offspring or even by biasing their provisioning efforts towards lower quality offspring. The surplus of resources in these environments could potentially allow parents to preferentially invest in smaller or weaker offspring in order to "catch them up" to their more developed siblings (Bize et al. 2006), ultimately increasing the total number of successful offspring.

In our study population male and female bluebirds respond differently to the brightness of their sons. As expected, females varied their feeding efforts based on natural differences in brightness between sons. However, males did not appear to allocate food differently to sons based on natural differences in plumage brightness. Females and males both responded to experimental changes in the relative brightness of their sons, but males increased feeding attempts to sons regardless of habitat quality while females did so only in low quality habitats. We suggest three, non-mutually exclusive explanations for these discrepancies. First, the control period may have been of an insufficient duration to accurately assess paternal feeding patterns. Although we limited our analyses to those trials in which fathers fed sons at least ten times during the control period, the average number of paternal feeding attempts during the control period was still significantly lower than the average number of maternal feeding attempts during the same period (average maternal feeds during control period = 18.8, average paternal feeds = 13.6, paired t-test p = 0.009). It is possible that the generally higher feeding rates of mothers during the control period contributed to the stronger observed feeding trend and the observed consistency between control and experimental periods.

Second, in the hierarchy of offspring signals that males assess, plumage brightness may rank lower for fathers than for mothers. If additional traits are assessed before plumage brightness, then differences in these traits may explain why there was no correlation between male feeding rate and natural differences in plumage brightness. Our control period allowed us to correct for these natural differences between male fledglings and assess only relative changes in feeding rate during the experimental period. That female feeding attempts were correlated to initial differences in offspring brightness and to changes in relative brightness during the experimental period suggests that plumage ranks higher in the hierarchy of signals assessed by females when making provisioning decisions to fledglings.

Third, males may be more likely to feed brighter and fitter offspring in all habitat qualities in order to maximize returns from their relatively limited feeding attempts. In this study, the number of paternal feeding attempts to fledglings was less than the number of maternal feeding attempts in 55 of 86 trials (Sign test; M = 12, p = 0.013), suggesting a consistently lower effort by fathers during the fledgling stage, contrary to previously published results (Plissner & Gowaty 1990). Although our feeding observations represent only a snapshot of fledgling care, if fathers provision offspring at lower rates than mothers then they may attempt to minimize risk of complete brood failure by consistently feeding better, brighter offspring. This strategy may not be shared by mothers because their increased feeding efforts should better allow them to respond to habitat quality and optimize reproductive output by provisioning offspring accordingly.

Changes in offspring proximity between nestling and fledgling stages make the likelihood that signals used by parents to assess young in the nest will be less useful outside the nest. Mouth color, used by adults of many bird species to assess nestling need and quality (Gotmark & Ahlstrom 1997; de Ayala et al. 2007; Ewen et al. 2008), is probably not as useful a signal outside the confines of the nest because fledged offspring are less likely to beg simultaneously when spatially separated (personal observation), at least early in the fledgling stage. Relative begging volume may also be more difficult for parents to assess after fledging, when nestlings are spatially separated (D. Mennill personal communication). Furthermore, begging by juveniles attracts predators (Haskell 1994; Leech & Leonard 1997). The risks associated with extended periods of begging likely contribute to the begging behaviors we observed, namely, begging only after parents have already approached fledglings. If our observations are representative of fledgling begging behavior in the wild, specifically in the first few days after leaving the nest, then parents are likely to rely on cues other than vocalizations when provisioning offspring. By assessing condition-dependent plumage traits, parents are able to assess the relative quality of their offspring without forcing them to reveal themselves through overt begging displays.

Natural selection and phylogenetic constraints have long been assumed to shape the appearance of juvenal plumage. However, birds represent a group in which we can explore potential intraspecific signaling functions of juvenile traits through various experimental studies. Birds possess many well-understood, sexually-selected, intraspecific signals of quality and condition and their readily observed behavioral patterns make them an ideal group in which to explore interactions between adults and juveniles. Recent work exploring such interactions makes it clear that signals of various types (quality and age) are likely to exist. Future work will elaborate on the type of signals used in parent-offspring communication, the environmental conditions that favor the use of such signals, and the mechanisms ensuring the honesty and stability of these traits.

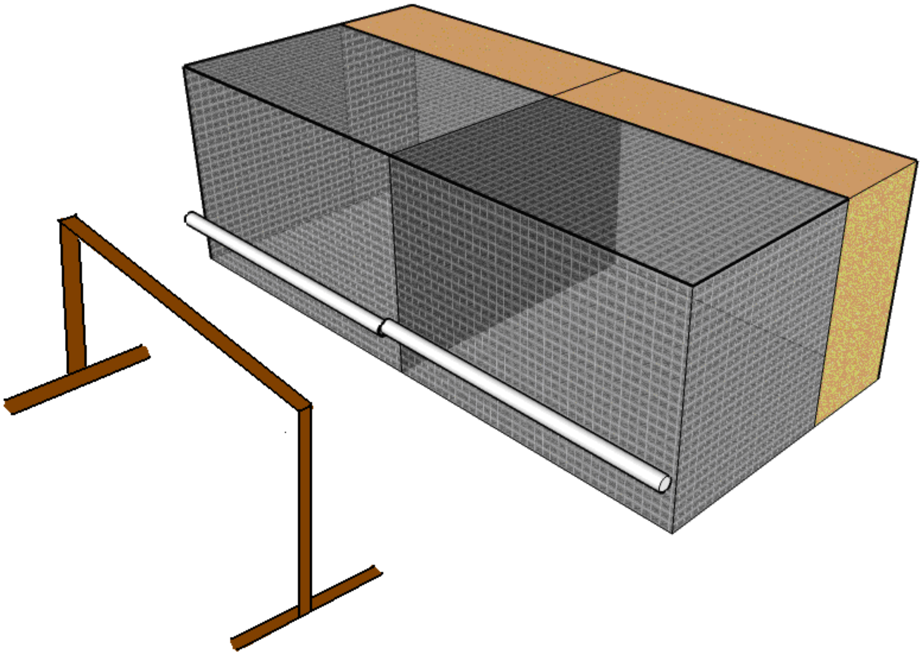

Figure 1. Experimental setup that allowed parental access to offspring while facilitating a side-by-side comparison and preventing visual or physical contact between sons.

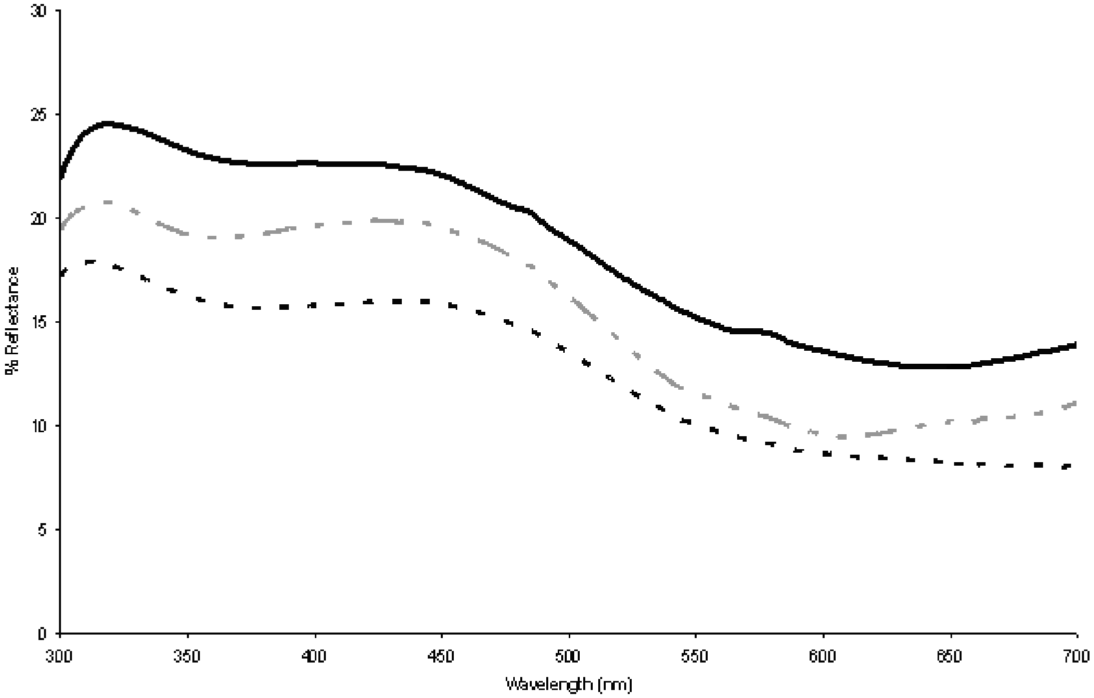

Figure 2. Average reflectance curves for unmanipulated juvenile males (solid black line), semi-darkened males (gray dashed line), and darkened males (dashed black line).

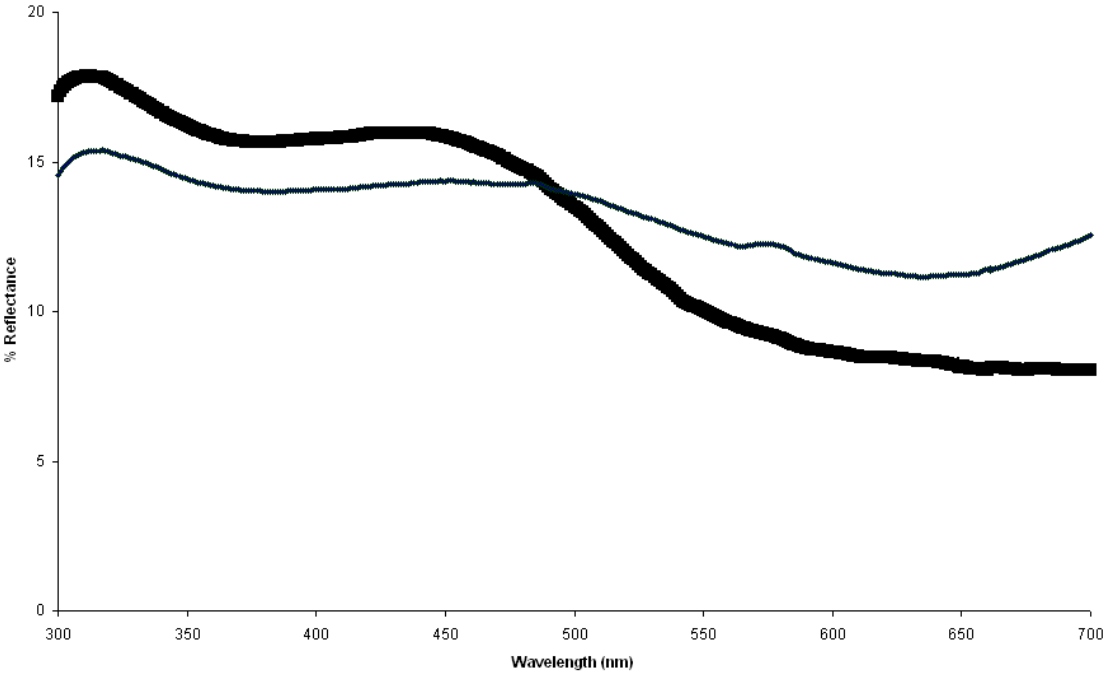

Figure 3. Average reflectance curves for darkened juvenile males (thick line) and unmanipulated juvenile females (thin line).

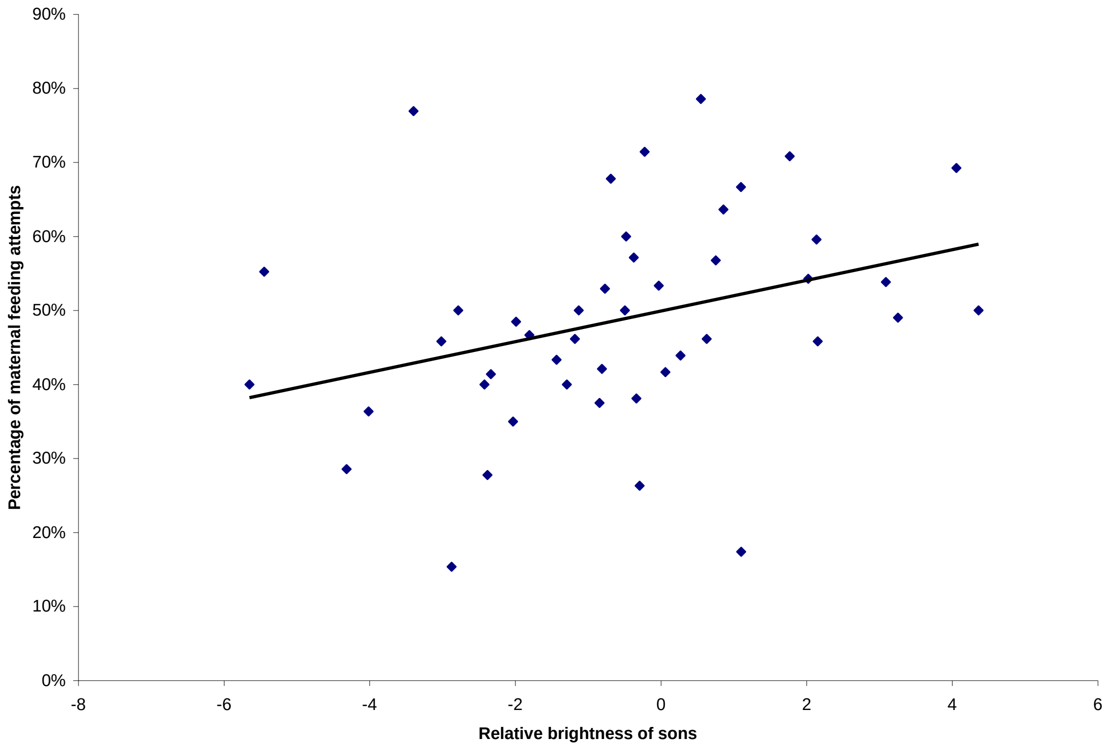

Figure 4. Relationship between the female feeding attempts and the relative brightness of sons during the control period.

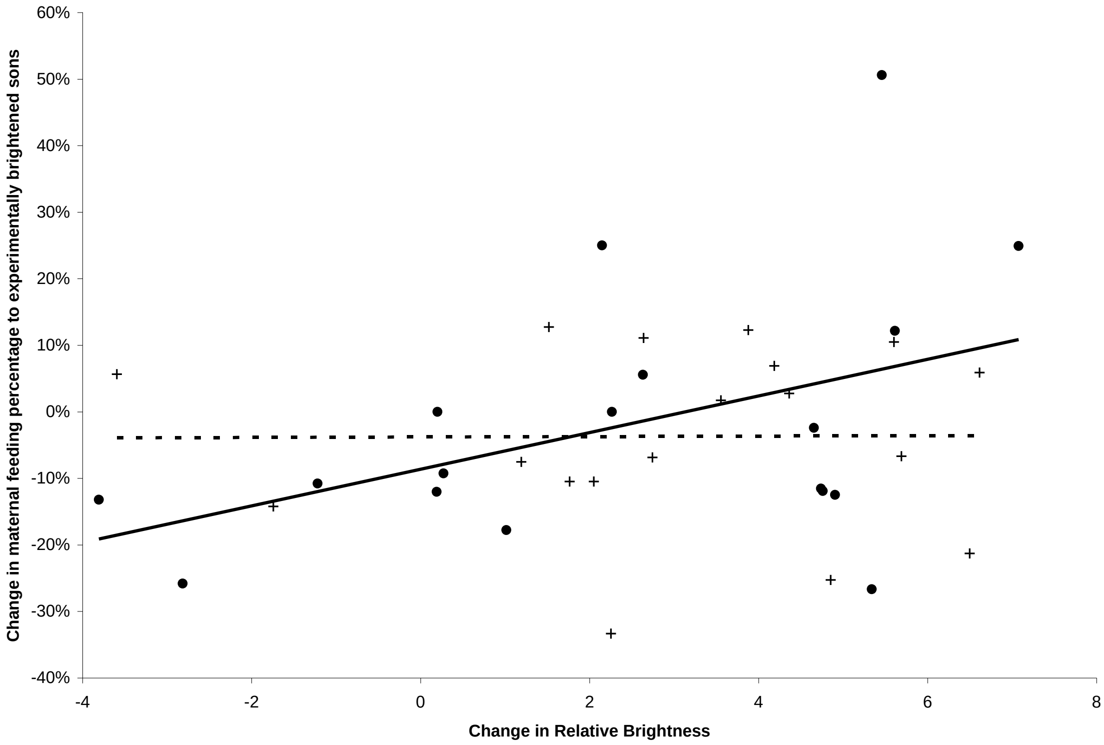

Figure 5. Relationship between the change in maternal feeding attempts and the change in relative brightness of sons during the experimental period in low quality (solid black line, circles) and high quality (dashed regression line, + symbols) habitats.

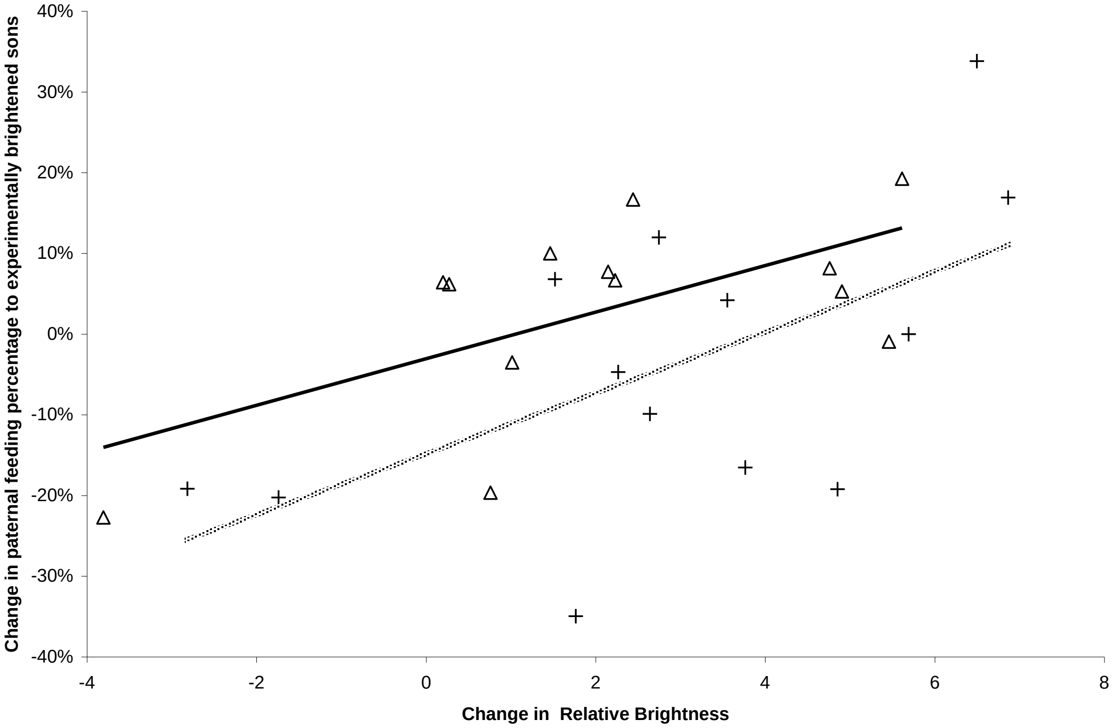

Figure 6. Relationship between change in paternal feeding attempts and the change in relative brightness of sons during experimental period in low quality (solid black line, triangles) and high quality (gray line, + symbols) habitats.

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