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## Is the juvenal plumage of altricial songbirds an honest signal of age? Evidence from a comparative study of thrushes (Passeriformes: Turdidae)

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### Abstract

The function and evolution of avian plumage colouration 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 colours and patterns of juvenal plumage, which is worn by altricial songbirds only for the first few months of life, have been the focus of few studies. 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 phylogenetic 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. Because many tropical bird species exhibit year-round territoriality and elongated breeding seasons, we used breeding latitude as a proxy for these variables. As predicted, distinctive juvenile appearance was significantly correlated with occupancy of tropical latitudes. While alternative explanations cannot be ruled out and more tests of the hypothesis are needed, the observed associations between breeding latitude and distinctiveness of juvenal plumage are consistent with our hypothesis that distinctive juvenal plumage evolved as a signal of sexual immaturity.

**Key words:** Juvenal plumage – honest signals – aggression – latitude – Turdidae

### Introduction

Ontogenetic colour changes, defined by Booth (1990) as 'non-reversible colour changes associated with normal progressive development of an individual of a species', occur across a wide taxonomic spectrum (Booth 1990). Examples of ontogenetic colour change include spiders that mimic different species of ants as they age (Reiskind 1970), insects that gain thermoregulatory advantages as dark early instar nymphs before becoming cryptic adults (Johnson 1985), fish that mimic predators to gain protection and escape detection when they are young and vulnerable (Zaret 1977), reptiles that mimic insects at small sizes before becoming cryptic once they outgrow their insect models (Huey and Pianka 1977), and mammals whose juvenile colour elicits protection and care (Alley 1980). Apparently, the functions of ontogenetic colour change vary as widely as the groups exhibiting such change (reviewed in Booth 1990).

At every stage of development, the external colouration of diurnal animals is likely to be shaped by three distinctly different forms of selection: thermoregulation, risk of capture by visual predators and the benefits of communication with conspecifics (Cott 1940; Williams 1996). From the time of Darwin and Wallace, communication and crypsis have been recognized as often opposing influences, with predation selecting for camouflage or mimicry and intraspecific interactions promoting bold and brilliant colouration. Numerous studies have confirmed that both influences shape the colouration of animals, and functional explanations of bird colouration in particular have received a great deal of attention (reviewed in Hill and McGraw 2006). The well-supported theory on the function and evolution of plumage colouration, however, has focused almost entirely on the basic and alternate

plumages (i.e. 'adult plumage') of birds. Juvenal plumage has largely 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 (Bonnievie 2007). Although the colour and pattern of juvenal plumage could play a central role in survival during this critical period, juvenal plumage colour and pattern have received little attention by researchers. A number of papers have proposed one benefit or another for the colours of downy and juvenal plumage in precocial birds (Chaniot 1970; Dorward and Ashmole 1963; Buckley and Buckley 1972; Stoutejesdijk 2002), but the possible functions of the colouration of juvenal plumage in altricial birds has only recently begun to receive attention (Tanner and Richner 2008; Galván et al. 2008; Griggio et al. 2009; Ligon and Hill 2009, 2010; Moreno and Soler 2011).

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 and 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 a hazard for yearling birds throughout their first winter and first breeding season. Consequently, the benefit of signalling subordination 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 and European

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passerine birds (Rohwer et al. 1980; Senar 2006; Hawkins et al. 2012). 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 (Delayed Plumage Maturation) is likely 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 colouration 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 benefit from a signal of immaturity by avoiding the directed attacks of territorial adults. Adults would benefit by not expending time and energy engaging individuals that pose no reproductive threat.

We propose that juvenal plumages that are distinct from adult plumages in colour 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 signalling juvenile and the responding adult, would be in the immediate recognition of non-reproductive status.

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), often making them recognizable as members of their species at the time they leave the nest (Collar 2005). Any plumage characteristics shared with older individuals 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, 2–3 times longer in tropical regions than are the breeding seasons of closely related taxa in the temperate zone (Stutchbury and 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 more common in tropical birds (Stutchbury and Morton 2001), with territorial aggression even higher during the non-breeding season for some tropical species (Fedy and Stutch-

bury 2005). Year-round territoriality is estimated to occur in at least 60% of Panamanian passerine species (Stutchbury and Morton 2001). The combination of lengthy breeding seasons and the prevalence of year-round territoriality amplify the risk that juveniles 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 species. Of course, there are other important differences between temperate and tropical habitats (e.g. light, predators, competitors and parasite-load) that might also shape the colouration of young birds.

We tested our prediction by tracing changes in plumage distinctiveness and changes in temperate versus tropical breeding range across a phylogeny of thrushes (Turdidae) and looking for congruence between breeding latitude and distinctiveness of juvenal plumage. A correlation between these traits 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 study, 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*, *Hyllocichla*, *Ridgwayia*, *Ixoreus*, *Platycichla*, *Cichlherminia*, *Psophocichla*, *Chlamydochaera*, *Cataponera*, *Geomalia*, *Nesocichla*, *Cichlopsis*, *Myadestes* and *Sialia*; Collar 2005) by joining several recently published phylogenies (see Fig. 3 for complete list of species included). In total, we included 91 of the roughly 336 species within Turdidae based on the availability of molecularly informed phylogenetic data and colour plates of adult and juvenal plumages.

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). The placement of species within *Myadestes* was obtained from Miller et al. (2007), and that of species within the genera *Turdus*, *Cichlherminia*, *Nesocichla* and *Platycichla* 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*, *Entomodestes*, *Psophocichla*, *Sialia* and *Ixoreus*.

We used equal branch lengths because of the difficulty associated with combining branch lengths from several different studies (difficulties highlighted by Winker and Pruett 2006), each using different combinations of molecular markers. In previous studies (e.g. Martins and Garland 1991; 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 breeding range occurred between the tropics of Capricorn and Cancer. Species were characterized as 'non-tropical' if the majority of their breeding range occurred outside of the tropics. Distribution and range maps were obtained from published accounts (Clement and Hathway 2000; Collar 2005). Scoring of geographic distribution was done by one of us (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 colouration or (2) plumage pattern (e.g. *Turdus dissimilis*, *Turdus pallidus*; Fig. 1). Adults and juveniles that were readily distinguishable at first glance were considered to exhibit strong dissimilarity. If adults and juveniles of a species were determined not to exhibit strong differences with respect to plumage (1) colour or (2) pattern, then that species were categorized as 'not distinct' (e.g. *Turdus philomelos*, *Zoothera dauma*). For the 20 sexually dichromatic species (e.g. *Turdus merula*, *Turdus obscurus*) in our analysis, we compared juvenile appearance to both adult males and females, such that 'distinct' juveniles were readily distinguishable from adults of both sexes. 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 'not distinct'. Although it would be interesting to trace the evolution of adult and juvenal plumage patterns independently, a complete reconstruction of the multiple evolutionary pathways of juvenile and adult thrushes is beyond the scope of the current study and, more importantly, does not address the goal of supporting or disproving our hypothesis regarding the signalling function of distinctive juvenile appearance. The classification of each species as either 'distinct' or 'not distinct' allowed us to focus on instances when plumage differences between adults and juveniles might serve a signalling function.

Information regarding plumage traits was obtained from published colour plates (Clement and Hathway 2000). Plumage character assignments were made by five volunteers unfamiliar with the species in question and blindly with respect to geographic range. Specifically,

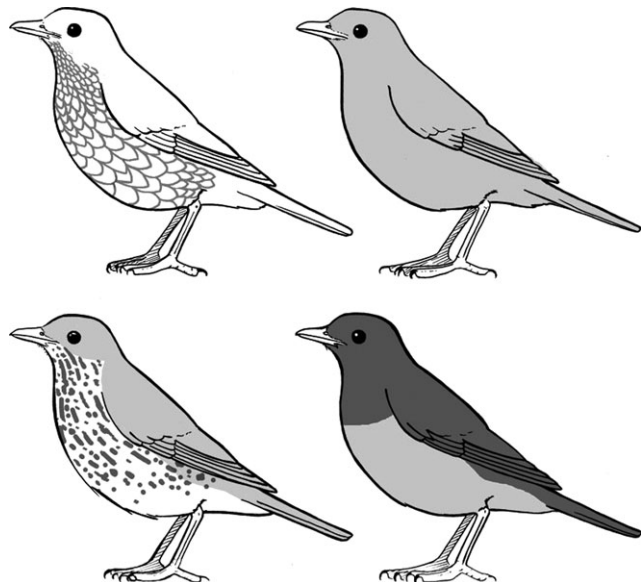


Fig. 1. General plumage patterns, commonly seen in adult and juvenile Turdids, that would be classified as 'distinct' from one another based on the scoring system we used. Each plumage pattern in this figure would be classified as 'distinct' with respect to colouration, pattern or both when compared to the other plumage patterns represented

each species was assigned to a plumage category by scorers presented only with colour plates of adults and juveniles, without any additional information (including range maps or species names). When plumage assignments were not unanimous (14 out of 91 species), 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 and 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 and discrete character.

### Correlated character evolution

To examine the relationship between current distribution (year-round tropical versus 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 and 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 and 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 2000, 2006) to test for correlation between plumage distinctiveness and latitude on our composite phylogeny in the program MESQUITE v2.0 (Maddison and 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 and 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 analysed only such contrasting pairs. Comparisons of these pairings allowed us to ask whether species that contrast in latitude also contrast in a predictable manner with respect to plumage distinctiveness.

## Results

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. 2). For a summary of the interspecific differences in location and distinctiveness, organized by clade, see Table 1.

### Ancestral state reconstruction

Distinctive juvenile appearance appears to have evolved independently 6–14 times among the species we analysed, and indistinct juvenile appearance arose independently 9–15 times (Fig. 3).

### Correlated character evolution

Using Pagel's (1994) test of correlated character evolution, we found a significant association between geographic distribution and distinct juvenile plumage relative to adult plumage ( $p = 0.006$ , 1000 simulations; Fig. 3).

The results of the pairwise comparisons agree with those obtained from Pagel's test for correlated character evolution (Pagel 1994). Fifty thousand pairings in which both character

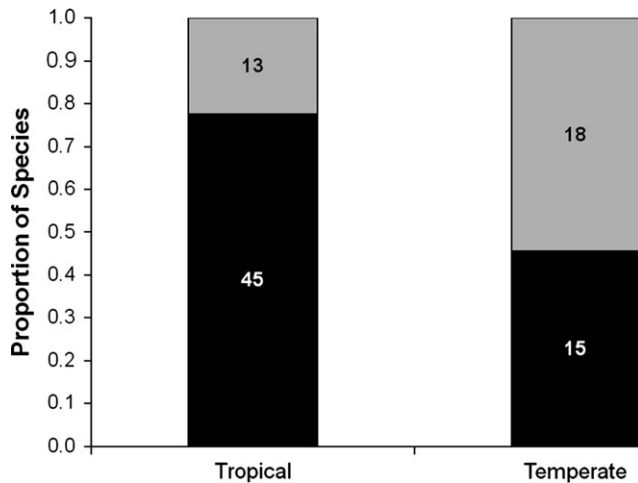


Fig. 2. The proportion of species exhibiting distinctive plumage (black) relative to the proportion of species exhibiting indistinct plumage (grey) for tropical and temperate thrushes. Numbers shown are total number of species exhibiting the different plumage characteristics

states of pair members differed showed that latitude and plumage distinctiveness are significantly related (best tail  $p = 0.046$ ; range: 0.005–0.291).

## Discussion

Drab juvenal plumage has often been presumed to be an ancestral appearance lacking functional significance (Maley and Winker 2007). Alternatively, it has also been assumed that juvenile appearance is shaped primarily by natural selection and a need for crypsis (Graber 1955). Recently, however, numerous studies have shown that the colour and pattern of juvenal plumage are important in mediating intraspecific interactions (Penteriani et al. 2007; Tanner and Richner 2008; Galván et al. 2008; Griggio et al. 2009; Ligon and Hill 2009, 2010).

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 colour and pattern serve as a signal of age, and sexual immaturity places distinctive juvenile colouration into the category of a 'status-related strategy signal' within Dale's classification system. The features of juvenal plumage colouration classified as distinct in our study are consistent with the predicted qualities of such status-related strategy signals – plumage colouration 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 juvenal 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 relative costs and benefits of signalling reproductive immaturity are likely to be, at least partially,

responsible for the repeated gains and losses of plumage distinctiveness within the thrush species we examined. Furthermore, 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 if they are perceived as reproductive competitors. Similar benefits of distinctive juvenile appearance have been discovered among taxonomically diverse groups including lizards (Clark and Hall 1970), fish (Fricke 1980) and primates (Alley 1980).

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 colour of some bird species, and particularly tropical jays (Family Corvidae), serve as a signal of age. He performed experiments altering the bill colouration 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 when the intruder's bill resembled that of a juvenile. The distinctive appearance of young birds, in this case achieved through age-specific colouration 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; Clark and Hall 1970; Fricke 1980; Alley 1980), despite the fact that individuals bearing such an appearance often have fully formed sex organs (Lawton and Lawton 1986 and references therein).

## Alternative hypotheses

Although our results are consistent with the hypothesis that distinctive juvenal plumage evolved as a signal of immaturity, the observed relationship between tropical distribution and distinctive juvenal plumage is consistent with alternative hypotheses as well.

The preponderance of distinctive juvenal plumage in the tropics could represent an increased predation risk for juveniles fledging in the tropics. Although drab juvenal plumage has often been presumed to represent an ancestral appearance (Maley and Winker 2007), when a functional explanation has been applied to juvenal plumage colouration it is usually that such plumage colouration aids in camouflaging young birds. Few studies, however, have demonstrated that any aspect of juvenal plumage colour 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. Although crypsis and signalling immaturity are not mutually exclusive functions for the colour and pattern of juvenal plumage, further studies will be required

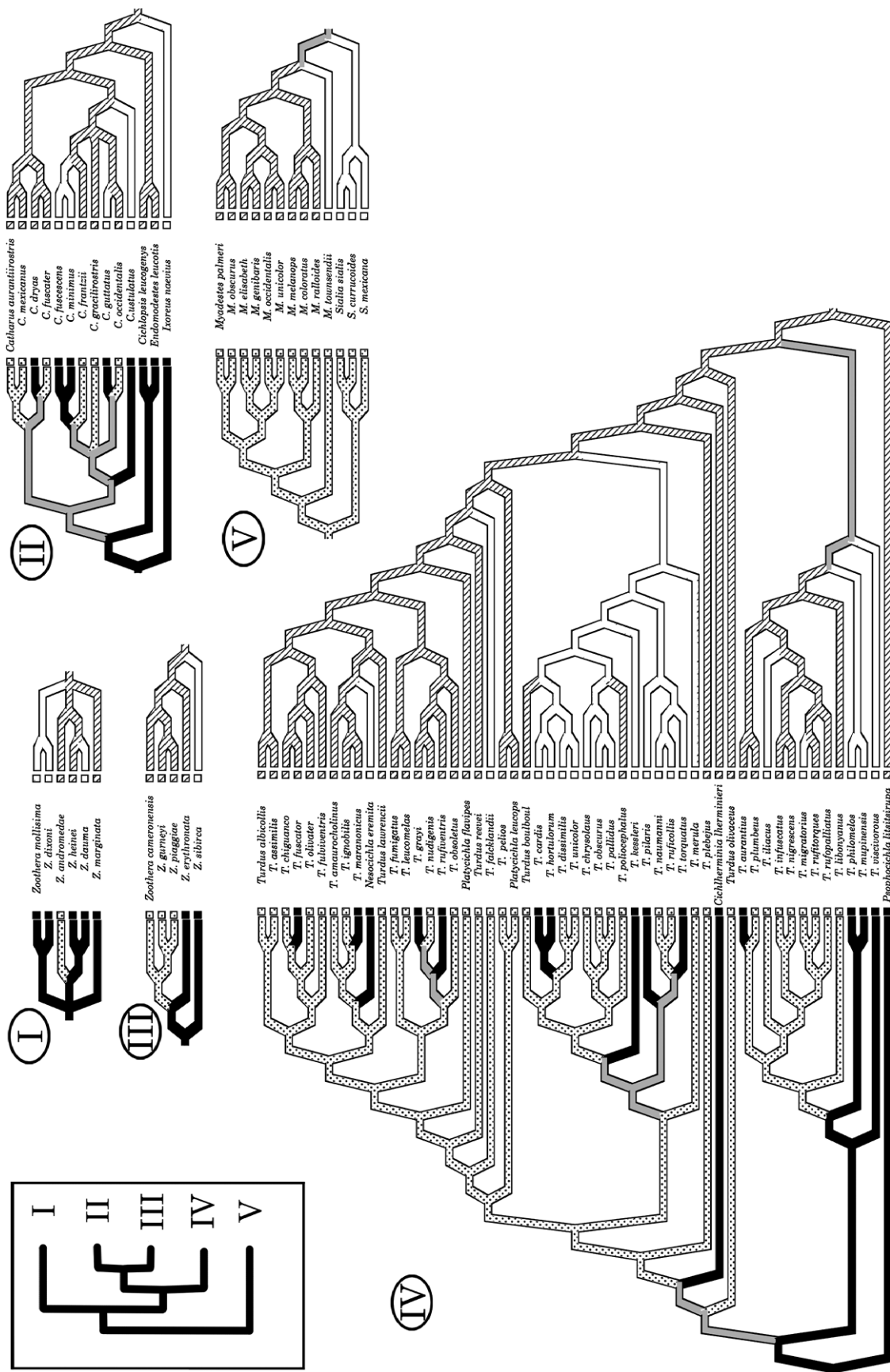


Fig. 3. Reconstruction of plumage differences and breeding latitude using a composite phylogeny of the Turdidae. Overall tree topology is presented in the top left corner of the figure, and major clades are represented by Roman numerals (defined in Table 1). Plumage was characterized as distinct between adults and juveniles (polka dot pattern) or indistinct between adults and juveniles (black) and is represented on the left side of each mirrored clade. Breeding latitude was characterized as tropical (diagonal line pattern) or temperate (white) and is represented on the right side of each mirrored clade. Grey denotes an equivocal state. Plumage type and breeding latitude were reconstructed as discrete characters using maximum likelihood in MESQUITE (Maddison and Maddison 2006)

Table 1. Turdidae traits (distinct versus not distinct, tropical versus temperate) broken down by clade. Clade numbers refer to Fig. 3

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

to determine the relative importance of these pressures in shaping the 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 be useful in assessing the relative importance of intra- and interspecific factors affecting plumage appearance. However, in this study, we assessed only strong differences in plumage pattern and colour, not subtle variation or gradation in colour quality, and spectrophotometric data would, therefore, contribute little to the interpretation of our results.

Differences in mating systems and territory use between temperate and tropical species might also contribute to the observed trend of increased juvenile distinctiveness in tropical thrush species. The year-round territoriality exhibited by many tropical passerine species (Stutchbury and Morton 2001) may increase the benefits of costly, bold or colourful signals for adults defending their territories (West-Eberhard 1983; Amundsen 2000; Murphy et al. 2009). Because participation in territory defence by both sexes is common (approximately 87% of resident Neotropical passerine species; Stutchbury and Morton 2001), adult females may experience social selection favouring appearances similar to those of their mates. Therefore, benefits associated with particular adult plumages might lead to differences between adults and juveniles, irrespective of the benefits such distinctiveness confers on sexually immature juveniles.

#### Exceptions proving the rule?

Empirical analysis of plumage patterns across thrushes showed that our predictions regarding breeding latitude and plumage distinctiveness were far from perfect. Although juvenal plumage did not always match our predictions, some of the exceptions (e.g. temperate species exhibiting distinctive juvenal plumage) might actually strengthen our hypothesis. Exceptional species include temperate breeders that have prolonged breeding seasons, increasing the likelihood that young from early-season broods will fledge into an environment with actively breeding and aggressive adults. In the south-eastern 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. In fact, it has recently been shown that adult males use plumage colour and pattern as cue when attacking territorial intruders and direct significantly less aggression towards models bearing juvenal plumage (Ligon and Hill 2009).

#### Conclusions

In the present study, we have attempted to build on recent experimental work in an attempt to uncover the broader scale ecological and life-history characteristics that promote intra-specific plumage signals in juveniles. While alternative explanations cannot be ruled out and more tests of the hypothesis are needed, the observed associations between breeding latitude and distinctiveness of juvenal plumage are consistent with our hypothesis that distinctive juvenal plumage evolved as a signal of 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. Although 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.

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#### Resumen

*¿Es el plumaje juvenil de passeriformes altriciales una señal honesta de inmadurez reproductiva? Evidencia de un estudio comparativo en los tordos (Familia Turdidae)*

La función y evolución de la coloración en el plumaje de aves ha sido objeto de numerosos estudios durante la última década. Sin embargo, la gran mayoría de estos estudios se han concentrado en el plumaje de individuos maduros sexualmente. Los colores y patrones del plumaje juvenil, el cual es vestido por paseriformes altriciales solo durante los primeros meses de vida, han sido poco estudiados. Nosotros teorizamos que la distintiva apariencia juvenil de estas aves puede ser una señal de inmadurez sexual, la cual sirve para reducir la agresión de adultos congéneres. Nosotros utilizamos un enfoque filogenético comparativo para examinar esta hipótesis en los tordos (Familia Turdidae). Señales honestas de inmadurez reproductiva deben ser más importantes en las aves juveniles que abandonan el nido en entornos donde hay adultos congéneres agresivos. Por lo tanto, nosotros predijimos que es más probable que una apariencia juvenil distintiva haya evolucionado en especies que presentan temporadas reproductivas extendidas y altos niveles de territorialidad. Muchas especies de aves tropicales exhiben territorialidad a lo largo de todo el año y temporadas reproductivas extendidas, por lo tanto nosotros utilizamos la latitud donde estas especies se reproducen como sustituto de esas dos variables. La apariencia distintiva juvenil estuvo significativamente correlacionada con las latitudes tropicales según lo previsto. Mientras que otras hipótesis no pueden ser descartadas y más investigaciones examinando estas hipótesis son necesarias, las asociaciones observadas entre latitud de reproducción y plumajes juveniles distintivos son consistentes con nuestra hipótesis original planteando que el plumaje juvenil distintivo evoluciono como una señal de inmadurez sexual.

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