ECOLOGICAL CO-OPTATION IN BIRDS

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ABSTRACT

ECOLOGICAL CO-OPTATION IN BIRDS

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Natural selection is commonly thought as the engine of ecological diversification, where sexual selection has a secondary role in promoting speciation. Sexual selection is also attributed a primary role in the origin of species, where it produces divergence not in ecological traits, but in sexually selected traits. Ecological co-optation suggests an alternative to these prevailing ideas. Sexual selection alone could drive ecological diversification, where a sexually selected trait is co-opted for a novel viability trait. Such an ecological co-optation will then enable species with newly co-opted trait to exploit a novel niche. In the present study, we test the prediction of ecological co-optation in antbirds, tanagers, and blackbirds. We use sexually selected plumage coloration in these groups, and check whether the birds with colorful plumage differ in their niche use (*i.e.* habitat range, altitudinal range, and distributional range), by using phylogenetically independent contrasts method, and sister taxa comparisons. Our results show that increasing plumage coloration produces changes in niche uses. Similarly, increasing plumage color differences between sexes leads to changes in niche width, which is a trend consistent with ecological co-optation hypothesis.

Keywords: Speciation, ecological diversification, sexual selection, plumage coloration, niche width.

ÖZ

KUŞLARDA EKOLOJİK ATAMA

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Genel kanıya göre ekolojik farklılaşmaya neden olan temel mekanizma doğal seçilimdir. Bu farklılaşma süresince, eşeysel seçilimin türleşmeye katkısı ikincildir. Bunun yanı sıra, türleşmede eşeysel seçilimin birincil bir rolü olabileceği kanısı da mevcuttur. Burada türler arasında farklılaşan özellikler ekolojik olanlar değil, eşeysel olanlardır. Bu görüşlere alternatif olan görüş ekolojik atamadır. Bu görüşe göre, eşeysel bir karakterin yaşamsal bir karaktere atanması ile eşeysel seçilim başlı başına ekolojik farklılaşma yaratabilir. Ekolojik atama, bu şekilde yaşamsal faaliyetler için atanan karaktere sahip türlerde yeni niş kullanımını öngörür. Biz bu çalışmamızda, ekolojik atamanın tahminini, Amerika kıtasında yaşayan üç kuş grubundaki renklenmelere bakarak test ettik. Filogenetik analizler ve kardeş tür karşılaştırmaları ile, ekolojik atamanın tahmin ettiği doğrultuda, renklilikteki artışa bağlı olarak niş kullanımı bakımından (*i.e.* habitat, yükseklik, dağılım) göze çarpan farklılıklar tespit ettik. Benzer şekilde, eşeyler arasındaki renk farklılığının da niş kullanımını etkilediğini gözlemledik ki bu da ekolojik atamayı destekleyen bir bulgudur.

Anahtar Kelimeler: Türleşme, ekolojik farklılaşma, eşeysel seçilim, tüylerde renklilik, niş genişliği

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CHAPTER 1

INTRODUCTION

Darwin (1859) endeavored to illuminate how lineages split as early as 1859 in his extraordinary book *On the Origin of Species*. Since then, elucidating the significant diversity of life has been a major challenge in evolutionary biology. Previous discussions on how new species arise mainly center around the role of geography such that geographic circumstances have been used to classify speciation (Gavrilets 2003). Three geographic modes of speciation cover allopatric, parapatric, and sympatric speciation. Allopatric and sympatric speciation represent the two extremes where new species emerge from geographically isolated populations with no gene flow between them in the former, and from a single local population with panmixia in the latter. Although allopatric speciation has been commonly accepted as the null model of speciation (Coyne & Orr 2004), parapatric speciation with intermediate levels of gene flow is probably the most common from of speciation (Gavrilets 2003). Nonetheless, recent studies suggest that speciation despite gene flow is also a plausible form of species formation (*e.g.* (Maynard Smith 1966; Bush 1969; Rice & Salt 1990; Dieckmann & Doebeli 1999; Van Doorn *et al.* 2009).)

Apart from the focus on geographical context of speciation, there is also a focus on the processes driving speciation (Ritchie 2007). One such focus questions the role of sexual selection in speciation. On the one hand, studies focusing on the role of ecology in speciation attribute a secondary role to sexual selection, where ecological divergence of populations evolves initially. Sexual selection will then contribute to the ecological divergence generated by natural selection (see references below). On the other hand, some studies attribute a primary role to sexual selection, where the evolution of sexual traits directly leads to reproductive isolation and speciation without producing ecological differences (Price 1998).

The main driving force of speciation is commonly thought as ecological divergence (Schluter 2001). Allopatric or sympatric populations initially diverge in their ecological attributes in response to divergent or disruptive natural selection, respectively (Dobzhansky 1940; Maynard Smith 1966; Bush 1969; West-Eberhard 1983; Dieckmann & Doebeli 1999; Van Doorn *et al.* 2009). Once populations become adapted to different environmental conditions, reproductive isolation will evolve between populations (Schluter 2001). This could occur if the trait adapting individuals to different environments directly causes nonrandom mating (Maynard Smith 1966; Schluter 2001), or if the trait under selection

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becomes genetically correlated to the trait(s) responsible for nonrandom mating (Maynard Smith 1966; Schluter 2001; Gavrilets 2003). Examples for the former scenario (where a given ecological trait has a pleiotropic effect) would be: host fruit choice in *Rhagoletis* flies affects mate choice (Bush 1969); copper tolerance, and floral traits preferred by pollinators in monkeyflower results in reproductive incompatibility (MacNair & Christie 1983), and strong premating reproductive isolation (Schemske & Bradshaw 1999), respectively; beak morphology and body size in Darwin's ground finches shape vocal features, which probably used as a mate recognition signal (Podos 2001); habitat selection in threespine sticklebacks affects female preference (McKinnon *et al.* 2004). In both cases, ecological conditions that vary from one habitat to the other is what drives divergence between populations. Sexual selection in the form of assortative mating promotes the divergence initiated by ecology-driven processes. In other words, sexual selection links adaptation to speciation (Price 1998).

Rather than ecological divergence, sexual selection by itself may produce biological species. In that case, it is not ecological specialization, but reproductive specialization (*e.g.* change in mating systems due to changes in morphology or behavior) that will lead to diversification (Heard & Hauser 1995). In fact, this idea dates back to Darwin's observations across a wide range of taxa including crustaceans, insects, fish, birds, reptiles, mammals that closely related species mostly vary in secondary sexual characters (West-Eberhard 1983). Evidences for the role of sexual selection in causing speciation come both from theoretical and empirical studies (Lande 1981; Kirkpatrick 1982; Lande 1982; Wu 1985; Barraclough *et al.* 1995; Mitra *et al.* 1996; Payne & Krakauer 1997; Moller & Cuervo 1998; Owens *et al.* 1999; Seehausen & van Alphen 1999; Irwin 2000; Uy & Borgia 2000; Wilson *et al.* 2000; Masta & Maddison 2002).

Theoretical studies modelling the evolution of speciation by pure sexual selection (Lande 1981; Kirkpatrick 1982; Lande 1982; Wu 1985; Payne & Krakauer 1997) is mainly inspired by the verbal model of Fisher's runaway sexual selection. Fisher (1930) proposed a genetic mechanism to explain the evolution of mating preferences in females, and subsequent coevolution of exaggerated traits in both sexes: exaggerated secondary sexual characters in males, and exaggerated mating preferences in females. The key point of this process is the establishment of a genetic correlation between sexes such that any increase in the frequency of male trait will be corresponded by an increase in the frequency of female preference (Futuyma 2009). These models based on Fisher's runaway sexual selection indicate that the joint evolution of female preference and male secondary sexual trait could produce sexual isolation, which, in turn, imply reproductive isolation and speciation.

Empirical studies also provide evidence in support of speciation by sexual selection. If it is sexual selection that gives rise to several distinct species, it is expected that clades with intense sexual selection will be more speciose (Barraclough *et al.* 1995; Mitra *et al.* 1996; Moller & Cuervo 1998; Owens *et al.* 1999). This expectation is confirmed in comparative studies with birds (but also see Price 1998; Panhuis *et al.* 2001), where species richness is high in sexually dichromatic clades (Barraclough *et al.* 1995; Owens *et al.* 1999), in promiscuously mating clades (Mitra *et al.* 1996), and in clades sexually dimorphic in feather ornamentation (Moller & Cuervo 1998), as well as in case studies where variation in morphology and behavior is usually related to courtship and mating [*e.g.* in Hawaiian *Drosophila* (Ringo 1977), in cichlid fishes (Seehausen & van Alphen 1999; Wilson *et al.* 2000), in field crickets (Gray & Cade 2000), in greenish warblers (Irwin 2000), in Vogelkop bowerbird (Uy & Borgia 2000), and in jumping spiders (Masta & Maddison 2002)].

Studies on speciation that either attribute an initiative role to ecology, or to sexual selection in the origin of species have a tendency to seperate traits into two discrete classes: sexual traits whose functions are restricted to a sexual context, and viability traits whose functions are restricted to a viability context. Nonetheless, it is often difficult to categorize an already complex trait in one of the two classes. In moth *Utetheisa ornatrix* and tiger moths, for example, males produce alkaloids both to avoid predation and to produce a pheromone during precopulatory interaction with the female (Eisner & Meinwald 1995; Weller *et al.* 1999). Similarly, in the poison frog *Oophaga pumilio*, aposematic coloration in males deter predators, and is subject to female choice at the same time (Maan & Cummings 2009). Hence, it is possible that a given trait serves both in a sexual and viability context over the long course of its evolutionary history.

In line with the view that the function of a given trait can change during its history, ecological co-optation suggests an alternative to the classical view of ecological diversification (Bonduriansky 2011). Here, sexual selection initiates ecological divergence, which is later driven to speciation by natural selection. This idea dates back to Lande & Kirkpatrick (1988) who in their model suggest that when the sexually selected trait in males have an ecologically important function, sexual selection could carry a population to a new niche. The mechanism of ecological co-optation differs from models of ecological speciation in that it attributes a primary role to sexual selection in ecological diversification, and also differs from other models of speciation by sexual selection in that it does not only produce reproductive isolation, but ecological differentiation, as

well.

Ecological co-optation hypothesis is based on a process with three main stages (Bond">(Bonduriansky 2011). At the first stage, sexual selection counteracts natural selection and displaces a population from its viability optimum. At the second stage, sexually selected trait is co-opted for a novel viability trait. This can occur when environmental conditions change, or when the evolution of sexual trait brings about individuals that are capable of exploiting a new niche. At the final stage, the novel viability trait expressed in the sexually selected sex is cross-transferred to the other sex, increasing the viability of both sexes. If ecological co-optation occurs when sexual selection produces phenotypes capable of invading a new niche, the final stage will refer to niche shift of a given population. Ecological co-optation hypothesis predicts that an ancestrally sexually dimorphic population with only males having a sexually selected trait will evolve to a sexually monomorphic population with both males and females having the sexually selected trait co-opted for a viability-related function. That sexually monomorphic population will then be able to exploit a novel ecological niche, becoming ecologically diversified (Bonduriansky 2011).

The mutual ornamentation prediction of ecological co-optation can also be explained by other hypotheses. Genetic correlation, for example, could produce mutual ornamentation, where females do not benefit from the ornament, but express it as a genetically correlated result of male ornament under sexual selection (Amundsen 2000; Kraaijeveld *et al.* 2007). Alternatively, social competition (competition over sexual resources, *i.e.* mates, and non-sexual resouces *i.e.* food, hibernation space, nesting material) could generate similar or monomorphic expression of ornaments in both sexes (West-Eberhard 1983). Mutual mate choice where both sexes are choosy could also produce ornamental traits both in males and females (Amundsen 2000). Lastly, sexual mimicry, where females concealing their sex, and appearing as "pseudomales" are favored by selection, could again result in mutual ornamentation (Amundsen 2000; Kraaijeveld *et al.* 2007). Nonetheless, ecological co-optation does not only predict mutual ornamentation, but also novel niche use in mutually ornamented species, which makes its prediction unique.

In the present study, we used plumage coloration in birds to examine whether colorful plumage in both males and females represent an example of an ecologically co-opted trait. Indeed, plumage coloration corresponds well to each premise of ecological co-optation. As suggested in the first premise, sexual selection on conspicuous plumage colors in male birds could drive them away

from the viability optimum since they will have a higher risk of predation. As mentioned in the second premise, conspicuous plumage color in males could eventually enable individuals to invade a new niche. Conspicuous plumage, for instance, may signal predators that the prey is unprofitable (Gotmark 1993), allowing males to exploit previously unoccupied habitats under high predation pressure. A comparative analysis in antbirds (Tobias & Seddon 2009) also reveals a pattern consistent with the second premise ecological co-optation (Bonduriansky 2011): clades with intense sexual selection occupy a greater number of habitats, and a wider altitudinal range, which may reflect the propensity to adapt to novel environments if the sexual trait is to be co-opted for a viability trait. As in the last premise of ecological co-optation, conspicuous plumage that is co-opted for such a viability-related function in males will then start to be expressed in females, as well.

Previous studies in birds provide further support for their suitability to test the prediction of ecological co-optation. Phylogenetic analyses of plumage coloration in tanagers (Burns 1998) and New World blackbirds (Irwin 1994) indicate that sexually dimorphic species with colorful males and drab females is ancestral, and changes in plumage coloration occur more frequently in females than males. In tanagers, it was also revealed that plumage coloration in females evolves from drab to colorful (Burns 1998). These findings seem compatible with the prediction of ecological co-optation that an ancestrally sexually dimorphic population with only males having colorful plumage will evolve to a sexually monomorphic population with both males and females having colorful plumage.

Inspired by the results of these previous studies (Irwin 1994; Burns 1998; Tobias & Seddon 2009), we chose antbirds (Thamnophilidae), tanagers (Thraupidae), and New World blackbirds (Icteridae) as our study groups to test the ecological co-optation hypothesis by (Bonduriansky 2011). Antbirds have low interspecific variation in terms of migratory behavior, feeding, and habitat preferences (Tobias & Seddon 2009): nonmigratory insectivorous antbirds occupy forested areas. In addition, both sexes have duties during incubation. Tanagers also have low variation with respect to migratory behavior and breeding biology: they are mainly nonmigratory (Brush 1967), and both sexes feed nestlings (Burns 1998). On the whole, all these features helped keep many variables constant so that interspecific variation is mostly due to plumage coloration in antbirds (Tobias & Seddon 2009) and tanagers. However, there exists an interspecific variation in blackbirds (Jaramillo & Burke 1999): some species are migratory while some other are nonmigratory; some species build their own nests while others are brood parasitic. Together with that, many aspects of their mating system and foraging activity

remains unknown (Jaramillo & Burke 1999).

To distinguish ecological co-optation from other hypotheses on mutual ornamentation, we focused on the third premise of ecological co-optation, which suggest that species where both sexes are equally ornamented will differ in their niche use from species where only males are ornamented. Following the determination of bird groups, we scored both plumage ornamentation and surrogates of niche width (*i.e.* habitat range, altitudinal range, and distributional range). We developed a novel method where both sexes of a given species can be scored as colorful or drab, using ornaments like bright color and noticable parts. Apart from these scores assigned to a given species (*i.e.* species plumage ornamentation), we also included female plumage ornamentation scores in the analyses. Interestingly, although female ornamentation is examined in its contribution to mating success and offspring quality (references in Kraaijeveld *et al.* 2007; Nordeide *et al.* 2013), its role in ecological attributes remains largely unexplored (but see Martin & Badyaev 1996). We carried out phylogenetically independent contrasts to examine the relationship between plumage ornamentation and niche width. We should note that we will use the term niche loosely just to refer to three variables, (*i.e.* habitat range, altitudinal range, and distributional range) rather than referring to a multidimensional space proposed by Hutchinson (1957).

Focusing on the relationship between sexual selection and ecological generalism could be informative about ecological co-optation, as well. If sexual selection is the engine of the evolution of traits that can later be co-opted for viability-related functions, species experiencing more intense sexual selection may be expected to have more such traits and thus be more effective in invading a new niche (R. Bonduriansky, *pers. comm.*). Such an invasion will then lead to broader niche use in species where sexual selection is strong. To examine such a relationship between sexual selection and ecological generalism, we used plumage dichromatism as an index of sexual selection, and the same indices of niche width for ecological generalism, and carried out phylogenetically independent contrasts.

The relationship between plumage ornamentation and niche width will provide information on how ecological co-optation affects habitat use. More specifically, the presence of any significant relationship will indicate whether an increase in plumage coloration is accompanied by an increse or a decrease in the compared variable (*i.e.* habitat, altitudinal, or distributional range). If, for instance, there appears a positive correlation between plumage ornamentation and habitat range, it could imply that species with colorful males and colorful females occur in a greater number of habitats. This, in turn, could imply novel niche use in species

where both sexes are ornamented. Nonetheless, the correlation analysis will fail to provide an answer to the question of whether any change in niche use will correspond to novel niche use in equally ornamented species, which is the main prediction of ecological co-optation hypothesis (Bonduriansky 2011). To separately examine novel niche exploitation, we performed sister taxa comparisons. We estimated niche overlap for sister species pairs where ecological co-optation is present, and also for sister species pairs where ecological co-optation is absent. We then compared these two groups if they differ from each other in their niche overlaps.

1.1 Objectives

In this study, using plumage coloration in antbirds, tanagers, and blackbirds, we test the predictions of ecological co-optation hypothesis (Bonduriansky 2011) that:

  (i) species with colorful males and colorful females differ in their niche use from species with colorful males and drab females, by carrying out phylogenetically independent contrasts.

 (ii) highly dichromatic species will have a wider niche width, by using phylogenetically independent contrasts.

(iii) the change in niche use tested in (i) corresponds to novel niche use, by carrying out sister taxa comparisons.

CHAPTER 2

MATERIALS and METHODS

2.1 Study species

We chose three different bird groups, namely, antbirds, tanagers, and blackbirds to test our predictions. These birds are all found widely across South America (Ridgely & Tudor 2009). New World blackbirds also extend to North America (Lowther 1975). There exist both sexually monomorphic and dimorphic species with respect to plumage in these birds (Lowther 1975; Burns 1998; Ridgely & Tudor 2009). Both antbirds and tanagers are monogamous (Burns 1998; Tobias & Seddon 2009) while blackbirds are either monogamous or polygynous (Irwin 1994). Antbird species share incubation duties (Tobias & Seddon 2009). Tanagers build an open nest, and unlike antbirds, only females incubate eggs but both males and females feed nestlings (Burns 1998). Blackbirds show variation in nesting dispersion (Lowther 1975). Solitary nesting species have territories for breeding, nesting, and feeding while colonial nesting species have territories for nesting only or breeding and nesting. There are also brood parasitic species in this group (Jaramillo & Burke 1999).

2.2 Plumage ornamentation scoring

Plumage ornamentation scoring based on human vision has been a widely used measure (Irwin 1994; Moller & Birkhead 1994; Owens & Bennett 1994; Gray 1996; Burns 1998; Badyaev & Hill 2000; Dunn *et al.* 2001). Almost all methods of plumage scoring identifies color differences between sexes with the assumption that sexual dichromatism reflects the strength of sexual selection (Hamilton & Zuk 1982; Gray 1996; Badyaev & Hill 2000; Tobias & Seddon 2009). Accordingly, sexual dichromatism is recorded in two ways: 1) each sex of a given species is scored separately on a scale of brigthness where the maximum value represents the most conspicuous and bright, and sexual dichromatism is estimated as the difference between male and female scores (Moller & Birkhead 1994; Martin & Badyaev 1996), 2) both sexes of a given species are compared across specified body regions, for each of which dichromatism is scored on a given scale with the maximum value representing high dicromatism, and sexual dichromatism is estimated as the sum of dichromatism scores (Irwin 1994; Owens & Bennett 1994; Gray 1996; Badyaev & Hill 2000; Dunn *et al.* 2001; Tobias & Seddon 2009). Both methods have problems: the former method is based on subjective decisions of scorers on the brightness of a sex (Owens &

Hartley 1998), and the latter method fails to score sexes of a given species separately since it is based on the degree of difference between sexes. Yet, we want to have separate scores for each sex of a species to be able to test the hypothesis by Bonduriansky (2011), which proposes differences in niche uses in sexually monomorphic populations with colorful males and colorful females from, sexually dimorphic populations with colorful males and drab females. Hence, we develop a novel method in present study to quantify plumage ornamentation in both sexes.

Our method differs from previous studies (Hamilton & Zuk 1982; Irwin 1994; Moller & Birkhead 1994; Owens & Bennett 1994; Gray 1996; Martin & Badyaev 1996; Burns 1998; Badyaev & Hill 2000; Dunn *et al.* 2001; Tobias & Seddon 2009) on several aspects. First, we score for each sex separately. Second, even though we score for five body regions [*i.e.* head (eye, forecrown, crown, nape), upperside (mantle, rump), underside (throat, breast, belly, thighs, undertail coverts), wings, and tail], we score for bright or contrasting color, which makes that particular body region stand out or more visible. Third, in addition to bright and contrasting plumage patterns, we also score for noticeable parts including crest, bill casque, tufts on forehead and below chin, bare skin around the eye, and bare cheek patch. Although there are several studies concentrating on the role of such distinct parts in sexual selection [*e.g.* ornamental tail feathers in black grouse (Höglund *et al.* 1992), head plume in quails (Hagelin 2003), eye ring pigmentation in red-legged patridge (Pérez-Rodríguez & Viñuela 2008)], these parts are usually ignored while scoring plumage ornamentation (Hamilton & Zuk 1982; Irwin 1994; Moller & Birkhead 1994; Owens & Bennett 1994; Gray 1996; Martin & Badyaev 1996; Burns 1998; Badyaev & Hill 2000; Dunn *et al.* 2001; Tobias & Seddon 2009). Fourth, in addition to scoring for five body regions, we scored overall plumage coloration, as well. We evaluated individuals as drab if they are colored in brown, gray, dull yellow or dull yellowish green (Burns 1998), and as colorful if they are colored in black, white, red, orange, blue, bright green or bright yellow (Burns 1998), when previously scored bright color(s) or noticeable structure(s) are ignored.

Our score for each body region can take either of two values: 0, which indicates the absence, and 1, which indicates the presence of such bright colors or distinct parts. Similarly, the score for overall plumage coloration can either be 0 or 1, where drab individuals are 0, and colorful individuals are 1. As a result, our total plumage score ranges from 0 to 6. We assessed plumage ornamentation from color plates (antbirds: Zimmer & Isler 2003; Ridgely & Tudor 2009, tanagers: Isler & Isler 1987; Ridgely & Tudor 2009, blackbirds: Jaramillo & Burke 1999). In cases where a given sex has multiple forms, we scored the widespread one.

To gain insight into how we score plumage, we will give a few examples. The male *Megastictus margaritatus* is mainly colored in grey (see Fig. A.1a). White bold spots on black wings and black tail in this antbird species can exemplify colors we define as bright or contrasting. Without considering these patterns, the bird has a grey color, which we consider as drab. Hence, male *Megastictus margaritatus* gets a score of 2 from two body regions (*i.e.* wings, and tail), and a score of 0 for overall coloration. The total score will then be 2 for this species. The male *Myrmotherula brachyura* has plumage streaked in black and white on the upperside (see Fig. A.1b). White spotted wings and lightly colored underside in this bird contrast with the overall plumage. Hence, *Myrmotherula brachyura* gets a score of 2 from two body regions (*i.e.* wings, and underside). Without considering these patterns, the bird has a vivid head and upperside, resulting in a score of 1 for overall coloration. The total score for this species will then add up to 3. Lastly, the male *Agelaius thilius* is a black icterid with yellow epaulets (Fig. A.2). Here, except its wings, all the remaining body regions are uniformly colored and do not present any contrast, thus will score 0. Eliminating yellow epaulets after getting a score of 1 from wings will leave a black color, which we consider as colorful. Hence, male *Agelaius thilius* will get a total score of 2 from wings and overall coloration. Our method seems to capture plumage ornamentation variation in three groups of birds, with lower scores in antbirds and higher scores in tanagers (see Fig. 2, 3 in Results section).

We use plumage ornamentation scores in three ways (see below). In the first case, we categorize them to obtain a score for a given species. In the second case, we use raw female scores. In the third case, we estimate plumage dichromatism scores by subtracting male score from female score.

First, to test the hypothesis by Bonduriansky (2011), we categorize species in one of the following three groups: i) species with colorful males and colorful females, ii) species with colorful males and drab females, and iii) species with drab males and drab females based on our plumage ornamentation score. Plumage ornamentation scores for antbirds and blackbirds (Fig. 2 and 3) indicate that the majority of males have a score of 2. Considering the high frequency of males with the score 2, we developed two scenarios where an individual bird with a score of 2 can be regarded as drab in one scenario or colorful in the other scenario (Table 1). In scenario A, we considered an individual bird as drab if it has a score less than 2, and colorful if it has a score greater than or equal to 2. In scenario B, we considered an individual bird as drab if it has a score less than 3, and colorful if it has a score greater than or equal to 3. We assigned a new score of 0

to a drab bird, and a new score of 1 to a colorful bird (Table 1). To obtain a single plumage score for a given species, we summed the scores of males and females. The new scale now varies from 0 to 2 where 0 indicates species with drab males and drab females, 1 indicates species with colorful males and drab females, and 2 indicates species with colorful males and colorful females. Here, we assume that the increase from 0 to 2 represents an increase in species coloration. Sec-

Table 1: Categorization of plumage ornamentation scores. Scores ranging from 0 to 6 are grouped into two categories under two different scenarios. In scenario A, individuals with a score lower than 2 are regarded as drab and assigned with a new score of 0. Individuals with a score greater than or equal to 2 are regarded as colorful and assigned with a new score of 1. In scenario B, individuals with a score lower than 3 are regarded as drab and assigned with a new score of 0. Individuals with a score greater than or equal to 3 are regarded as colorful and assigned with a new score of 1. Each sex, then, has a score of 0 (drab) or 1 (colorful).

	Plumage score						
	0	1	2	3	4	5	6
Scenario A	Drab (0)		Colorful (1)				
Scenario B	Drab (0)			Colorful (1)			

ond, we use raw female plumage ornamentation scores to see whether there is any shift in niche use in species where females are more colorful. Since Bonduriansky (2011) focuses on species where both sexes are colorful, increasing female coloration can represent females gaining color following ecological co-optation. Hence, we used female plumage ornamentation scores to discover the relationship between female coloration and niche width.

Third, we used plumage dichromatism as an index of sexual selection, where plumage dichromatism is simply estimated as the difference between male plumage score and female plumage score, to examine the relationship between sexual selection and ecological generalism.

2.3   Niche width

We used habitat range, altitudinal range, and distributional range, as indices of niche width since they can capture the ability to exploit various habitats, foraging niches, and the ability to tolerate different environmental conditions (Badyaev & Ghalambor 1998; Tobias & Seddon 2009). We gathered habitat and altitude information for each species of blackbirds, tanagers, and antbirds from BirdLife International (2013). Habitat range is estimated as the sum of different habitat types (see Appendix D for habitat types) occupied by each species (Tobias & Seddon 2009). Altitudinal range is calculated as the difference between maximum altitude and minimum altitude. Distributional range is quantified using digital distribution maps of the birds of the Western Hemisphere (Ridgely & Birdlife International 2011). All raw data are given in Appendix E.

2.4   Phylogenetic analyses

We used species level phylogenetic trees for the bird groups included in the study. We modified the phylogeny of antbirds from Gómez *et al.* (2010) by reducing two populations of *Gymnopithys leucaspis* to a single population (143 species, Fig. A.4, A.5, A.6 & A.7). We used the phylogeny in Sedano & Burns (2010) for tanagers (93 species, Fig. A.8, A.9, A.10 & A.11). For blackbirds, we removed *Icterus chrysocephalus* from the phylogeny in Price *et al.* (2009) as no data exists for this species in BirdLife International (2013) [64 species, Fig. A.12 & A.13]. Mitochondrial DNA data providing branch length information in the form of genetic distance was available only for antbirds. For tanagers and blackbirds, we redraw the trees in Drawgram 3.66 (Felsenstein 1989; Dereeper *et al.* 2008, 2010) from the published manuscripts (Price *et al.* 2009; Sedano & Burns 2010).

To examine the relationship between plumage ornamentation and niche width, we calculated Felsenstein's independent contrasts (Felsenstein 1985) using the module PDAP:PDTREE (Midford *et al.* 2010) in the program Mesquite 2.75 (Maddison & Maddison 2011). Because this method compares continuous variables across a phylogeny, we treated our species plumage scores (*i.e.* 0, 1 and 2) as continuous variables where increasing from 0 to 1 represents an increase in male coloration, and increasing from 1 to 2 represents an increase in female coloration. Such treatment of species plumage scores is justified by similar results we obtained using female plumage scores, which vary on a continous scale of 0 to 6 (see Results section). A correlation analysis between two characters across a range of taxa cannot be conducted using an ordinary regression as individual

species cannot be regarded as independent samples (Felsenstein 1985). This non-independence of taxa can be corrected by obtaining contrasts for each character between pairs of adjacent tips and assuming that characters evolve by Brownian motion. Statistically independent contrasts determined by the phylogeny will then be used in correlation analysis. To carry out phylogenetic analyses, we performed Felsenstein's (1985) independent contrasts.

Prior to each analysis, we tested the adequacy of the standardization of branch lengths in Mesquite 2.75 (Maddison & Maddison 2011) using the analysis suggested by Garland *et al.* (1992). In this analysis, standardized independent contrasts are plotted against their standard deviations (Garland *et al.* 1992). If a significant trend comes out, this will imply inadequate standardization of branch lengths for the statistical purposes. For antbirds, tanagers, and blackbirds, there were significant correlations between contrasts and their standard deviations (Table A.9). Thus, we performed analyses both by assuming branch lengths to be proportional to the number of taxa in each clade for a gradual model evolution (Maddison & Maddison 2011), and by assigning all branch lengths equal to 1 for a punctuated model of evolution (see Appendix G for modified trees). In addition, we log transformed altitudinal and distributional range data to reduce variation since they differ by three orders of magnitude. In all cases, we analyzed the relationship between 1) species plumage ornamentation and niche width, 2) female plumage ornamentation and niche width, and 3) plumage dichromatism and niche width.

2.5   Sister taxa comparisons

Although phylogenetically independent contrasts approach corrects for nondependence of taxa that share a common evolutionary history, it will provide results only in terms of correlation. In other words, it will just reveal whether two variables are correlated, without giving any further information. Hence, testing the prediction of novel niche use in species with equally ornamented sexes or with colorful females will require another approach. We employed sister taxa comparisons as an alternative approach to test the prediction of novel niche use. Similar to phylogenetically independent contrasts, this approach circumvents the problem of phylogenetic dependence of taxa since they share a common ancestor. To carry out sister taxa comparisons, we identified sister species pairs in three bird groups. We classified sister species pairs into two main groups: one with a potential of experiencing ecological co-optation and the other with no potential of experiencing ecological co-optation (Fig. 1). The former group includes species pairs where only one of the sister species has colorful males and

colorful females (with score 2), while the other sister species has either drab males and drab females (with score 0), or colorful males and drab females (with score 1) [Fig. 1a]. The latter group covers sister species pairs that have combinations of drab males and drab females (0) and colorful males and drab females (1) [Fig. 1b]. We then compared sister species pairs with respect to niche overlaps. We estimated 1) altitudinal overlap as the range of altitude where sister species co-occur divided by the altitudinal range of sister species with the smaller altitudinal range (Kozak & Wiens 2007), 2) distributional overlap as the area where sister species co-occur divided by the distributional range of sister species with the smaller distributional range (Chesser & Zink 1994), 3) habitat overlap as the number of habitats where sister species co-occur divided by the habitat range of sister species with the smaller habitat range. As predicted by ecological co-optation (Bonduriansky 2011), we expect to see less niche overlap between sister species pairs with the sexually monomorphic and colorful species, if ecological co-optation causes novel niche (Fig. 1a), and greater niche overlap between sister species pairs both of which lack the ecologically co-opted trait (Fig. 1b).

a. "Ecological co-optation present"

2

0 or 1
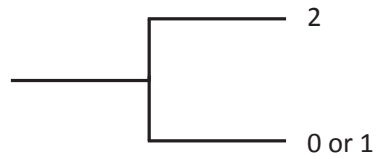
b. "Ecological co-optation absent"

0 or 1

0 or 1
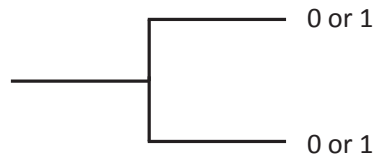
Figure 1: Schematic representation of the classification of sister species pairs into two groups. The group where ecological co-optation is present (a) includes one sister species with a plumage ornamentation score of 2, while the group where ecological co-optation is absent (b) includes no species with a plumage ornamentation score of 2. We expect to see less niche overlap between sister species pairs in (a) if colorful plumage enables novel niche use in species with score 2, and greater niche overlap between sister species pairs in (b) since these species lack colorful plumage, and thus the potential to invade a novel niche.

CHAPTER 3

RESULTS

Our novel plumage scoring method captured the coloration pattern in antbirds, tanagers, and blackbirds successfully where drab-looking antbird species have lower scores, and colorful-looking tanager species have higher scores (Fig. 2, 3). When we look at the frequency distribution of plumage scores in males and females, a few expected trends are appearent (Fig. 2). For example, females and males usually have similar scores (most appearent in sexually monomorphic and colorful tanagers in Fig. 3b), or females have lower scores than males (appearent in antbirds and blackbirds in Fig. 3a & Fig. 3c, respectively). There are also some cases in antbirds where females seem more colorful than males (Fig. 3a, see also Table A.1 & Fig. A.3). However, these cases are few in number, where only 7 females out of 143 species appear more colorful (see Table A.1 for species list). In these cases, we readjusted female scores by reducing them to match the scores of males. The reason for such readjustement stems from our categorization of plumage ornamentation scores where no species have females more colorful than males. Since we are interested in species with both sexes colorful, increasing male scores to match that of females in an alternative readjustement would result in inflated results for these species.

Using two different scenarios to categorize total plumage scores, and two different models of evolution, we obtained four results for each comparison between species plumage ornamentation and any index of niche width (Table 2). There is a significant correlation between species plumage ornamentation and altitudinal range both in antbirds and tanagers. There is also a significant correlation with respect to habitat range in these bird groups. However, there is no significant pattern for distributional range in any of the bird groups (except in antbirds under gradual model with $p<0.1$). Our results do not seem to be sensitive to the model of evolution in phylogenetically independent contrasts analysis and to our different plumage scoring methods. With respect to the model of evolution, only in three cases out of 18 correlations (*i.e.* altitudinal range in antbirds, and tanagers, distributional range in antbirds), the results differed between gradual and punctuated model of evolution, where gradual model yielded significant results. Of nine correlations, only two (*i.e.* habitat range in antbirds, and tanagers) showed different results according to our plumage scoring scenarios A and B.
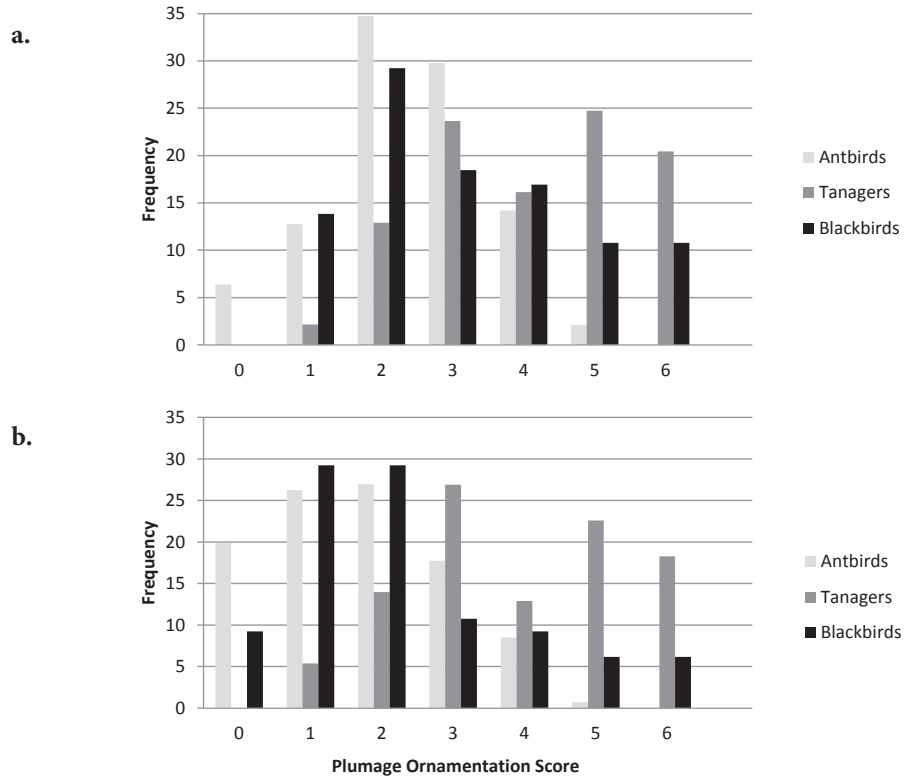
Figure 2: The frequency distribution of plumage ornamentation scores in a) males and b) females of antbirds, tanagers, and blackbirds. This plumage score distribution indicates that our novel method successfully captures the variation in these bird groups. Antbirds are usually colored in shades of brown and grey, and have low ornamentation scores in general. There are no males or females with the maximum score of 6 in these birds. Most tanagers are colored vividly, and have a minimum score of 1, with majority of males and females getting a score of 5 and 3, respectively. Blackbirds are mainly colored in shades of brown and black, and have scores somewhat in between antbirds and tanagers.
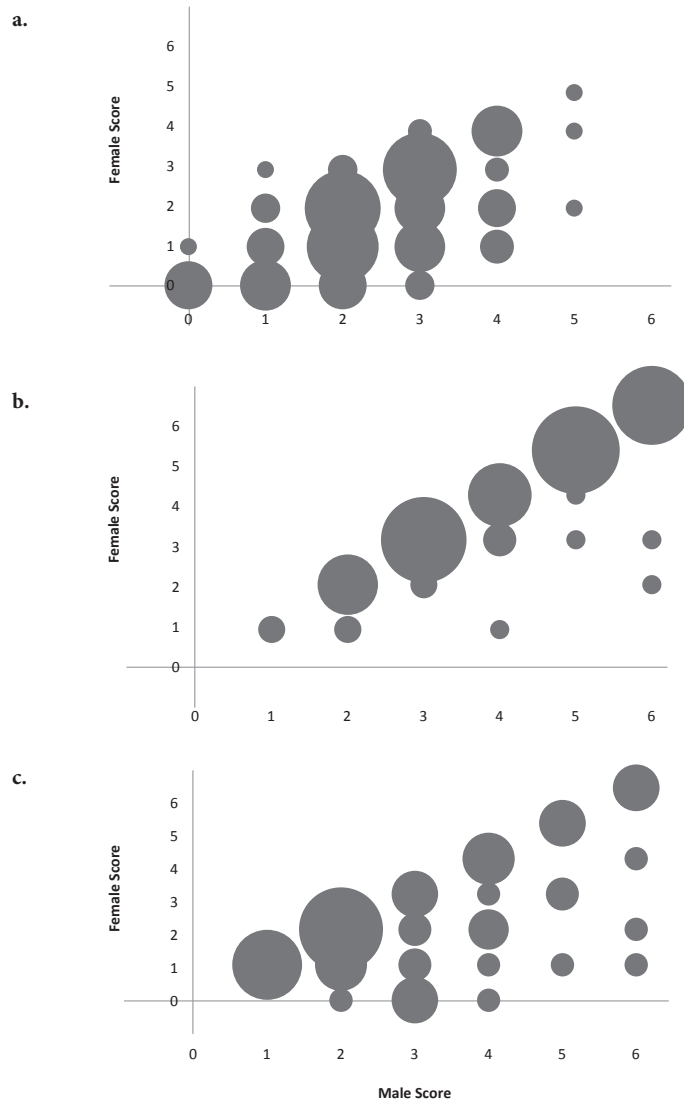
Figure 3: The distribution of male and female plumage ornamentation scores in a) antbirds, b) tanagers, and c) blackbirds. Bubble size indicates the frequency of a female score for a given male score. A few trends are visible: females have similar plumage ornamentation scores as males (*e.g.* in b, tanagers are mostly colorful and sexually monomorphic), or they have less scores than males (*e.g.* as in blackbirds in c). Antbirds, however, show a few relatively rare case where females of some species appear more colorful than males (see Fig. A.3 and Table A.1).

Analyses using female ornamentation scores under two models of evolution largely agreed with the results of analyses using species plumage scores: there is a significant correlation between female plumage ornamentation and altitudinal range in antbirds, and tanagers, plus there exists no detectable pattern for distributional range (Table 3). Distinctively, a different trend emerges in regard to habitat range: the significant correlation obtained for antbird, and tanager species (Table 2) is now obtained only for blackbird females. Results for gradual and punctuated models of evolution did not differ in these analyses.

The patterns observed in Tables 2 and 3 suggest that increasing plumage coloration in antbird and tanager species correspond to a wider altitudinal ranges. Table 2 further suggests that increasing plumage coloration in antbird species corresponds to occuring in a greater number of habitats, and being distributed over larger areas. However, increasing plumage coloration in tanager species corresponds to occupying less number of habitats. The analysis using female plumage scores suggests that increasing coloration in female blackbirds correspond to occupying wider range of habitats.

When we examined the association between plumage dichromatism and niche width under two models of evolution, we see that there exist positive correlations between plumage dichromatism and distributional range in all bird groups (Table 4). But the results are sensitive to the model of evolution used in phylogenetically independent contrasts. Habitat range in antbirds and tanagers are also correlated with dichromatism scores, where it is positive in the former, and negative in the latter. Again the results are sensitive to the model of evolution. No significant pattern emerges with respect to altitudinal range.

Sister taxa comparisons of groups where ecological co-optation is present or absent provide significant results for antbirds under scenario A (Fig. 4) and for tanagers under scenario B (Fig. 5). Distributional range overlap is significantly different between two antbird groups (Fig. 4). Antbird species with colorful males and colorful females have a greater distributional range overlap with species having at least one sex drab, which contradicts with Bonduriansky's (2011) prediction. However, species with at least one sex drab have less overlap, and thus more frequently occur in different areas. Distributional range overlap differs significantly between tanager groups, as well. Here, however, the pattern is just the reverse: species with both sexes colorful have less overlap than species having at least one sex drab as expected from Bonduriansky's (2011) hypothesis. Habitat range overlap also differs significantly between these tanager groups. Species with both sexes colorful have greater habitat range overlap with species having

at least one sex drab, whcih again contradicts with Bonduriansky's (2011) prediction. Unlike antbirds and tanagers, sister species pairs in blackbirds do not show any significant difference in their niche overlaps (Fig. 6).

All the results we obtained are summarized in Table 5. Altitudinal range is positively correlated with increasing species and female plumage coloration both in antbirds and tanagers. However, no significant correlation exists between plumage dichromatism and altitudinal range in any bird group. Distributional range is also positively correlated with increasing species plumage coloration in antbirds. Nonetheless, this result is sensitive both to the model of evolution, and to our different plumage scoring methods. Despite the lack of an overall pattern for distributional range for species and female plumage coloration, there is a positive correlation between plumage dichromatism and distributional range in all bird groups. The results are interesting for habitat range. Both species plumage coloration and plumage dichromatism are correlated with habitat range, positively in antbirds, and negatively in tanagers. Nonetheless, in blackbirds, habitat range is positively correlated with female plumage coloration, but not with plumage dichromatism. Overall, these results suggest that species and female plumage coloration explain the variation in altitudinal range, whereas plumage dichromatism explains the variation in distributional range.

Table 2: Results of correlation between species plumage coloration and habitat, altitudinal, and distributional ranges. Values refer to Pearson product-moment correlation coefficients estimated from regression of independent contrasts through the origin. Correlations are estimated for alternative threshold values of total plumage scores (scenarios A and B) under gradual and punctuated models of evolution. (two-tailed p values: *$p<0.1$, **$p<0.05$, ***$p<0.01$.)

			Habitat range	Altitudinal range	Distributional range
Antbirds	Scenario A	Gradual model	0.035	**0.219*****	**0.149***
		Punctuated model	0.063	**0.165****	0.107
	Scenario B	Gradual model	**0.137***	**0.159****	0.105
		Punctuated model	**0.148***	0.127	0.089
Tanagers	Scenario A	Gradual model	**-0.385*****	**0.173***	-0.089
		Punctuated model	**-0.250****	0.161	0.044
	Scenario B	Gradual model	-0.102	**0.400*****	0.107
		Punctuated model	-0.155	**0.402*****	0.052
Blackbirds	Scenario A	Gradual model	-0.121	0.072	0.054
		Punctuated model	-0.087	-0.013	0.059
	Scenario B	Gradual model	0.147	-0.009	-0.029
		Punctuated model	0.166	-0.072	0.035

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Table 3: Results of correlation between female plumage coloration and habitat, altitudinal, and distributional ranges. Values refer to Pearson product-moment correlation coefficients estimated from regression of independent contrasts through the origin under gradual and punctuated models of evolution. (two-tailed p values: *$p<0.1$, **$p<0.05$, ***$p<0.01$.)

		Habitat range	Altitudinal range	Distributional range
Antbirds	Gradual model	0.129	**0.228***	0.026
	Punctuated model	0.110	**0.188**	0.014
Tanagers	Gradual model	-0.021	**0.288***	0.035
	Punctuated model	-0.111	**0.244**	0.007
Blackbirds	Gradual model	**0.220***	0.032	-0.096
	Punctuated model	**0.222***	-0.030	-0.092

Table 4: Results of correlation between plumage dichromatism and habitat, altitudinal, and distributional ranges. Values refer to Pearson product-moment correlation coefficients estimated from regression of independent contrasts through the origin. Correlations are estimated under gradual and punctuated models of evolution. (two-tailed p values: *$p<0.1$, **$p<0.05$, ***$p<0.01$.)

		Habitat range	Altitudinal range	Distributional range
Antbirds	Gradual model	0.110	0.060	**0.150***
	Punctuated model	**0.141***	0.035	0.118
Tanagers	Gradual model	**-0.195***	0.057	**0.218**
	Punctuated model	-0.016	0.093	**0.241**
Blackbirds	Gradual model	-0.110	-0.099	0.179
	Punctuated model	-0.104	-0.069	**0.231***
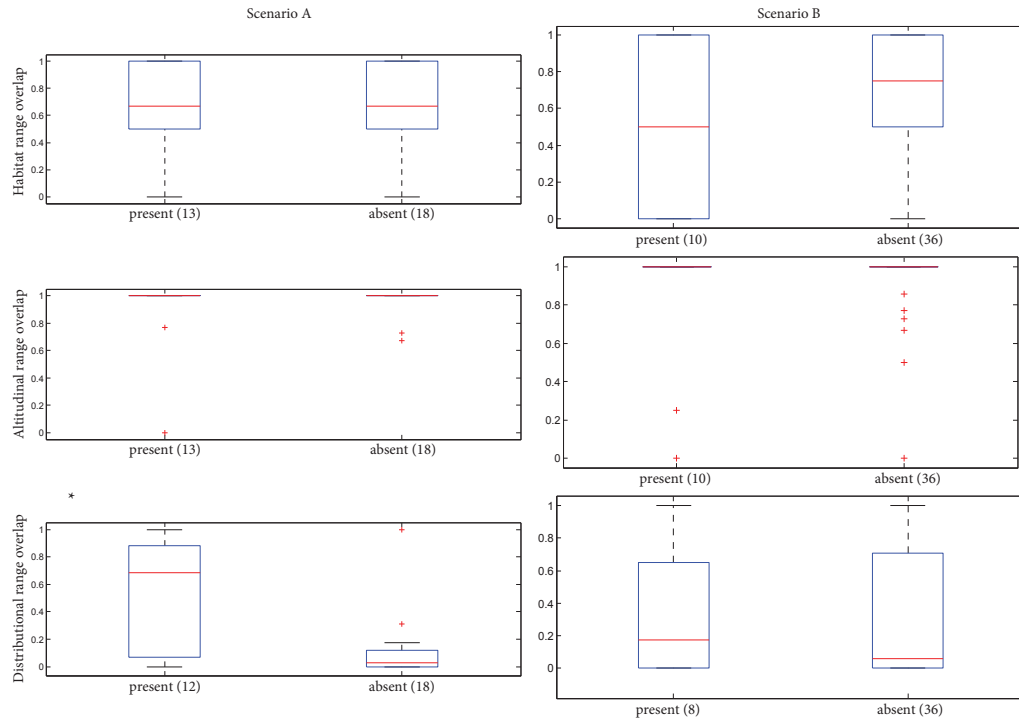
Figure 4: Box plots of habitat, altitudinal, and distributional range overlap in sister species pairs of antbirds under scenarios A and B. Sister species in these bird groups are classified into two groups where ecological co-optation is *present* in one sister species only, and where ecological co-optation is *absent* in both sister species. The number of sister species pairs for a given group is shown in parentheses. In both groups, range overlap is estimated as the ratio of overlap to the range of sister species with the smaller range. Box plots designate the median (inner red line), the 25th and 75th percentiles (upper and lower blue edges, respectively), extreme data (black lines above or below the box), and outliers (+). Asteriks (*) indicate significant range overlap difference between compared groups, determined by two-sample Kolmogorov-Smirnov test.
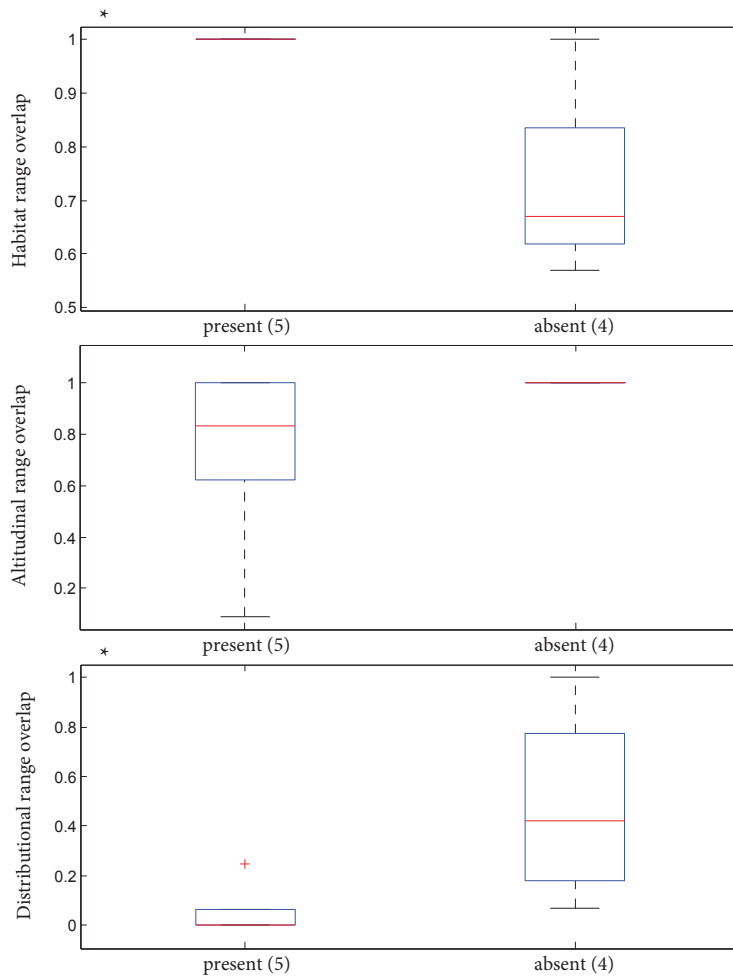
Figure 5: Box plots of habitat, altitudinal, and distributional range overlap in sister species pairs of tanagers under scenario B. No result is available for tanagers under scenario A since no sister species is identified where ecological co-optation is absent. See the caption in Fig. 4 for additional information.

24
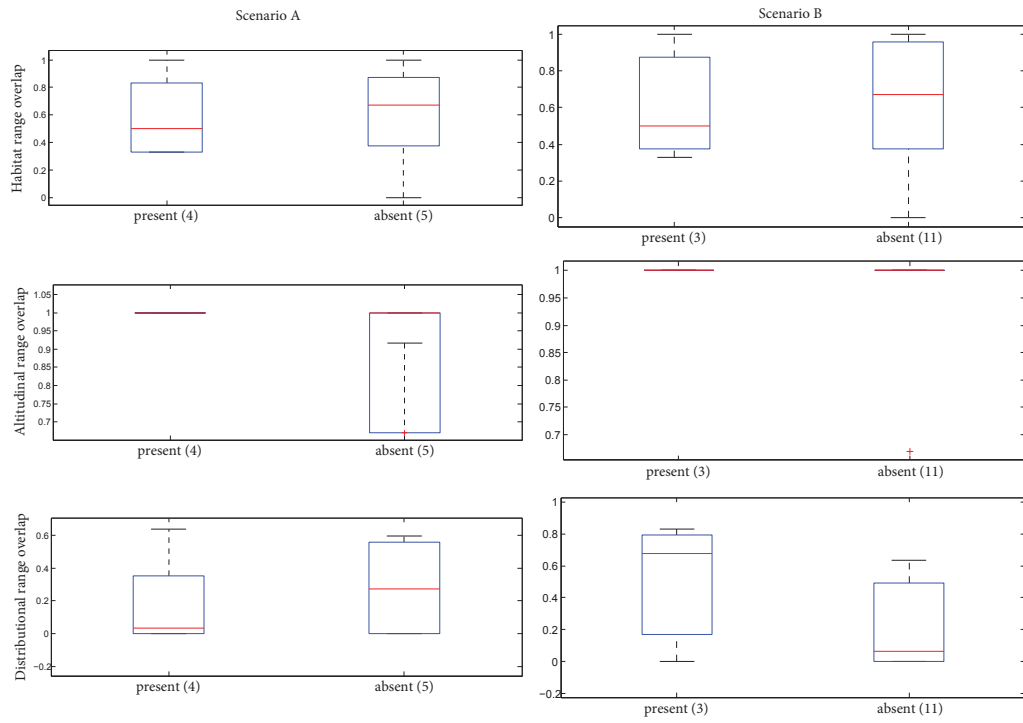
Figure 6: Box plots of habitat, altitudinal, and distributional range overlap in sister species pairs of blackbirds under scenarios A and B. See the caption in Fig. 4 for additional information.

Table 5: Summary table for all results obtained from phylogenetic comparative analyses and sister taxa comparisons. The conditions of significant correlation between plumage coloration/dichromatism and niche width are shown in parentheses. Nonsignificant correlation is indicated as n.s.

	Habitat range	Altitudinal range	Distributional range
Antbirds	Increase in species coloration correlated positively with habitat range (scenario B)	Increase in species and female coloration correlated positively with altitudinal range (except punctuated model of scenario B for species coloration)	Increase in species coloration correlated positively with distributional range (only in gradual model of scenario A)
	Color difference in sexes correlated positively with (punctuated model)		Color difference in sexes correlated positively with distributional range (gradual model)
			Distributional range overlap significantly different between sister species pairs (scenario A)
Tanagers	Increase in species coloration correlated negatively with habitat range	Increase in species and female coloration correlated positively with altitudinal range (except punctuated model of scenario A for species coloration)	Color difference in sexes correlated positively with distributional range
	Color difference in sexes correlated negatively with habitat range (gradual model)		Distributional range overlap significantly different between sister species pairs
	Habitat range overlap significantly different between sister species pairs		
Blackbirds	Increase in female coloration correlated positively with habitat range	n.s.	Color difference in sexes correlated positively with distributional range (punctuated model)

CHAPTER 4

DISCUSSION

The processes driving speciation has been an enigma despite Darwins's (1859) *magnum opus*. Several studies on speciation reemphasize the role of natural selection on speciation (Dobzhansky 1940; Maynard Smith 1966; Bush 1969; West-Eberhard 1983; MacNair & Christie 1983; Dieckmann & Doebeli 1999; Schemske & Bradshaw 1999; Podos 2001; Schluter 2001; McKinnon *et al.* 2004; Van Doorn *et al.* 2009) as Darwin originally proposed. In "ecological speciation" as now called (Schluter 2001), sexual selection acts as a link between adaptation and speciation (Price 1998). Sexual selection could also have a primary role where divergence in sexually selected traits will be enough to result in reproductive isolation and speciation (Lande 1981; Kirkpatrick 1982; Lande 1982; Wu 1985; Barraclough *et al.* 1995; Mitra *et al.* 1996; Payne & Krakauer 1997; Moller & Cuervo 1998; Owens *et al.* 1999; Seehausen & van Alphen 1999; Irwin 2000; Uy & Borgia 2000; Wilson *et al.* 2000; Masta & Maddison 2002).

An alternative idea to ecological speciation and speciation by pure sexual selection is ecological co-optation (Bonduriansky 2011), which suggests sexual selection as the engine of ecological diversification. Here, a sexually selected trait in males is co-opted for a novel viability trait such that males driven away from their viability optimum under sexual selection will become capable of invading a new niche if newly co-opted trait confers an advantage in the new niche. The male-limited trait will be also expressed in females, enabling niche shift of a population as a whole. Overall, ecological co-optation predicts that evolution from an ancestral population where only males have the sexual trait to a population where both sexes have the ecologically co-opted sexual trait will be accompanied by change in niche use.

In the present study, we used plumage coloration in antbirds, tanagers, and blackbirds to elucidate whether equal plumage ornamentation in both sexes of a species exemplifies a case of ecological co-optation. We carried out phylogenetically independent contrasts to examine the relationship between species plumage coloration and niche width, female plumage coloration and niche width, and plumage dichromatism and niche width. We also compared sister species pairs to determine whether any change in niche use of species with equally ornamented sexes corresponds to a novel niche use. The relationship between species plumage ornamentation and niche width will show whether increasing plumage coloration in species will correspond to an increase in their habitat range, alti-

tudinal range, and/or distributional range. Similarly, the relationship between female plumage ornamentation and niche width will show whether increasing plumage coloration in females will correspond to an increase in their habitat range, altitudinal range, and/or distributional range. As an indirect test of ecological co-optation, the relationship between plumage dichromatism and niche width will show whether highly sexually dichromatic species occupy wider habitat, altitudinal, and/or distributional ranges compared to less sexually dichromatic or monochromatic species. The comparison between sister species pairs will show whether niche overlap is less between sister species pairs where one species have the ecologically co-opted trait than sister species pairs where both lack the ecologically co-opted trait.

Our results indicate that in birds, an increase in conspicuity of both sexes could produce changes in habitat, altitudinal, and, to a lesser extent, in distributional ranges (Tables 2 and 3). Both in antbird and tanager species, increasing plumage coloration correspond to occupying wider altitudinal range (Table 2). The same is true for antbird and tanager females: increasing plumage coloration in females correspond to occupying wider altitudinal range (Tables 3 and 5). There appears a trend with respect to habitat range, as well: increasing plumage coloration in antbird species corresponds to inhabiting a greater number of habitats, whereas increasing plumage coloration in tanager species corresponds to inhabiting less number of habitats. Similar to the pattern in antbirds (Tables 2), increasing plumage coloration in female blackbirds corresponds to occuring in a greater number of habitats (Table 3). Additionally, a slight correlation exists for antbirds in regard to distributional range, implying that increasing plumage coloration in antbird species corresponds to being distributed over larger areas (Table 2).

The results of correlation between plumage dichromatism and niche width also provide evidence in support of ecological co-optation. Species under strong sexual selection (*i.e.* with high plumage dichromatism scores) seem to occupy wider areas in all bird groups (Table 4). Actually, the pattern we detect for distributional range is found in two seperate studies, as well (Badyaev & Ghalambor 1998; Tobias & Seddon 2009): a positive correlation between sexual dichromatism and altitudinal range in cardueline finches (Badyaev & Ghalambor 1998), and a positive correlation between sexual dichromatism and habitat range, and altitudinal range in antbirds (Tobias & Seddon 2009). One interpretation of this pattern is that sexual selection promotes ecological generalism by favoring high-quality individuals (*i.e.* good genes models of sexual selection, Tobias & Seddon 2009). Alternative interpretation is that ecological generalism promotes sexual selection, where a broad niche increases population density, and thus the inten-

sity of competition between mates (Tobias & Seddon 2009). Distinct from these interpretations, a positive correlation between sexual dichromatism and niche width may throw light on the role of sexual selection in ecological co-optation, where sexual selection has the potential to produce secondary sexual traits that will later be co-opted for viability traits. If, for instance, a given species has several populations, and these populations vary in the expression of the sexually-selected trait, each population with its differenatially expressed sexual trait will come to occupy a new niche when the sexual trait starts to serve as a novel viability trait (R. Bonduriansky, *pers. comm.*). Invasion of a variety of niches by different populations of a given species will then lead to a wider distributional range in that species.

Our results of sister taxa comparisons show that antbird species where ecological co-optation is present have a greater distributional range overlap than antbird species where ecological co-optation is absent (Fig. 4) while the pattern is just the reverse for tanagers (Fig. 5). There is also a signifcant difference between sister species pairs in tanagers with respect to habitat range: tanager species where ecological co-optation is present have a greater habitat range overlap than tanager species where ecological co-optation is absent. Nonetheless, the patterns observed for tanagers could be artefacts resulting from low number of sister species pairs.

It is noticeable that we obtained significant results mostly for antbirds and tanagers, but not for blackbirds (Table 5). This could be due to interspecific variation observed in blackbirds (Jaramillo & Burke 1999): there exist both migratory and nonmigratory species, and also both nest-building and brood parasitic species. In addition, there are many unknowns regarding their mating system and foraging activity (Jaramillo & Burke 1999), which may also vary between species.

Our results summarized in Table 5 indicate that plumage coloration predicts the variation in altitudinal range, while plumage dichromatism predicts the variation in distributional range. These results suggest that ecological co-optation could result in change in niche width with respect to habitat, altitude and distribution. Although we detect the unique prediction of novel niche use only in one case (*i.e.* less distributional range overlap in tanagers where ecological co-optation is present), an increase or a decrease in niche width (Table 5) would both imply novel niche use.

The interpretations of these results rest on the methodology and the assump-

tions of the phylogenetic analyses. Referring to the methodology, our plumage color scoring is based on human vision, and thus fails to capture ultraviolet (UV) plumage reflectance in birds. However, most of the birds are sensitive to UV light (Odeen & Hastad 2003), which may create differences between human and avian perception of plumage color. Nonetheless, there are some results that could justify human vision based scoring: 1) dense vegetation inhabited by antbirds lowers UV penetration and reduces UV reflectance in plumage (Seddon *et al.* 2010), 2) black, brown, rufous plumage in antbirds and blackbirds, and red plumage in blackbirds and tanagers have low level of UV reflectance (Gotmark 1996; Eaton & Lanyon 2003; Seddon *et al.* 2010). For plumage dichromatism scoring, the method could be more promising since human perception of dichromatism is found to be strongly correlated with avian perception of dichromatism (Seddon *et al.* 2010). Again in reference to methodology, we used plumage color variation between sexes (*i.e.* plumage dichromatism) as an index of sexual selection. Actually, a positive relationship between plumage dichromatism and other measures of sexual selection (*i.e.* degree of polygyny, frequency of extra-pair paternity and testes size) supports the use of plumage dichromatism as a metric to assess sexual selection in birds (Seddon *et al.* 2008).

The assumptions of the phylogenetic analyses are also important to note. Our comparative analyses assume gradual or punctuated model of evolution. In the former case, the height of node is proportional to the number of species it includes, and branch length is the difference between the height of the upper and lower nodes (Grafen 1989). In the latter, all branches are of equal length (all equal to 1 in our analyses). In fact, many comparative studies employ these models (*e.g.* Polo & Carrascal 1999; Irschick & Losos 1998; Smith 2012; Watanabe *et al.* 2012; Matysiokova & Remes 2013) especially when branch length information is unavailable or controversial. Further phylogenetic studies covering higher number of species in a better resolution will definitely confirm whether the traits under analysis follows the pattern predicted by evolution models.

To best of our knowledge, this study is the first to test ecological co-optation hypothesis proposed by Bonduriansky (2011), which we hope will initiate further studies on the topic. As suggested by this hypothesis, and partly supported by this study, it is plausible that sexual selection could generate ecological diversity.

REFERENCES

Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology Evolution*, **15**(4), 149–155.

Badyaev, A. V., & Ghalambor, C. K. 1998. Does a trade-off exist between sexual ornamentation and ecological plasticity? Sexual dichromatism and occupied elevational range in finches. *Oikos*, **82**, 319–324.

Badyaev, A. V., & Hill, G. E. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnean Society*, **69**(2), 153–172.

Barraclough, T. G., Harvey, P. H., & Nee, S. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society B Biological Sciences*, **259**(1355), 211–215.

BirdLife International. 2013. *IUCN Red List for birds. Downloaded from http://www.birdlife.org on 13/12/2012.*

Bonduriansky, R. 2011. Sexual selection and conflict as engines of ecological diversification. *The American Naturalist*, **178**(6), 729–45.

Brush, A. H. 1967. Pigmentation in the scarlet tanager, *Piranga olivacea*. *The Condor*, **69**(6), 549–559.

Burns, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): The role of female versus male plumage. *Evolution*, **52**(4), 1219–1224.

Bush, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution*, **23**(2), 237–251.

Chesser, R. T., & Zink, R. M. 1994. Modes of speciation in birds: a test of Lynch's method. *Evolution*, **48**(2), 490–497.

Coyne, J. A., & Orr, H. A. 2004. *Speciation*. Sunderland, MA: Sinauer.

Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J. F., Guindon, S., Lefort, V., Lescot, M., Claverie, J. M., & Gascuel, O. 2008. Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research*, **36**(Web Server issue), W465–W469.

Dereeper, A., Audic, S., Claverie, J. M., & Blanc, G. 2010. BLAST-EXPLORER helps you building datasets for phylogenetic analysis. *BMC Evolutionary Biology*, **10**(1), 8.

Dieckmann, U., & Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**(6742), 354–7.

Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. *The American Naturalist*, **74**(753), 312–321.

Dunn, P. O., Whittingham, L. A., & Pitcher, T. E. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, **55**(1), 161–175.

Eaton, M. D., & Lanyon, S. M. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proceedings of the Royal Society B Biological Sciences*, **270**(1525), 1721–1726.

Eisner, T., & Meinwald, J. 1995. The chemistry of sexual selection. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 50–55.

Felsenstein, J. 1985. Phylogenies and the comparative method. *The American Naturalist*, **125**(1), 1–15.

Felsenstein, J. 1989. PHYLIP - Phylogeny Inference Package (Version 3.2). *Cladistics*, **5**, 164–166.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Futuyma, D. J. 2009. Runaway sexual selection. *Chap. 15, pages 402–403 of: Evolution*, 2nd edn. Sunderland, USA: Sinauer Associates.

Garland, T., Harvey, P. H., & Ives, A. R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*, **41**(1), 18–32.

Gavrilets, S. 2003. Models of speciation: what have we learned in 40 years? *Evolution*, **57**(10), 2197–2215.

Gómez, J. P., Bravo, G. A., Brumfield, R. T., Tello, J. G., & Cadena, C. D. 2010. A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly of Neotropical forest birds. *Journal of Animal Ecology*, **79**(6), 1181–1192.

Gotmark, F. 1993. Conspicuous coloration in male birds is favoured by predation in some species and disfavoured in others. *Proceedings of the Royal Society of London series B*, **253**, 143–146.

Gotmark, F. 1996. Simulating a colour mutation: Conspicuous red wings in the European Blackbird reduce the risk of attacks by Sparrowhawks. *Functional Ecology*, **10**(3), 355–359.

Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, **326**(1233), 119–157.

Gray, D. A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. *The American Naturalist*, **148**(3), 453–480.

Gray, D. A., & Cade, W. H. 2000. Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences of the United States of America*, **97**(26), 14449–14454.

Hagelin, J. C. 2003. A field study of ornaments, body size, and mating behavior of the Gambel's Quail. *The Wilson Bulletin*, **115**(3), 246–257.

Hamilton, W. D., & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**(4570), 384–387.

Heard, S. B., & Hauser, D. L. 1995. Key evolutionary innovations and their ecological mechanisms. *Historical Biology*, **10**(2), 151–173.

Höglund, J., Alatalo, R., & Lundberg, A. 1992. The effects of parasites on male ornaments and female choice in the lek-breeding black grouse (*Tetrao tetrix*). *Behavioral Ecology and Sociobiology*, **30**(2), 71–76.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Irschick, D. J., & Losos, J. B. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean Anolis lizards. *Evolution*, **52**(1), 219–226.

Irwin, D. E. 2000. Song variation in an avian ring species. *Evolution*, **54**(3), 998–1010.

Irwin, R. E. 1994. The evolution of plumage dichromatism in the new world blackbirds: social selection on female brightness? *The American Naturalist*, **144**(6), 890–907.

Isler, M. L., & Isler, P. R. 1987. *The Tanagers*. Washington, DC: Smithsonian Institution Press.

Jaramillo, A., & Burke, P. 1999. *New World Blackbirds The Icterids*. London: Christopher Helm Ltd.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution*, **36**(1), 1–12.

Kozak, K. H., & Wiens, J. J. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B Biological Sciences*, **274**, 2995–3003.

Kraaijeveld, K., Kraaijeveld-Smit, F. J. L., & Komdeur, J. 2007. The evolution of mutual ornamentation. *Animal Behaviour*, **74**(4), 657–677.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America*, **78**(6), 3721–3725.

Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution*, **36**(2), 213–223.

Lande, R., & Kirkpatrick, M. 1988. Ecological speciation by sexual selection. *Journal of Theoretical Biology*, **133**(1), 85–98.

Lowther, P. E. 1975. Geographic and ecological variation in the Family Icteridae. *The Wilson Bulletin*, **87**(4), 481–495.

Maan, M. E., & Cummings, M. E. 2009. Sexual dimorphism and directional sexual selection on aposematic signals in a poison frog. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19072–19077.

MacNair, M. R., & Christie, P. 1983. Reproductive isolation as a pleiotropic effect of copper tolerance in *Mimulus guttatus*? *Heredity*, **50**(3), 295–302.

Maddison, W. P., & Maddison, D. R. 2011. *Mesquite: A modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org*.

Martin, T. E., & Badyaev, A. V. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution*, **50**(6), 2454–2460.

Masta, S. E., & Maddison, W. P. 2002. Sexual selection driving diversification in jumping spiders. *Proceedings of the National Academy of Sciences of the United States of America*, **99**(7), 4442–4447.

Matysiokova, B., & Remes, V. 2013. Faithful females receive more help: the extent of male parental care during incubation in relation to extra-pair paternity in songbirds. *Journal of Evolutionary Biology*, **26**, 155–162.

Maynard Smith, J. 1966. Sympatric speciation. *The American Naturalist*, **100**(916), 637–650.

McKinnon, J. S., Mori, S., Blackman, B. K., David, L., Kingsley, D. M., Jamieson, L., Chou, J., & Schluter, D. 2004. Evidence for ecology's role in speciation. *Nature*, **429**, 294–298.

Midford, P. E., Garland Jr., T., & Maddison, W. P. 2010. *PDAP:PDTREE package for Mesquite, version 1.16.*

Mitra, S., Landel, H., & Pruett-Jones, S. 1996. Species richness covaries with mating system in birds. *The Auk*, **113**(3), 544–551.

Moller, A. P., & Birkhead, T. R. 1994. The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution*, **48**(4), 1089–1100.

Moller, A. P., & Cuervo, J. J. 1998. Speciation and feather ornamentation in birds. *Evolution*, **52**(3), 859–869.

Nordeide, J. T., Kekalainen, J., Janhunen, M., & Kortet, R. 2013. Female ornaments revisited are they correlated with offspring quality? *Journal of Animal Ecology*, **82**, 26–38.

Odeen, A., & Hastad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution*, **20**(6), 855–861.

Owens, I. P. F., & Bennett, P. M. 1994. Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society B Biological Sciences*, **257**(1348), 1–8.

Owens, I. P. F., & Hartley, I. R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society B Biological Sciences*, **265**(1394), 397–407.

Owens, I. P. F., Bennett, P. M., & Harvey, P. H. 1999. Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society B Biological Sciences*, **266**(1422), 933–939.

Panhuis, T. M., Butlin, R., Zuk, M., & Tregenza, T. 2001. Sexual selection and speciation. *Trends in Ecology Evolution*, **16**(7), 364–371.

Payne, R. J. H., & Krakauer, D. C. 1997. Sexual selection, space, and speciation. *Evolution*, **51**(1), 1–9.

Pérez-Rodríguez, L., & Viñuela, J. 2008. Carotenoid-based bill and eye ring coloration as honest signals of condition: an experimental test in the red-legged partridge (*Alectoris rufa*). *Die Naturwissenschaften*, **95**(9), 821–830.

Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, **409**, 185–188.

Polo, V., & Carrascal, L. M. 1999. Shaping the body mass distribution of Passeriformes: habitat use and body mass are evolutionarily and ecologically related. *Journal of Animal Ecology*, **68**(2), 324–337.

Price, J. J., Lanyon, S. M., & Omland, K. E. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proceedings of the Royal Society B Biological Sciences*, **276**(1664), 1971–1980.

Price, T. 1998. Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society B Biological Sciences*, **353**(1366), 251–260.

Rice, W. R., & Salt, G. W. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution*, **44**(5), 1140–1152.

Ridgely, R. S., & Birdlife International. 2011. *Digital distribution maps of the birds of the western hemisphere, version 4.0 . In BirdLife International and NatureServe (2011) Bird species distribution maps of the world*.

Ridgely, R. S., & Tudor, G. 2009. *Field guide to the songbirds of South America*. Vol. 127. University of Texas Press.

Ringo, J. M. 1977. Why 300 species of Hawaiian *Drosophila*? The sexual selection hypothesis. *Evolution*, **31**(3), 694–696.

Ritchie, M. G. 2007. Sexual selection and speciation. *Annual Review of Ecology, Evolution, and Systematics*, **38**(79-102).

Schemske, D. W., & Bradshaw, H. D. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences of the United States of America*, **96**(21), 11910–11915.

Schluter, D. 2001. Ecology and the origin of species. *Trends in Ecology Evolution*, **16**(7), 372–380.

Sedano, R. E., & Burns, K. J. 2010. Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). *Journal of Biogeography*, **37**(2), 325–343.

Seddon, N., Merrill, R. M., & Tobias, J. A. 2008. Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *The American naturalist*, **171**(5), 620–631.

Seddon, N., Tobias, J. A., Eaton, M., Ödeen, A., & Byers, B. E. 2010. Human Vision Can Provide a Valid Proxy for Avian Perception of Sexual Dichromatism. *The Auk*, **127**(2), 283–292.

Seehausen, O., & van Alphen, J. J. M. 1999. Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? *Ecology Letters*, **2**(4), 262–271.

Smith, N. D. 2012. Body mass and foraging ecology predict evolutionary patterns of skeletal pneumaticity in the diverse "waterbird" clade. *Evolution: International Journal of Organic Evolution*, **66**(4), 1059–1078.

Tobias, J. A., & Seddon, N. 2009. Sexual selection and ecological generalism are correlated in antbirds. *Journal of Evolutionary Biology*, **22**, 623–636.

Uy, J. A., & Borgia, G. 2000. Sexual selection drives rapid divergence in bowerbird display traits. *Evolution*, **54**(1), 273–278.

Van Doorn, G. S., Edelaar, P., & Weissing, F. J. 2009. On the origin of species by natural and sexual selection. *Science*, **326**(5960), 1704–1707.

Watanabe, Y. Y., Lydersen, C., Fisk, A. T., & Kovacs, K. M. 2012. The slowest fish: Swim speed and tail-beat frequency of Greenland sharks. *Journal of Experimental Marine Biology and Ecology*, **426-427**, 5–11.

Weller, S. J., Jacobson, N. L., & Conner, W. E. 1999. The evolution of chemical defences and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society*, **68**, 557–578.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, **58**(2), 155–183.

Wilson, A. B., Noack-kunnmann, K., & Meyer, A. 2000. Incipient speciation in sympatric Nicaraguan crater lake cichlid fishes: sexual selection versus ecological diversifcation. *Proceedings of the Royal Society of London Series B Biological Sciences*, **267**, 2133 –2141.

Wu, CI. 1985. A stochastic simulation study on speciation by sexual selection. *Evolution*, **39**(1), 66–82.

Zimmer, K. J., & Isler, M. L. 2003. Family Thamnophilidae (typical antbirds). *Pages 448–681 of:* del Hoyo, J., Elliott, A., & Christie, D. (eds), *Handbook of Birds of the World, Vol. 8*. Lynx Edicions, Barcelona.

APPENDIX A

Plumage Ornamentation Scoring
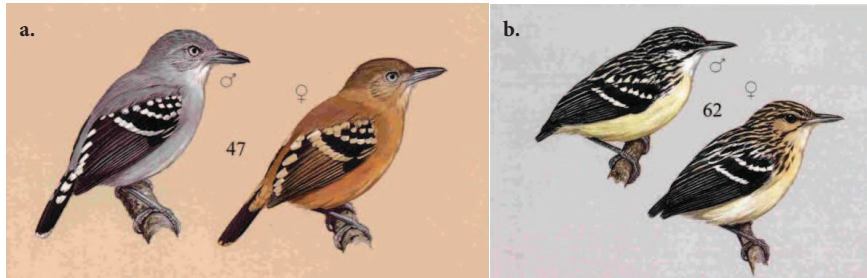
Figure A.1: Example species pairs (a) *Megastictus margaritatus* and (b) *Myrmotherula brachyura* [reproduced from Zimmer & Isler (2003)] showing different plumage ornamentation in antbirds. Five body regions for plumage scoring include head, upperside, underside, wings, and tail. The score can either be 0 or 1 for each body region, where 0 indicates the absence and 1 indicates the presence of a conspicuous ornament. a) Male *Megastictus margaritatus* on the left gets a score of 2 for conspicuousness due to black and white patterns on two regions: wings and tail, which contrast with the remaining dull grey plumage. Without considering these patterns, the bird has a drab color (*i.e.* grey), resulting in a score of 0 for overall coloration. Similar to the male, the female *Megastictus margaritatus* on the right gets a score of 2 for conspicuousness due to dark brown colored wings and tail, which look vivid on a dull brown background. Without considering these patterns, the bird again has a drab color (*i.e.* brown), resulting in a score of 0 for overall coloration. So, plumage ornamentation score will add up to 2 both in male and female of *Megastictus margaritatus*. b) Male and female *Myrmotherula brachyura* have similar plumage. White spotted wings and lightly colored underside in both sexes contrast with upper parts streaked in black and white. Hence, both sexes get a score of 2 from two body regions: wings and underside. Without considering these patterns, the bird has vivid head and upperside, resulting in a score of 1 for overall coloration. So, plumage ornamentation score will add up to 3 both in male and female of *Myrmotherula brachyura*.

Figure A.2: Example blackbird species *Agelaius thilius* [male (58a) on the left, and female (58b) on the right; reproduced from Jaramillo & Burke (1999)]. The male gets a score of 1 for conspicuousness due to yellow epaulets contrasting with black plumage. Due to black plumage, which we consider as colorful, the male also gets an additional score of 1 for overall coloration. The female gets a score of 1 for conspicuousness due to buffy supercilium contrasting with the brown head. The female bird otherwise, is drab (*i.e.* brown), resulting in a score of 0 for overall coloration. Hence, male and female *Agelaius thilius* will have a plumage ornamentation score of 2 and 1, respectively.

APPENDIX B

Exceptional Cases in Plumage Ornamentation Scoring

Table A.1: Antbird species that represent exceptional cases where females appear more colorful than males. Total plumage scores of females are reduced to that of males. Hence, both sexes of these species are considered as equally ornamented.

		Females	
Species	**Males**	**Original score**	**Adjusted Score**
Neoctantes niger	1	2	1
Myrmeciza berlepschi	1	3	1
Myrmeciza nigricauda	2	3	2
Frederickena viridis	2	3	2
Rhegmatorhina melanosticta	2	3	2
Thamnophilus nigriceps	1	2	1
Thamnophilus praecox	1	2	1

Figure A.3: One of the exceptional cases in antbird *Frederickena viridis* where female antbird (on the right) appears more colorful than male antbird (on the left; reproduced from Zimmer & Isler 2003). The male gets a score of 1 for its crest, and a score of 1 for its overall black plumage. So, it will have a score of 2 for plumage ornamentation. The female gets a score of 3 for plumage ornamentation due to its crest, black-white patterned underside and tail, both of which contrast with orange-brown upperside and wings. Without considering these ornaments, the bird has a color of dull brown, and thus a score of 0 for overall coloration. So, the female will have a score of 3 for plumage ornamentation.

APPENDIX C

Plumage Ornamentation Scores

Table A.2: Plumage ornamentation scores in male and female antbirds. Total score is obtained from ornaments across five body regions (*i.e.* head, upperside, underside, wings, tail) and overall coloration evaluated without considering the ornaments. Values of 0 and 1 indicate the absence and presence of a conspicuous ornament, respectively, for a given body region. Values of 0 and 1 for overall coloration refer to a drab and a colorful bird, respectively. Hence, total score varies between 0 and 6. Species with a single asteriks (*) have different scientific names in BirdLife International (2013).

Species	Males					Overall Coloration	Total Score	Females					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Pipra mentalis	1	0	1	0	0	1	3	0	0	0	0	0	0	0
Liosceles thoracicus	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Hylopezus berlepschi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terenura sharpei	1	1	1	1	0	0	4	1	1	1	1	0	0	4
Terenura humeralis	1	1	1	1	0	0	4	0	1	1	1	0	0	3
Myrmornis torquata	1	1	1	1	0	0	4	1	1	1	1	0	0	4
Pygiptila stellaris	1	0	0	1	0	0	2	0	0	0	0	0	0	0
Thamnistes anabatinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microrhopias quixensis	0	0	0	1	1	1	3	0	0	1	1	1	1	4
Neoctantes niger	0	0	0	0	0	1	1	0	0	1	0	0	1	2
Epinecrophylla fulviventris	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Epinecrophylla ornata	0	1	1	1	0	0	3	0	1	1	1	0	0	3
Epinecrophylla leucophthalma	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Epinecrophylla erythrura	0	0	1	1	0	0	2	0	0	0	1	0	0	1
*Epinecrophylla gutturalis**	0	0	1	1	0	0	2	0	0	0	0	0	0	0
Epinecrophylla spodionota	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Epinecrophylla haematonota	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Myrmorchilus strigilatus	1	1	1	1	1	0	5	1	1	0	1	1	0	4

Table A.2: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Myrmeciza atrothorax	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Myrmeciza pelzelni	0	0	1	1	0	0	2	0	0	1	1	0	0	2
Myrmotherula schisticolor	0	0	1	1	0	0	2	0	0	0	0	0	0	0
Myrmotherula behni	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Myrmotherula grisea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Formicivora melanogaster	1	0	1	1	1	0	4	1	0	1	1	1	0	4
Formicivora rufa	1	0	1	1	0	0	3	1	0	1	1	0	0	3
Formicivora grisea	1	0	1	1	1	0	4	0	0	0	1	1	0	2
Myrmotherula axillaris	0	0	1	1	1	0	3	0	0	1	0	0	0	1
Myrmotherula longipennis	0	0	1	1	0	0	2	0	0	0	0	0	0	0
Myrmotherula menetriesii	0	0	1	1	0	0	2	0	0	0	0	0	0	0
Myrmotherula assimilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrmotherula longicauda	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Myrmotherula klagesi	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Myrmotherula sclateri	0	0	1	1	0	1	3	0	0	1	1	0	1	3
Myrmotherula ambigua	0	0	1	1	0	1	3	0	0	1	1	0	1	3
*Myrmotherula obscura**	0	0	1	1	0	1	3	0	0	1	1	0	1	3
Myrmotherula brachyura	0	0	1	1	0	1	3	0	0	1	1	0	1	3
Myrmotherula multostriata	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Myrmotherula pacifica	0	0	0	1	0	1	2	0	1	0	1	0	0	2
Myrmochanes hemileucus	0	0	1	1	0	1	3	0	0	1	1	0	1	3
Myrmotherula cherriei	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Myrmeciza ferruginea	1	0	1	1	0	0	3	1	0	1	1	0	0	3
Myrmeciza loricata	1	0	1	1	0	0	3	1	0	0	1	0	0	2
Myrmeciza squamosa	1	0	1	1	0	0	3	1	0	0	1	0	0	2
Hypocnemoides maculicauda	0	0	1	1	1	0	3	0	0	1	1	1	0	3
Hylophylax punctulatus	1	1	1	1	0	0	4	1	1	1	1	0	0	4
Hylophylax naevioides	1	0	1	1	0	0	3	0	0	0	1	0	0	1
Hylophylax naevius	0	1	1	1	0	0	3	0	1	1	1	0	0	3
Myrmeciza longipes	1	0	1	0	0	0	2	1	0	0	0	0	0	1

Table A.2: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Percnostola lophotes	1	0	0	1	0	1	3	1	0	0	0	0	0	1
Myrmoborus myotherinus	1	0	1	1	0	0	3	1	0	1	1	0	0	3
Pyriglena leuconota	1	1	0	0	0	1	3	1	1	0	0	1	0	3
Gymnocichla nudiceps	1	0	0	1	0	1	3	1	0	0	0	0	0	1
Percnostola rufifrons	1	0	1	1	0	0	3	0	0	0	0	0	0	0
Myrmeciza goeldii	1	0	0	0	0	1	2	1	0	0	0	0	0	1
Myrmeciza melanoceps	0	0	0	1	0	1	2	1	0	1	0	0	0	2
Myrmeciza immaculata	1	0	0	0	0	1	2	1	0	0	0	0	0	1
Myrmeciza fortis	1	0	0	0	0	1	2	1	0	0	0	0	0	1
Myrmeciza exsul	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Myrmeciza laemosticta	1	0	1	1	0	0	3	1	0	1	1	0	0	3
Myrmeciza berlepschi	0	0	0	0	0	1	1	0	0	1	1	0	1	3
Myrmeciza nigricauda	1	0	0	1	0	0	2	1	0	1	1	0	0	3
Sclateria naevia	0	0	1	1	0	0	2	0	0	1	0	0	0	1
Myrmeciza hyperythra	1	0	0	1	0	0	2	1	0	0	1	0	0	2
Schistocichla schistacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomacra manu	0	0	0	1	1	1	3	0	0	0	1	1	0	2
Cercomacra brasiliana	0	0	0	1	1	0	2	0	0	0	0	0	0	0
Cercomacra cinerascens	0	0	0	0	1	0	1	0	0	0	0	1	0	1
Cercomacra melanaria	0	0	0	1	1	1	3	0	0	0	1	1	0	2
Cercomacra nigricans	0	0	0	1	1	1	3	0	0	0	1	1	0	2
Cercomacra carbonaria	0	0	0	1	1	1	3	0	0	1	1	1	0	3
Myrmeciza castanea	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Myrmeciza hemimelaena	0	0	1	1	0	0	2	0	0	0	1	0	0	1
Cercomacra laeta	0	0	0	1	0	1	2	1	0	0	0	0	0	1
Cercomacra parkeri	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Cercomacra nigrescens	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Cercomacra tyrannina	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Cercomacra serva	0	0	0	1	0	1	2	0	0	0	0	0	0	0
Drymophila genei	1	1	1	1	0	0	4	1	0	0	1	0	0	2

Table A.2: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Hypocnemis peruviana	1	1	1	1	0	0	4	1	1	1	1	0	0	4
Willisornis poecilinotus	0	0	0	1	1	0	2	0	0	0	1	1	0	2
Phaenostictus mcleannani	1	1	1	1	1	0	5	1	1	1	1	1	0	5
Pithys castaneus	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Pithys albifrons	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Phlegopsis nigromaculata	1	1	1	1	0	0	4	1	1	1	1	0	0	4
Phlegopsis erythroptera	1	1	0	1	0	1	4	0	0	0	1	0	0	1
Rhegmatorhina melanosticta	1	0	1	0	0	0	2	1	1	0	1	0	0	3
Rhegmatorhina gymnops	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Rhegmatorhina hoffmannsi	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Gymnopithys leucaspis	0	0	1	0	0	0	1	0	0	1	0	0	0	1
Gymnopithys rufigula	1	1	0	0	0	0	2	1	0	0	0	0	0	1
Gymnopithys lunulata*	1	0	1	0	0	0	2	0	0	1	0	0	0	1
Gymnopithys salvini	1	0	1	0	1	0	3	0	0	0	0	0	0	0
Megastictus margaritatus	0	0	0	1	1	0	2	0	0	0	1	1	0	2
Dichrozona cincta	0	1	1	1	0	0	3	0	0	1	1	0	0	2
Batara cinerea	1	1	0	1	1	0	4	1	1	0	1	1	0	4
Hypoedaleus guttatus	0	0	1	0	0	1	2	0	0	1	0	0	1	2
Mackenziaena severa	1	0	0	0	0	1	2	1	0	0	0	1	0	2
Mackenziaena leachii	0	0	1	0	1	1	3	0	0	0	0	1	0	1
Frederickena viridis	1	0	0	0	0	1	2	1	0	1	0	1	0	3
Frederickena unduligera*	1	0	0	0	0	1	2	1	0	0	0	1	0	2
Taraba major	1	0	1	1	1	1	5	1	0	1	0	0	0	2
Cymbilaimus lineatus	1	0	0	0	0	1	2	1	0	1	0	0	0	2
Thamnophilus bernardi*	1	0	1	1	1	0	4	1	0	1	1	0	0	3
Thamnophilus atrinucha	1	1	0	1	1	0	4	0	0	0	1	0	0	1
Thamnophilus bridgesi	0	0	0	1	0	1	2	0	0	1	1	0	0	2
Thamnophilus schistaceus	1	0	0	0	0	1	2	0	0	0	0	0	0	0
Thamnophilus murinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thamnophilus nigrocinereus	1	0	0	1	1	0	3	1	0	0	0	0	0	1

Table A.2: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Thamnophilus cryptoleucus	0	1	0	1	0	1	3	0	0	0	0	0	1	1
Thamnophilus punctatus	1	0	0	1	1	0	3	0	0	0	1	0	0	1
Thamnophilus stictocephalus	1	1	0	1	1	0	4	0	0	0	1	0	0	1
Thamnophilus caerulescens	1	1	0	1	1	0	4	0	0	0	1	0	0	1
Thamnophilus unicolor	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Thamnophilus aroyae	0	0	0	1	0	0	1	1	0	0	0	0	0	1
Thamnophilus aethiops	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Thamnophilus nigriceps	0	0	0	0	0	1	1	1	0	1	0	0	0	2
Thamnophilus praecox	0	0	0	0	0	1	1	1	0	1	0	0	0	2
Thamnophilus amazonicus	1	1	0	1	1	0	4	0	0	0	1	1	0	2
Thamnophilus insignis	1	1	0	1	1	0	4	1	1	0	1	1	0	4
Thamnophilus divisorius	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Thamnophilus doliatus	1	0	1	0	0	1	3	1	0	0	0	0	0	1
Thamnophilus torquatus	1	0	1	0	1	0	3	1	0	1	0	0	0	2
Thamnophilus ruficapillus	1	0	1	0	1	0	3	0	0	0	0	0	0	0
Thamnophilus zarumae	1	0	0	0	0	1	2	1	0	0	0	0	0	1
Thamnophilus palliatus	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Thamnophilus tenuepunctatus	1	0	0	0	0	1	2	1	0	1	0	0	0	2
Sakesphorus luctuosus	1	0	0	1	0	1	3	1	0	0	1	0	1	3
Sakesphorus canadensis	1	0	1	1	1	0	4	1	0	0	1	0	0	2
Dysithamnus mentalis	1	0	1	1	0	0	3	1	0	1	0	0	0	2
Dysithamnus leucostictus	0	0	0	1	0	1	2	0	0	1	0	0	0	1
Herpsilochmus axillaris	1	0	1	1	1	0	4	1	0	0	1	0	0	2
Herpsilochmus longirostris	1	0	0	1	1	0	3	0	0	0	1	1	0	2
Herpsilochmus rufimarginatus	1	0	1	1	1	0	4	1	0	1	1	1	0	4
Herpsilochmus atricapillus	1	0	0	1	1	0	3	1	0	1	1	1	0	4
Herpsilochmus parkeri	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Herpsilochmus motacilloides	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Herpsilochmus stictocephalus	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Herpsilochmus dorsimaculatus	1	0	0	1	1	0	3	1	0	0	1	1	0	3

Table A.2: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Myrmotherula hauxwelli	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Thamnomanes saturninus	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Thamnomanes ardesiacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thamnomanes caesius	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thamnomanes schistogynus	0	0	0	0	0	0	0	0	0	1	0	0	0	1

Table A.3: Plumage ornamentation scores in male and female tanagers. See the subtitle of Table A.2 for detailed explanation.

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Tangara vassorii	1	0	0	1	1	1	4	1	0	0	1	1	1	4
Tangara nigroviridis	1	1	0	1	1	1	5	1	1	0	1	1	1	5
Tangara dowii	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara fucosa	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Tangara cyanotis	1	1	0	1	1	1	5	1	1	0	1	1	1	5
Tangara labradorides	1	0	1	1	1	0	4	1	0	1	1	1	0	4
Tangara gyrola	1	0	1	1	0	1	4	1	0	1	1	0	1	4
Tangara lavinia	1	1	1	1	0	1	5	0	1	1	1	0	1	4
Tangara chrysotis	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara xanthocephala	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara arthus	1	1	0	1	1	1	5	1	1	0	1	1	1	5
Tangara florida	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara icterocephala	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara parzudakii	1	1	1	1	0	1	5	1	1	1	1	0	1	5
Tangara johannae	1	1	1	1	1	0	5	1	1	1	1	1	0	5
Tangara schrankii	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara inornata	0	0	1	1	0	0	2	0	0	1	1	0	0	2
Tangara mexicana	1	1	1	1	0	1	5	1	1	1	1	0	1	5
Tangara chilensis	1	1	1	1	0	1	5	1	1	1	1	0	1	5
Tangara callophrys	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara velia	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara cyanocephala	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara cyanoventris	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara desmaresti	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara fastuosa	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara seledon	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara varia	0	0	0	1	1	0	2	0	0	0	1	1	0	2
Tangara punctata	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Tangara rufigula	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Tangara guttata	1	0	1	1	1	1	5	1	0	1	1	1	1	5

Table A.3: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Tangara xanthogastra	0	0	1	1	1	0	3	0	0	1	1	1	0	3
Tangara ruficervix	1	0	0	1	1	1	4	1	0	0	1	1	1	4
Thraupis sayaca	0	0	0	1	1	0	2	0	0	0	1	1	0	2
Thraupis episcopus	0	0	0	1	1	0	2	0	0	0	1	1	0	2
Thraupis cyanoptera	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Thraupis abbas	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Thraupis ornata	0	0	0	1	1	1	3	1	0	0	1	0	0	2
Thraupis palmarum	0	0	0	1	0	0	1	0	0	0	1	0	0	1
Tangara palmeri	1	0	1	1	1	0	4	1	0	1	1	1	0	4
Tangara larvata	1	1	1	1	0	1	5	1	1	1	1	0	1	5
Tangara cyanicollis	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara nigrocincta	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Tangara cyanoptera	1	0	0	1	1	1	4	0	0	1	0	0	0	1
Tangara viridicollis	1	0	1	0	0	0	2	1	0	0	0	0	0	1
Tangara argyrofenges	1	1	1	0	0	1	4	1	1	1	0	0	0	3
Tangara heinei	1	0	1	0	0	0	2	0	0	1	0	0	0	1
Tangara preciosa	1	1	1	1	0	1	5	1	0	1	1	0	0	3
Tangara meyerdeschauenseei	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Tangara vitriolina	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Tangara cayana	1	0	1	1	1	0	4	1	0	0	1	1	0	3
Tangara cucullata	1	0	0	1	1	0	3	1	0	0	1	1	0	3
Chlorochrysa phoenicotis	1	0	0	1	0	1	3	1	0	0	1	0	1	3
Chlorochrysa calliparaea	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Chlorochrysa nitidissima	1	1	1	1	1	1	6	1	0	1	0	0	1	3
Stephanophorus diadematus	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Diuca diuca	1	0	1	0	1	0	3	1	0	1	0	1	0	3
Neothraupis fasciata	1	0	0	1	0	0	2	1	0	0	1	0	0	2
Lophospingus griseocristatus	1	0	0	0	1	0	2	1	0	0	0	1	0	2
Lophospingus pusillus	1	0	1	1	1	0	4	1	0	0	1	1	0	3
Cissopis leverianus	1	1	1	1	1	1	6	1	1	1	1	1	1	6

Table A.3: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Schistochlamys melanopis	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Schistochlamys ruficapillus	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Paroaria dominicana	1	0	1	1	0	1	4	1	0	1	1	0	1	4
Paroaria coronata	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Paroaria capitata	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Paroaria gularis	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Wetmorethraupis sterrhopteron	0	0	1	1	0	1	3	0	0	1	1	0	1	3
Bangsia/Buthraupis arcaei	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Bangsia melanochlamys	0	0	1	1	1	1	4	0	0	1	1	1	1	4
Bangsia rothschildi	0	0	1	0	0	1	2	0	0	1	0	0	1	2
Bangsia aureocincta	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Bangsia edwardsi	1	0	1	1	0	1	4	1	0	1	1	0	1	4
Pipraeidea melanonota	1	0	1	0	0	1	3	1	0	1	0	0	0	2
Thraupis bonariensis	1	1	1	1	1	1	6	1	0	0	1	0	0	2
Iridosornis analis	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Iridosornis porphyrocephalus	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Iridosornis jelskii	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Iridosornis reinhardti	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Iridosornis rufivertex	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Calochaetes coccineus	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Delothraupis castaneoventris	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Dubusia taeniata	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Buthraupis wetmorei	1	0	0	1	1	1	4	1	0	0	1	1	1	4
Thraupis cyanocephala	1	0	1	1	0	0	3	1	0	1	1	0	0	3
Anisognathus notabilis	1	0	0	1	1	1	4	1	0	0	1	1	1	4
Anisognathus somptuosus	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Anisognathus melanogenys	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Anisognathus igniventris	1	1	1	1	0	1	5	1	1	1	1	0	1	5
Anisognathus lacrymosus	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Buthraupis montana	1	0	1	1	0	1	4	1	0	1	1	0	1	4

Table A.3: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Chlorornis riefferii	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Buthraupis aureodorsalis	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Buthraupis eximia	1	0	1	1	1	1	5	1	0	1	1	1	1	5

Table A.4: Plumage ornamentation scores in male and female blackbirds. See the subtitle of Table A.2 for detailed explanation.

Species	Males					Overall Coloration	Total Score	Females					Overall Coloration	Total Score
	Ornaments							Ornaments						
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Psarocolius angustifrons	0	0	0	0	1	0	1	0	0	0	0	1	0	1
Psarocolius atrovirens	0	0	0	0	1	0	1	0	0	0	0	1	0	1
Psarocolius wagleri	1	1	0	1	1	0	4	1	1	0	1	1	0	4
Psarocolius decumanus	1	0	0	0	1	1	3	1	0	0	0	1	1	3
Psarocolius viridis	1	0	0	0	1	0	2	1	0	0	0	1	0	2
*Gymnostinops bifasciatus**	1	0	0	0	1	0	2	1	0	0	0	1	0	2
*Gymnostinops guatimozinus**	1	0	0	0	1	1	3	1	0	0	0	1	1	3
*Gymnostinops montezuma**	1	0	0	0	1	0	2	1	0	0	0	1	0	2
Cacicus solitarius	0	0	0	0	0	1	1	0	0	0	0	0	1	1
*Psarocolius oseryi**	1	0	1	1	1	0	4	1	0	1	1	1	0	4
Cacicus haemorrhous	1	1	0	0	0	1	3	0	1	0	0	0	1	2
Cacicus cela	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Cacicus uropygialis	1	1	0	0	0	1	3	1	1	0	0	0	1	3
Cacicus chrysopterus	1	1	0	1	0	1	4	1	1	0	1	0	1	4
Amblycercus holosericeus	1	0	0	0	0	1	2	1	0	0	0	0	1	2
Icterus spurius	0	0	1	1	0	1	3	0	0	0	1	0	0	1
Icterus cucullatus	1	1	1	1	1	1	6	0	0	0	1	0	0	1
Icterus icterus	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Icterus croconotus	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Icterus pectoralis	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Icterus mesomelas	1	1	1	1	1	1	6	1	1	1	1	1	1	6
Icterus pustulatus	1	1	1	1	1	1	6	1	0	1	1	0	1	4
Icterus bullockii	1	1	1	1	1	1	6	0	0	1	1	0	0	2
Icterus galbula	0	1	1	1	1	1	5	1	0	1	1	0	0	3
Icterus leucopteryx	1	0	1	1	1	0	4	1	0	1	1	1	0	4
Icterus parisorum	0	1	1	1	1	1	5	0	0	1	0	0	0	1
Icterus graduacauda	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Icterus chrysater	1	0	1	1	1	1	5	1	0	1	1	1	1	5
Agelaius phoeniceus	0	0	0	1	0	1	2	1	0	1	0	0	0	2
Agelaius assimilis	0	0	0	1	0	1	2	0	0	0	0	0	1	1

Table A.4: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Agelaius tricolor	0	0	0	1	0	1	2	0	0	0	0	0	0	0
Agelaius xanthomus	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Agelaius humeralis	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Nesopsar nigerrimus	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Quiscalus quiscula	1	0	1	1	0	1	4	1	0	1	0	0	1	3
Quiscalus lugubris	1	0	0	1	0	1	3	1	0	0	0	0	0	1
Quiscalus nicaraguensis	1	0	0	0	0	1	2	1	0	1	0	0	0	2
Quiscalus major	1	1	1	0	0	1	4	0	0	0	0	0	0	0
Quiscalus niger	1	0	0	0	0	1	2	1	0	0	0	0	1	2
Quiscalus mexicanus	1	1	1	0	0	1	4	1	0	0	0	0	0	1
Euphagus cyanocephalus	1	0	1	0	0	1	3	0	0	0	0	0	0	0
Euphagus carolinus	1	0	0	0	0	1	2	1	0	0	0	0	0	1
Dives dives	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Dives warszewiczi	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Chrysomus ruficapillus	1	0	1	0	0	1	3	0	0	0	0	0	0	0
Chrysomus icterocephalus	1	0	1	0	0	1	3	1	0	1	0	0	0	2
Xanthopsar flavus	1	1	1	1	0	1	5	1	1	1	0	0	0	3
Agelasticus thilius	0	0	0	1	0	1	2	0	0	0	1	0	0	1
Agelasticus xanthophthalmus	1	0	0	0	0	1	2	0	0	0	0	0	1	1
Gnorimopsar chopi	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Amblyramphus holosericeus	1	0	1	0	0	1	3	1	0	1	0	0	1	3
Curaeus forbesi	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Agelaioides badius	1	0	0	1	0	0	2	1	0	0	1	0	0	2
Gymnomystax mexicanus	1	0	1	1	0	1	4	1	0	1	1	0	1	4
Macroagelaius imthurni	0	0	0	1	0	1	2	0	0	0	1	0	1	2
Molothrus ater	0	1	1	0	0	1	3	0	0	0	0	0	0	0
Molothrus bonariensis	0	1	1	0	0	1	3	0	0	0	0	0	0	0
Molothrus aeneus	1	0	0	1	1	1	4	1	0	0	0	0	1	2
Molothrus oryzivorus	1	0	0	0	0	1	2	0	0	0	0	0	1	1
Molothrus rufoaxillaris	0	0	0	0	0	1	1	0	0	0	0	0	1	1

Table A.4: (continued)

Species	Males							Females						
	Ornaments					Overall Coloration	Total Score	Ornaments					Overall Coloration	Total Score
	Head	Upperside	Underside	Wings	Tail			Head	Upperside	Underside	Wings	Tail		
Sturnella magna	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Sturnella neglecta	1	0	1	0	0	0	2	1	0	1	0	0	0	2
Dolichonyx oryzivorus	1	1	0	1	0	1	4	1	0	1	0	0	0	2
Xanthocephalus xanthocephalus	1	0	1	1	0	1	4	1	0	1	0	0	0	2

APPENDIX D

Habitat Types

Table A.5: Habitat types used for all the species in this study. Numbers in parentheses correspond to codes for each habitat type (BirdLife International 2013). A full list of habitat types is available in BirdLife International (2013).

Habitat types
Subarctic forest (1.2)
Temperate forest (1.4)
Subtropical/tropical dry forest (1.5)
Subtropical/tropical lowland moist forest (1.6)
Subtropical/tropical mangrove (1.7)
Subtropical/tropical swamp forest (1.8)
Subtropical/tropical montane moist forest (1.9)
Dry savanna (2.1)
Moist savanna (2.2)
Temperate shrubland (3.4)
Subtropical/tropical (lowland) dry shrubland (3.5)
Subtropical/tropical (lowland) moist shrubland (3.6)
Subtropical/tropical high altitude shrubland (3.7)
Temperate grassland (4.4)
Subtropical/tropical (lowland) dry grassland (4.5)
Subtropical/tropical (lowland) seasonally wet/flooded grassland (4.6)
Rivers, streams, creeks - permanent (5.1)
Rivers, streams, creeks - seasonal/intermittent/irregular (5.2)
Bogs, marshes, swamps, fens, peatlands (5.4)
Freshwater lakes - permanent (5.5)
Saline, brackish/alkaline marshes/pools - permanent (5.16)
Hot desert (8.1)
Rocky shores (10.1)
Sand, shingle, pebble shores (10.2)
Intertidal marshes (10.5)
Coastal brackish/saline lagoons (10.6)
Arable land (11.1)
Pastureland (11.2)
Plantations (11.3)
Rural gardens (11.4)
Urban areas (11.5)
Subtropical/tropical heavily degraded former forest (11.6)
Tidepools

Niche Width Scores

Table A.6: Niche width scores in antbirds. Habitat range is estimated as the sum of different habitat types coded in BirdLife International (2013). Altitudinal range is estimated as the difference between maximum and minimum altitude, using the information in BirdLife International (2013). Note that these minimum and maximum values refer to the altitudes where a species usually occurs, excluding occasional records. Distributional range is estimated using digitalized maps provided by Ridgely & Birdlife International (2011). Species with the asteriks (*) have different scientific names in BirdLife International (2013). Species with double asteriks (**) have no data for distributional range in Ridgely & Birdlife International (2011). We performed the analyses excluding these species with the missing data.

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Pipra mentalis	1.6	1	0	750	750	46.83
Liosceles thoracicus	1.6, 1.8	2	0	1050	1050	186.07
Hylopezus berlepschi	1.6, 11.6	2	0	500	500	117.43
Terenura sharpei	1.6, 1.9, 11.3	3	1100	1700	600	0.22
Terenura humeralis	1.6	1	0	650	650	104.30
Myrmornis torquata	1.6	1	0	1300	1300	253.46
Pygiptila stellaris	1.6, 1.8	2	0	700	700	383.45
Thamnistes anabatinus	1.6, 1.9	2	0	1700	1700	46.83
Microrhopias quixensis	1.6, 1.8	2	0	1100	1100	336.85
Neoctantes niger	1.6, 1.8, 5.1	3	0	800	800	99.53
Epinecrophylla fulviventris	1.6, 1.9	2	0	2000	2000	23.12
Epinecrophylla ornata	1.6, 1.8, 5.1	3	0	1400	1400	171.01
Epinecrophylla leucophthalma	1.6	1	0	800	800	163.84
Epinecrophylla erythrura	1.6, 1.8	2	0	900	900	136.10
*Epinecrophylla gutturalis**	1.6	1	0	1000	1000	89.03
Epinecrophylla spodionota	1.6, 1.9	2	500	1600	1100	5.71
Epinecrophylla haematonota	1.6	1	0	1300	1300	214.08
Myrmorchilus strigilatus	2.1, 2.2, 3.5	3	0	1200	1200	146.53

Table A.6: (continued)

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Myrmeciza atrothorax	1.6, 1.8, 1.9, 2.2, 3.6, 5.1, 11.6	7	0	1200	1200	557.33
Myrmeciza pelzelni	1.5, 1.6, 2.1	3	0	350	350	4.11
Myrmotherula schisticolor	1.6, 1.9	2	900	2400	1500	40.49
Myrmotherula behni	1.6, 1.9	2	900	1850	950	22.63
Myrmotherula grisea	1.6, 1.9	2	600	1500	900	4.29
Formicivora melanogaster	1.5, 2.1, 3.5	3	0	1050	1050	222.54
Formicivora rufa	1.5, 2.1, 3.5, 4.6	4	0	1450	1450	336.03
Formicivora grisea	1.5, 1.6, 1.7, 1.9, 2.2, 3.5, 3.6	7	0	1600	1600	492.16
Myrmotherula axillaris	1.6, 1.8, 5.1, 11.6	4	0	1200	1200	654.82
Myrmotherula longipennis	1.6, 1.8	2	0	1100	1100	417.48
Myrmotherula menetriesii	1.5, 1.6, 2.1	3	0	1000	1000	517.57
Myrmotherula assimilis	1.6, 1.8, 3.6, 5.1	4	0	0	0	33.68
Myrmotherula longicauda	1.6, 1.8, 1.9, 3.6, 11.6	5	150	1800	1650	8.32
Myrmotherula klagesi	1.8, 5.1	2	0	100	100	4.02
Myrmotherula sclateri	1.6, 1.8	2	0	550	550	157.54
Myrmotherula ambigua	1.5, 1.6, 2.1	3	0	350	350	11.51
*Myrmotherula obscura**	1.6, 1.8, 5.1	3	0	1100	1100	116.33
Myrmotherula brachyura	1.6, 1.8, 11.6	3	0	1100	1100	506.41
Myrmotherula multostriata	1.6, 1.8, 3.6, 11.6	4	0	550	550	371.46
Myrmotherula pacifica	1.6, 1.9, 3.6, 5.1, 11.3, 11.4, 11.6	7	0	800	800	19.34
Myrmochanes hemileucus	1.6, 3.6	2	0	300	300	21.35
Myrmotherula cherriei	1.5, 1.8, 2.1, 3.5	4	0	550	550	47.60
Myrmeciza ferruginea	1.6, 2.1	2	0	550	550	88.02
Myrmeciza loricata	1.6, 1.9	2	700	1300	600	15.27
Myrmeciza squamosa	1.6, 2.1	2	0	1000	1000	21.67
Hypocnemoides maculicauda	1.6, 1.8, 5.1, 5.5	4	0	500	500	274.14
Hylophylax punctulatus	1.6, 1.8, 5.5	3	0	800	800	226.64
Hylophylax naevioides	1.6	1	0	900	900	30.64
Hylophylax naevius	1.6, 1.8	2	0	1350	1350	477.96
Myrmeciza longipes	1.5, 1.6, 2.1, 11.3	4	0	1750	1750	114.80
Percnostola lophotes	1.6, 1.8	2	0	1450	1450	14.32
Myrmoborus myotherinus	1.6, 1.9	2	0	1350	1350	391.75

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Pyriglena leuconota	1.5, 1.6, 1.9	3	0	2200	2200	132.30
Gymnocichla nudiceps	1.6, 1.8, 5.1, 11.3, 11.4, 11.6	6	0	1200	1200	29.39
Percnostola rufifrons	1.5, 1.6, 1.7, 1.8, 2.1	5	0	1100	1100	89.63
Myrmeciza goeldii	1.6, 1.8, 3.6	3	0	450	450	28.27
Myrmeciza melanoceps	1.6, 1.8	2	0	450	450	107.70
Myrmeciza immaculata	1.6, 1.9, 11.6	3	0	2300	2300	17.21
Myrmeciza fortis	1.6, 1.8	2	0	900	900	159.00
Myrmeciza exsul	1.6	1	0	900	900	29.36
Myrmeciza laemosticta	1.6, 1.9	2	0	1000	1000	12.03
Myrmeciza berlepschi	1.6	1	0	650	650	4.54
Myrmeciza nigricauda	1.6, 1.9	2	150	1500	1350	5.26
Sclateria naevia	1.6, 1.7, 1.8, 3.6, 5.5	5	0	700	700	504.93
Myrmeciza hyperythra	1.6, 1.8, 5.5	3	0	450	450	134.69
Schistocichla schistacea	1.6, 5.2	2	0	400	400	43.19
Cercomacra manu	1.6, 5.1, 11.6	3	0	1200	1200	11.77
Cercomacra brasiliana	1.5, 3.6	2	600	950	350	9.78
Cercomacra cinerascens	1.6	1	0	900	900	548.45
Cercomacra melanaria	1.5, 1.6, 2.2	3	0	800	800	37.80
Cercomacra nigricans	1.6, 1.9, 5.4, 11.3	4	0	1500	1500	44.81
Cercomacra carbonaria	1.6, 3.6, 5.1, 11.3	4	800	900	100	0.84
Myrmeciza castanea	1.5, 1.6, 1.9	3	0	1350	1350	6.53
Myrmeciza hemimelaena	1.6, 1.8, 1.9	3	0	1350	1350	216.96
Cercomacra laeta	1.6, 1.8, 2.1, 5.1, 11.6	5	0	900	900	32.02
Cercomacra parkeri	1.9, 3.6, 11.6	3	1130	1950	820	2.95
Cercomacra nigrescens	1.6, 1.8, 1.9, 3.6, 5.1, 11.3, 11.6	7	0	2200	2200	321.85
Cercomacra tyrannina	1.6, 1.9, 3.6, 5.1, 11.6	5	0	1900	1900	259.15
Cercomacra serva	1.6, 1.8, 5.5	3	0	1350	1350	90.52
Drymophila genei	1.9	1	1000	2200	1200	1.94
*Hypocnemis peruviana***	1.6, 1.8, 5.1, 11.6	4	0	1300	1300	-
Willisornis poecilinotus	1.6, 1.8	2	0	1350	1350	525.63
Phaenostictus mcleannani	1.6, 11.3, 11.6	3	0	1200	1200	20.98
Pithys castaneus	1.6, 1.8	2	200	250	50	0.19

Table A.6: (continued)

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Pithys albifrons	1.6	1	0	1350	1350	252.66
Phlegopsis nigromaculata	1.6, 1.8	2	0	900	900	318.91
Phlegopsis erythroptera	1.6, 2.1	2	0	550	550	158.33
Rhegmatorhina melanosticta	1.6	1	0	1350	1350	156.36
Rhegmatorhina gymnops	1.6, 1.8	2	0	200	200	12.86
Rhegmatorhina hoffmannsi	1.6	1	0	300	300	53.31
Gymnopithys leucaspis	1.6, 1.9	2	0	1700	1700	113.96
Gymnopithys rufigula	1.6	1	0	1200	1200	140.64
*Gymnopithys lunulata**	1.6, 1.8	2	0	950	950	24.21
Gymnopithys salvini	1.6	1	0	450	450	111.31
Megastictus margaritatus	1.5, 1.6	2	0	1250	1250	158.08
Dichrozona cincta	1.6	1	0	800	800	254.47
Batara cinerea	1.6, 1.9, 2.2, 3.5, 5.1	5	0	2600	2600	53.98
Hypoedaleus guttatus	1.6	1	0	900	900	106.53
Mackenziaena severa	1.6, 1.9, 11.3, 11.6	4	0	1400	1400	84.29
Mackenziaena leachii	1.5, 1.6, 1.9, 3.5, 3.6, 11.6	6	0	2150	2150	71.54
Frederickena viridis	1.5, 1.6	2	0	700	700	103.16
*Frederickena unduligera**	1.6	1	0	1100	1100	141.81
Taraba major	1.6, 1.9, 2.1, 2.2, 3.6, 11.6	6	0	2200	2200	1072.69
Cymbilaimus lineatus	1.6, 1.9, 3.6	3	0	1000	1000	543.89
*Thamnophilus bernardi**	1.5, 1.7, 1.9, 3.5, 3.6	5	0	1850	1850	9.07
Thamnophilus atrinucha	1.6, 1.9, 11.6	3	0	1500	1500	45.44
Thamnophilus bridgesi	1.7, 1.6, 11.6	3	0	1150	1150	2.32
Thamnophilus schistaceus	1.6, 1.8	2	0	1100	1100	327.97
Thamnophilus murinus	1.5, 1.6	2	0	1300	1300	342.52
Thamnophilus nigrocinereus	1.6, 1.9, 1.8, 2.1, 11.6	5	0	0	0	160.97
Thamnophilus cryptoleucus	1.6, 1.8, 5.1	3	0	0	0	16.58
Thamnophilus punctatus	1.5, 1.6, 2.1	3	0	1500	1500	127.90
Thamnophilus stictocephalus	1.5, 1.6	2	0	700	700	77.08
Thamnophilus caerulescens	1.5, 1.6, 1.9, 3.6, 5.1	5	0	2800	2800	350.83
Thamnophilus unicolor	1.6, 1.9	2	1200	2300	1100	9.70
Thamnophilus aroyae	1.6, 1.9, 3.6, 11.6	4	600	1700	1100	5.26

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Thamnophilus aethiops	1.6, 1.9, 5.1	3	0	2000	2000	385.12
Thamnophilus nigriceps	1.6, 11.6	2	0	600	600	17.26
Thamnophilus praecox	1.8, 5.1	2	200	250	50	0.72
Thamnophilus amazonicus	1.5, 1.6, 1.8, 2.1	4	0	0	0	506.82
Thamnophilus insignis	1.9, 3.7	2	900	2000	1100	4.28
*Thamnophilus divisorius***	1.5	1	0	0	0	-
Thamnophilus doliatus	1.6, 2.1, 3.6, 11.1, 11.4, 11.5, 11.6	7	0	2000	2000	888.07
Thamnophilus torquatus	1.6, 1.9, 2.1, 3.6, 11.2, 11.3	6	0	1750	1750	313.12
Thamnophilus ruficapillus	1.9, 3.6, 3.7, 11.6	4	0	3050	3050	136.19
Thamnophilus zarumae	1.5, 1.6, 3.5, 3.6, 11.6	5	800	2650	1850	2.27
Thamnophilus palliatus	1.6, 1.9, 11.3, 11.4, 11.5, 11.6	6	0	2200	2200	210.88
Thamnophilus tenuepunctatus	1.6, 1.9, 11.3, 11.4, 11.5, 11.6	6	300	2500	2200	8.77
Sakesphorus luctuosus	1.6, 1.8, 5.1	3	0	250	250	132.46
Sakesphorus canadensis	1.5, 1.6, 1.7, 1.8, 2.1, 3.5, 5.1, 11.5	8	0	900	900	157.90
Dysithamnus mentalis	1.6, 1.9, 1.8, 2.1	4	600	2500	1900	372.71
Dysithamnus leucostictus	1.9	1	0	600	600	3.67
Herpsilochmus axillaris	1.6, 1.9	2	500	1900	1400	8.97
Herpsilochmus longirostris	1.5, 1.6	2	150	1200	1050	168.63
Herpsilochmus rufimarginatus	1.5, 1.6, 1.9, 2.1, 3.5	5	0	1500	1500	259.32
Herpsilochmus atricapillus	1.5, 1.6	2	0	1450	1450	314.96
Herpsilochmus parkeri	1.5, 1.9	2	1350	1450	100	0.14
Herpsilochmus motacilloides	1.9	1	900	2100	1200	6.20
Herpsilochmus stictocephalus	1.6	1	0	700	700	42.97
Herpsilochmus dorsimaculatus	1.6, 1.8, 2.1	3	0	600	600	73.83
Myrmotherula hauxwelli	1.6, 1.8	2	0	600	600	348.19
Thamnomanes saturninus	1.6, 1.8	2	0	650	650	111.80
Thamnomanes ardesiacus	1.6, 1.8	2	0	1050	1050	275.49
Thamnomanes caesius	1.6, 1.8	2	0	1100	1100	495.31
Thamnomanes schistogynus	1.6, 1.8	2	0	1200	1200	101.00

Table A.7: Niche width scores in tanagers. See the subtitle of Table A.6 for detailed explanation.

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Tangara vassorii	1.9	1	2000	3400	1400	25.75
Tangara nigroviridis	1.9	1	1500	3000	1500	28.73
Tangara dowii	1.9	1	1300	2700	1400	1.00
Tangara fucosa	1.9	1	1400	2000	600	0.25
Tangara cyanotis	1.9	1	1250	2200	950	7.33
Tangara labradorides	1.6, 1.9, 11.6	3	1300	2000	700	6.63
Tangara gyrola	1.6, 1.9, 1.8, 11.3	4	0	1800	1800	326.53
Tangara lavinia	1.6, 11.6	2	0	800	800	11.04
Tangara chrysotis	1.9	1	1150	1750	600	8.23
Tangara xanthocephala	1.6, 1.9, 11.3, 11.6	4	1300	2600	1300	29.41
Tangara arthus	1.6, 1.9	2	1000	1500	500	36.01
Tangara florida	1.6, 1.9	2	0	900	900	3.15
Tangara icterocephala	1.6, 1.9, 11.6	3	600	1600	1000	6.07
Tangara parzudakii	1.9	1	1000	2600	1600	13.39
Tangara johannae	1.6	1	0	1000	1000	5.64
Tangara schrankii	1.6, 1.8	2	0	1200	1200	225.09
Tangara inornata	1.6, 11.3	2	0	200	200	14.79
Tangara mexicana	1.6, 1.8, 11.3, 11.4	4	0	1000	1000	588.60
Tangara chilensis	1.6, 1.8, 11.3	3	0	1100	1100	376.47
Tangara callophrys	1.6, 11.3	2	0	1000	1000	121.18
Tangara velia	1.6, 11.3, 11.6	3	0	500	500	420.08
Tangara cyanocephala	1.6, 2.1, 11.3	3	0	1000	1000	39.52
Tangara cyanoventris	1.6, 1.9, 11.6	3	0	1000	1000	40.95
Tangara desmaresti	1.6, 1.9, 11.3	3	800	1800	1000	19.25
Tangara fastuosa	1.6, 1.8	2	0	550	550	1.29
Tangara seledon	1.6, 11.3, 11.4	3	0	900	900	59.61
Tangara varia	1.6, 11.3, 11.6	3	0	0	0	99.61
Tangara punctata	1.6, 1.9	2	0	1700	1700	208.08
Tangara rufigula	1.9	1	400	2100	1700	1.23
Tangara guttata	1.6, 1.9, 11.3, 11.4	4	700	1500	800	29.86
Tangara xanthogastra	1.6, 1.9	2	0	1350	1350	227.80
Tangara ruficervix	1.6, 1.9, 11.6	3	1100	2400	1300	20.51

Table A.7: (continued)

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Thraupis sayaca	1.6, 3.5, 3.6, 11.1, 11.2, 11.4, 11.5, 11.6	8	0	1000	1000	582.53
Thraupis episcopus	1.6, 2.1, 3.6, 11.3, 11.4, 11.6	6	0	2600	2600	648.97
Thraupis cyanoptera	1.6	1	200	950	750	19.84
Thraupis abbas	1.6, 11.3, 11.6	3	0	1600	1600	49.53
Thraupis ornata	1.6, 1.9, 11.6	3	0	1750	1750	34.05
Thraupis palmarum	1.6, 1.8, 1.9, 2.1, 3.5, 3.6, 11.3, 11.6	8	0	1200	1200	1009.22
Tangara palmeri	1.6	1	0	1100	1100	3.48
Tangara larvata	1.6, 1.9, 3.6, 11.3, 11.6	5	0	1200	1200	39.90
Tangara cyanicollis	1.6, 1.9, 2.1, 3.5, 3.6, 3.7, 11.3, 11.6	8	0	2400	2400	102.77
Tangara nigrocincta	1.6, 1.8, 11.3	3	0	900	900	280.32
Tangara cyanoptera	1.9, 3.7, 11.6	3	600	2000	1400	22.67
Tangara viridicollis	1.5, 1.9, 3.6, 3.7, 11.6	5	1450	3050	1600	8.40
Tangara argyrofenges	1.9	1	1200	2700	1500	2.98
Tangara heinei	1.9, 11.6	2	1300	2200	900	10.74
Tangara preciosa	1.6, 11.3, 11.4, 11.6	4	0	1000	1000	101.98
Tangara meyerdeschauenseei	1.9, 3.7, 11.1, 11.3, 11.4	5	2000	2200	200	0.07
Tangara vitriolina	1.6, 1.9, 3.5, 3.6, 3.7, 11.4, 11.6	7	300	2500	2200	10.10
Tangara cayana	1.6, 2.1, 3.5, 4.6, 11.1, 11.6	6	0	1800	1800	473.81
Tangara cucullata	1.6, 1.9, 3.5, 3.6, 11.3, 11.4, 11.6	7	0	850	850	0.06
Chlorochrysa phoenicotis	1.9	1	700	2200	1500	2.28
Chlorochrysa calliparaea	1.9	1	900	2000	1100	0.02
Chlorochrysa nitidissima	1.9	1	900	2195	1295	1.42
Stephanophorus diadematus	1.6, 1.9, 3.6, 11.4, 11.6	5	0	2400	2400	100.69
Diuca diuca	1.6, 1.9, 3.5, 3.6, 3.7, 11.1, 11.4, 11.6	8	0	2000	2000	228.58
Neothraupis fasciata	2.1	1	0	1100	1100	189.58
Lophospingus griseocristatus	3.5, 3.7, 11.1, 11.6	4	1000	2500	1500	7.30
Lophospingus pusillus	3.5, 3.7	2	0	2200	2200	50.04
Cissopis leverianus	1.6, 1.8, 11.6	3	0	1200	1200	435.60
Schistochlamys melanopis	2.1, 3.5, 3.6, 11.1, 11.6	5	0	1700	1700	513.28
Schistochlamys ruficapillus	1.5, 2.1, 3.5	3	0	1100	1100	157.40
Paroaria dominicana	1.5, 3.5	2	0	1200	1200	99.95
Paroaria coronata	3.5, 11.6	2	0	500	500	222.00

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Paroaria capitata	3.6, 5.4, 11.6	3	0	500	500	111.49
*Paroaria gularis****	1.8, 2.2, 3.6, 4.6	4	0	300	300	-
Wetmorethraupis sterrhopteron	1.6	1	600	800	200	0.79
Bangsia/Buthraupis arcaei	1.6, 1.9	2	300	1500	1200	0.74
Bangsia melanochlamys	1.6, 1.9	2	1000	2285	1285	0.67
Bangsia rothschildi	1.6	1	0	1100	1100	1.63
Bangsia aureocincta	1.9	1	1600	2200	600	0.08
Bangsia edwardsi	1.6, 1.9	2	900	2100	1200	1.55
Pipraeidea melanonota	1.6, 1.9, 3.5, 3.6, 11.1, 11.2, 11.4, 11.6	8	0	2500	2500	183.65
Thraupis bonariensis	1.6, 1.9, 2.1, 3.6, 3.7, 11.3, 11.6	7	0	2550	2550	309.39
Iridosornis analis	1.9	1	1150	2600	1450	7.97
Iridosornis porphyrocephalus	1.9	1	1500	2200	700	1.36
Iridosornis jelskii	1.9	1	2500	3500	1000	8.21
Iridosornis reinhardti	1.9	1	2000	3400	1400	6.09
Iridosornis rufivertex	1.9	1	2000	3500	1500	6.00
Calochaetes coccineus	1.9	1	1100	2000	900	8.13
Delothraupis castaneoventris	1.9	1	2400	3400	1000	10.95
Dubusia taeniata	1.9	1	2500	3500	1000	23.02
Buthraupis wetmorei	1.9, 3.7	2	2900	3550	650	0.84
Thraupis cyanocephala	1.9, 3.6, 3.7, 11.3, 11.6	5	1500	3000	1500	35.20
Anisognathus notabilis	1.9	1	900	2200	1300	1.51
Anisognathus somptuosus	1.9	1	900	2300	1400	22.45
Anisognathus melanogenys	1.9, 3.7	2	2000	3000	1000	0.49
Anisognathus igniventris	1.9, 3.7	2	2600	3500	900	23.43
Anisognathus lacrymosus	1.9	1	2100	3600	1500	12.42
Buthraupis montana	1.9	1	1500	3200	1700	24.59
Chlorornis riefferii	1.9	1	1800	2800	1000	23.93
Buthraupis aureodorsalis	1.9, 3.7	2	3050	3500	450	0.20
Buthraupis eximia	1.9	1	2800	3500	700	4.33

Table A.8: Niche width scores in blackbirds. See the subtitle of Table A.6 for detailed explanation.

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Psarocolius angustifrons	1.6, 1.8, 1.9	3	0	2000	2000	182.75
Psarocolius atrovirens	1.6, 1.9	2	800	2600	1800	11.68
Psarocolius wagleri	1.6, 11.3	2	0	1200	1200	40.02
Psarocolius decumanus	1.6, 1.8, 11.3	3	0	2600	2600	878.91
Psarocolius viridis	1.6	1	0	1100	1100	401.81
*Gymnostinops bifasciatus**	1.6, 1.8	2	0	900	900	374.66
*Gymnostinops guatimozinus**	1.5, 1.6	2	0	800	800	8.81
*Gymnostinops montezuma**	1.6, 11.3	2	0	800	800	38.01
Cacicus solitarius	1.6, 1.8	2	0	500	500	737.18
*Psarocolius oseryi**	1.6, 1.8	2	0	750	750	50.35
Cacicus haemorrhous	1.6	1	0	1000	1000	668.94
Cacicus cela	1.5, 1.6, 1.8, 2.1	4	0	1100	1100	727.62
Cacicus uropygialis	1.9	1	1300	2300	1000	33.28
Cacicus chrysopterus	1.5, 1.6, 1.9	3	0	2000	2000	158.19
Amblycercus holosericeus	1.6, 1.9	2	0	3500	3500	96.41
Icterus spurius	1.5, 1.6, 2.1, 11.3	4	0	1800	1800	653.58
Icterus cucullatus	1.5, 11.5	2	0	1500	1500	213.25
Icterus icterus	1.5, 2.1, 3.5, 11.3, 11.4	5	0	500	500	36.35
Icterus croconotus	1.6	1	0	550	550	277.40
Icterus pectoralis	1.5, 1.6, 3.5, 11.3, 11.5	5	0	1500	1500	17.99
Icterus mesomelas	1.5, 1.6, 1.7, 1.8, 11.3, 11.6	6	0	500	500	83.05
Icterus pustulatus	1.5, 1.6, 1.9, 2.1, 3.5	5	0	2000	2000	47.89
Icterus bullockii	1.4, 1.5, 11.5	3	0	1800	1800	511.23
Icterus galbula	1.4, 1.6, 4.4, 11.4, 11.5	5	0	500	500	1270.64
Icterus leucopteryx	1.6, 1.7, 1.9, 11.3, 11.4	5	0	1000	1000	0.96
Icterus parisorum	3.5, 3.7, 8.1	3	0	3000	3000	176.45
Icterus graduacauda	1.5, 1.6, 1.9, 5.1	4	0	2500	2500	23.28
Icterus chrysater	1.5, 1.6, 1.9, 2.1, 11.6	5	0	2900	2900	64.54
Agelaius phoeniceus	5.4, 11.1, 11.2	3	0	3000	3000	1623.83
Agelaius assimilis	1.7, 5.4, 11.1, 11.2	4	0	0	0	0.36
Agelaius tricolor	5.4, 11.1	2	0	1300	1300	11.42
Agelaius xanthomus	1.7, 3.5, 11.1, 11.2	4	0	0	0	0.75

Table A.8: (continued)

Species	Habitat Code	Habitat range	Altitude (min)	Altitude (max)	Altitudinal range	Distributional range
Agelaius humeralis	1.2, 3.5, 11.1, 11.2	4	0	900	900	9.53
Nesopsar nigerrimus	1.9	1	500	2200	1700	0.15
Quiscalus quiscula	1.4, 3.4, 5.4, 11.1, 11.2, 11.4, 11.5	7	0	0	0	969.23
Quiscalus lugubris	1.7, 10.1, 10.2, 11.1, 11.2, 11.4, 11.5	7	0	600	600	57.51
Quiscalus nicaraguensis	5.4, 5.5, 11.2	3	0	0	0	0.59
Quiscalus major	5.4, 5.16, 10.6	3	0	0	0	19.61
Quiscalus niger	1.7, 5.4, 10.2, 11.4, 11.5, tidepools	6	0	1800	1800	17.73
Quiscalus mexicanus	1.4, 1.5, 1.6, 1.7, 4.4, 4.5, 5.4, 11.1, 11.2, 11.4, 11.5	11	0	2300	2300	469.42
Euphagus cyanocephalus	4.4, 10.2, 11.1, 11.2, tidepools	5	0	1300	1300	1106.25
Euphagus carolinus	5.4, 5.5	2	0	0	0	3269.54
Dives dives	1.5, 1.6, 3.5, 3.6, 11.1, 11.2, 11.4, 11.5, 11.6	9	0	1000	1000	50.34
Dives warszewiczi	1.5, 3.5, 3.7, 11.1, 11.2, 11.5	6	0	1500	1500	17.69
Chrysomus ruficapillus	4.5, 5.4, 11.1	3	0	500	500	484.30
Chrysomus icterocephalus	4.6, 5.4, 11.1	3	0	2600	2600	128.95
Xanthopsar flavus	4.5, 4.6, 5.4, 11.1	4	0	1100	1100	61.54
Agelasticus thilius	5.4, 10.5, 11.1, 11.2	4	0	4300	4300	269.53
Agelasticus xanthophthalmus	5.4	1	0	650	650	0.75
Gnorimopsar chopi	1.6, 1.8, 2.1, 3.6, 4.6, 11.1, 11.6	7	0	1000	1000	511.29
Amblyramphus holosericeus	5.4	1	0	600	600	116.09
Curaeus forbesi	1.6, 4.6	2	0	600	600	1.55
Agelaioides badius	1.2, 3.5, 11.1, 11.2, 11.5	5	0	2880	2880	386.74
Gymnomystax mexicanus	2.1, 3.6, 4.6, 11.1, 11.2	5	0	950	950	125.38
Macroagelaius imthurni	1.9	1	500	2000	1500	4.81
Molothrus ater	1.4, 1.5, 4.4, 4.5, 11.1, 11.2	6	0	2000	2000	1300.78
Molothrus bonariensis	1.5, 1.6, 3.5, 3.6, 4.5, 11.1, 11.2	7	0	700	700	1151.63
Molothrus aeneus	1.5, 1.6, 11.1, 11.2, 11.4	5	0	2200	2200	210.58
Molothrus oryzivorus	1.6, 11.1, 11.2, 11.3	4	0	2000	2000	890.92
Molothrus rufoaxillaris	1.2, 4.5, 11.1, 11.2	4	0	700	700	295.36
Sturnella magna	3.5, 4.4, 4.5, 11.1, 11.2, 11.4	6	0	3500	3500	624.11
Sturnella neglecta	3.5, 4.4, 4.5, 11.1, 11.2	5	0	2800	2800	926.83
Dolichonyx oryzivorus	2.2, 4.4, 4.5, 11.1	4	0	0	0	1204.61
Xanthocephalus xanthocephalus	5.4, 11.1, 11.2	3	0	1000	1000	876.01

APPENDIX F

Diagnostic Chart for Branch Length Analysis

Table A.9: Results of branch length analysis where standardized independent contrasts are plotted against their standard deviations (Garland *et al.* 1992). The analysis is performed for all variables including habitat range, altitudinal range, distributional range, species plumage coloration under scenario A, species plumage coloration under scenario B, female plumage coloration, and plumage dichromatism. Values refer to Pearson product-moment correlation coefficients. (two-tailed *p* values: *$p<0.1$, **$p<0.05$, ***$p<0.01$.)

	Antbirds	Tanagers	Blackbirds
Habitat range	-0.561***	-0.346***	-0.205
Altitudinal range	-0.380***	-0.287***	-0.300**
Distributional range	-0.514***	-0.407***	-0.461***
Speices plumage coloration (Scenario A)	-0.337***	-0.389***	-0.064
Speices plumage coloration (Scenario B)	-0.244***	-0.419***	-0.186
Female plumage coloration	-0.305***	-0.289***	-0.098
Plumage dichromatism	-0.532***	-0.389***	-0.136

Phylogenetic Trees
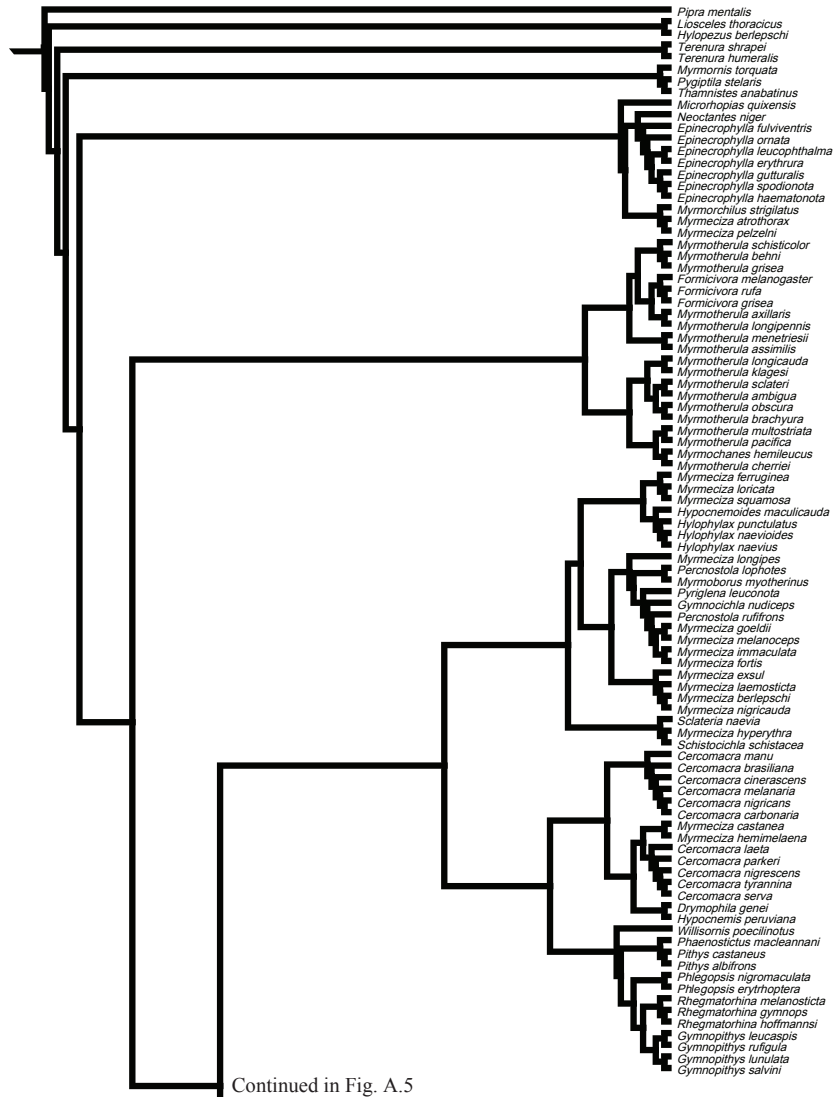
Figure A.4: Phylogenetic tree of antbirds under gradual model of evolution. The tree is modified from Gómez *et al.* (2010) by reducing two populations of *Gymnopithys leucaspis* to one in our phylogeny. The phylogeny is continued in Figure A.5.

Megastictus margaritatus
Dichrozona cincta
Batara cinerea
Hypoedaleus guttatus
Mackenziaena severa
Mackenziaena leachii
Frederickena viridis
Frederickena unduligera
Taraba major
Cymbilaimus lineatus
Thamnophilus bernardi
Thamnophlis atrinucha
Thamnophilus brdgesi
Thamnophilus schistaceus
Thamnophilus murinus
Thamnophilus nigrocinereus
Thamnophilus cryptoleucus
Thamnophilus punctatus
Thamnophilus stictocephalus
Thamnophilus caerulescens
Thamnophilus unicolor
Thamnophilus aroyae
Thamnophilus aethiops
Thamnophilus nigriceps
Thamnophilus praecox
Thamnophilus amazonicus
Thamnophilus insgnis
Thamnophilus divisorius
Thamnophilus doliatus
Thamnophilus torquatus
Thamnophilus ruficapillus
Thamnophilus zarumae
Thamnophilus palliatus
Thamnophilus tenuepunctatus
Sakesphorus luctuosus
Sakesphorus canadensis
Dysithamnus mentalis
Dysithamnus leucostictus
Herpsilochmus axillaris
Herpsilochmus longirostris
Herpsilochmus rufimarginatus
Herpsilochmus atricapillus
Herpsilochmus parkeri
Herpsilochmus motacilloides
Herpsilochmus stictocephalus
Herpsilochmus dorsimaculatus
Myrmotherula hauxwelli
Thamnomanes saturninus
Thamnomanes ardesiacus
Thamnomanes caesius
Thamnomanes schistogynus

Figure A.5: Phylogenetic tree of antbirds under gradual model of evolution. The phylogeny is continued in Figure A.4.

Figure A.6: Phylogenetic tree of antbirds under punctuated model of evolution. The phylogeny is continued in Figure A.7. See the caption in A.4.

Megastictus margaritatus
Dichrozona cincta
Batara cinerea
Hypoedaleus guttatus
Mackenziaena severa
Mackenziaena leachii
Frederickena viridis
Frederickena unduligera
Taraba major
Cymbilaimus lineatus
Thamnophilus bernardi
Thamnophlis atrinucha
Thamnophilus brdgesi
Thamnophilus schistaceus
Thamnophilus murinus
Thamnophilus nigrocinereus
Thamnophilus cryptoleucus
Thamnophilus punctatus
Thamnophilus stictocephalus
Thamnophilus caerulescens
Thamnophilus unicolor
Thamnophilus aroyae
Thamnophilus aethiops
Thamnophilus nigriceps
Thamnophilus praecox
Thamnophilus amazonicus
Thamnophilus insgnis
Thamnophilus divisorius
Thamnophilus doliatus
Thamnophilus   torquatus
Thamnophilus ruficapillus
Thamnophilus zarumae
Thamnophilus palliatus
Thamnophilus tenuepunctatus
Sakesphorus luctuosus
Sakesphorus canadensis
Dysithamnus mentalis
Dysithamnus leucostictus
Herpsilochmus axillaris
Herpsilochmus longirostris
Herpsilochmus rufimarginatus
Herpsilochmus atricapillus
Herpsilochmus parkeri
Herpsilochmus motacilloides
Herpsilochmus stictocephalus
Herpsilochmus dorsimaculatus
Myrmotherula hauxwelli
Thamnomanes saturninus
Thamnomanes ardesiacus
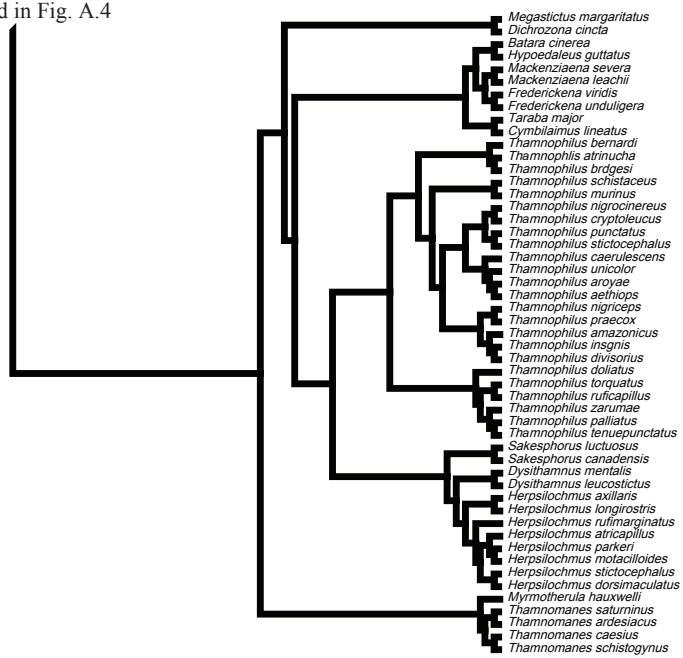*Thamnomanes caesius*
Thamnomanes schistogynus

Figure A.7: Phylogenetic tree of antbirds under punctuated model of evolution. The phylogeny is continued in Figure A.6.

Figure A.8: Phylogenetic tree of tanagers under gradual model of evolution (Sedano & Burns 2010). The phylogeny is continued in Figure A.9.

Continued in Fig. A.8

Chlorochrysa phoenicotis
Chlorochrysa calliparaea
Chlorochrysa nitidissima
Stephanophorus diadematus
Diuca diuca
Neothraupis fasciata
Lophospingus griseocristatus
Lophospingus pusillus
Cissopis leverianus
Schistochlamys melanopis
Schistochlamys ruficapillus
Paroaria dominicana
Paroaria coronata
Paroaria capitata
Paroaria gularis
Wetmothraupis sterrhopteron
Bangsia arcaei
Bangsia melanochlamys
Bangsia rothschildi
Bangsia aureocincta
Bangsia edwardsi
Pipraeidea melanonota
Thraupis bonariensis
Iridosornis analis
Iridosornis porphyrocephalus
Iridosornis jelskii
Iridosornis reinhardti
Iridosornis rufivertex
Calochaetes coccineus
Delothraupis castaneoventris
Dubusia taeniata
Buthraupis wetmorei
Thraupis cyanocephala
Anisognathus notabilis
Anisognathus somptuosus
Anisognathus melanogenys
Anisognathus iginiventris
Anisognathus lacrymosus
Buthraupis montana
Chlorornis riefferi
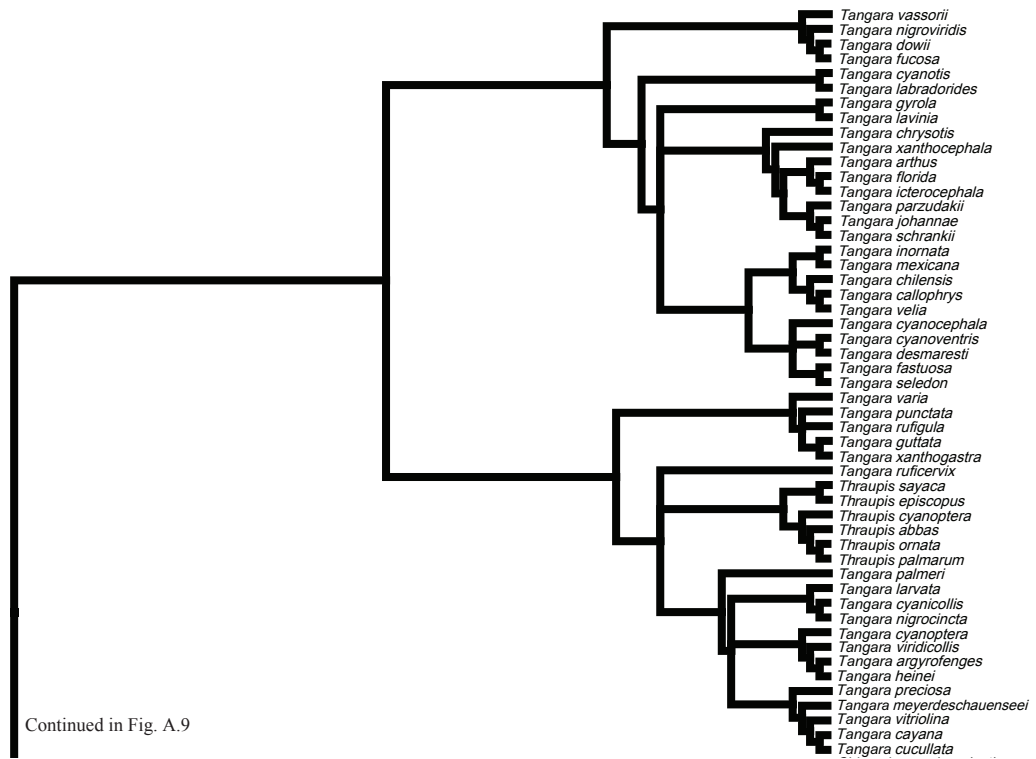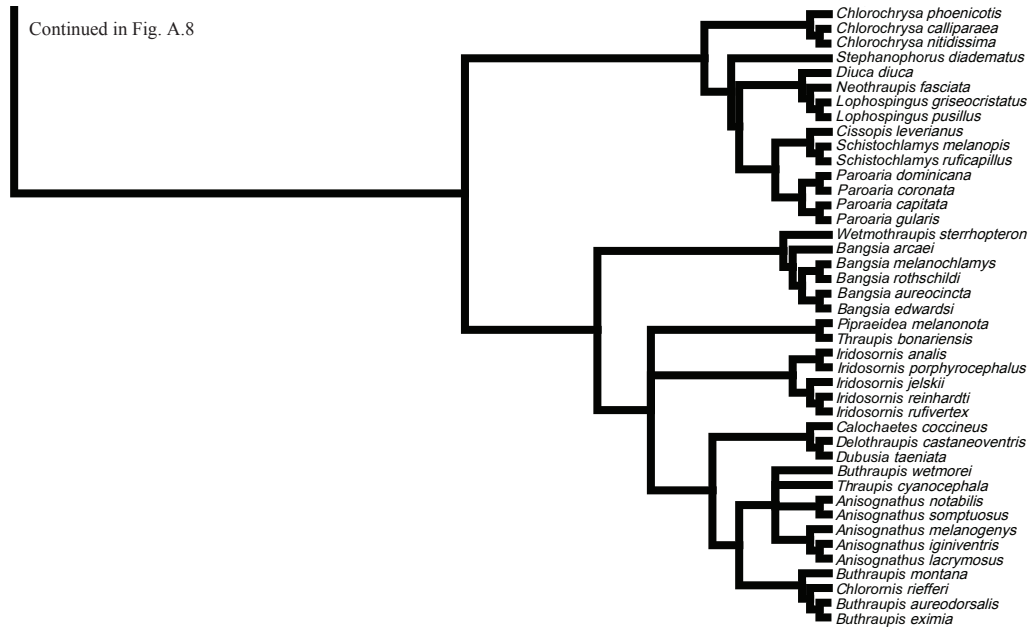*Buthraupis aureodorsalis*
Buthraupis eximia

Figure A.9: Phylogenetic tree of tanagers under gradual model of evolution (Sedano & Burns 2010). The phylogeny is continued in Figure A.8.
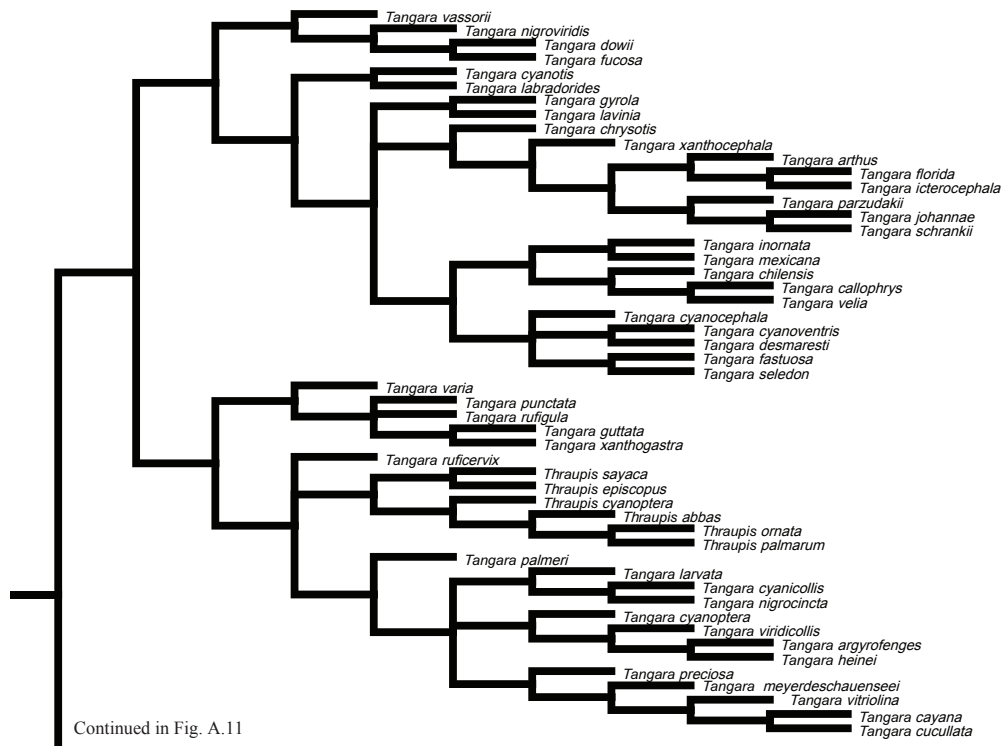
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Figure A.10: Phylogenetic tree of tanagers under punctuated model of evolution (Sedano & Burns 2010). The phylogeny is continued in Figure A.11.

Chlorochrysa phoenicotis
Chlorochrysa calliparaea
Chlorochrysa nitidissima
Stephanophorus diadematus
Diuca diuca
Neothraupis fasciata
Lophospingus griseocristatus
Lophospingus pusillus
Cissopis leverianus
Schistochlamys melanopis
Schistochlamys ruficapillus
Paroaria dominicana
Paroaria coronata
Paroaria capitata
Paroaria gularis
Wetmetharupis sterrhopteron
Bangsia arcaei
Bangsia melanochlamys
Bangsia rothschildi
Bangsia aureocincta
Bangsia edwardsi
Pipraeida melanonota
Thraupis bonariensis
Iridodornis analis
Iridodornis porphyrocephalus
Iridodornis jelskii
Iridodornis reinhardti
Iridodornis rufivertex
Calochaetes coccineus
Delothraupis castaneoventris
Dubusia taeniata
Buthraupis wetmorei
Thraupis cyanocephala
Anisognathus notabilis
Anisognathus somptuosus
Anisognathus melanogenys
Anisognathus iginiventris
Anisognathus lacrymosus
Buthraupis montana
Chlorornis riefferi
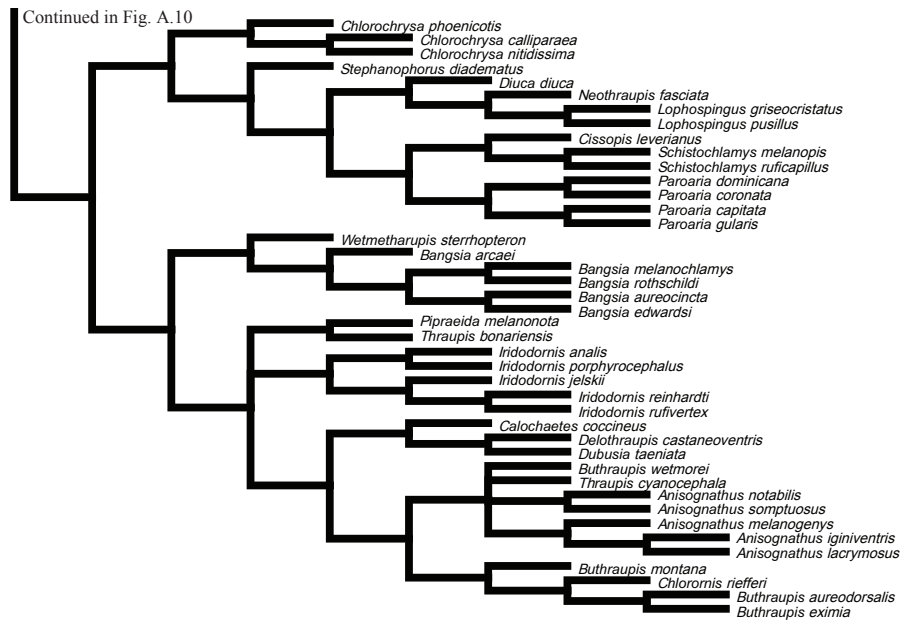*Buthraupis aureodorsalis*
Buthraupis eximia

Figure A.11: Phylogenetic tree of tanagers under punctuated model of evolution (Sedano & Burns 2010). The phylogeny is continued in Figure A.10.
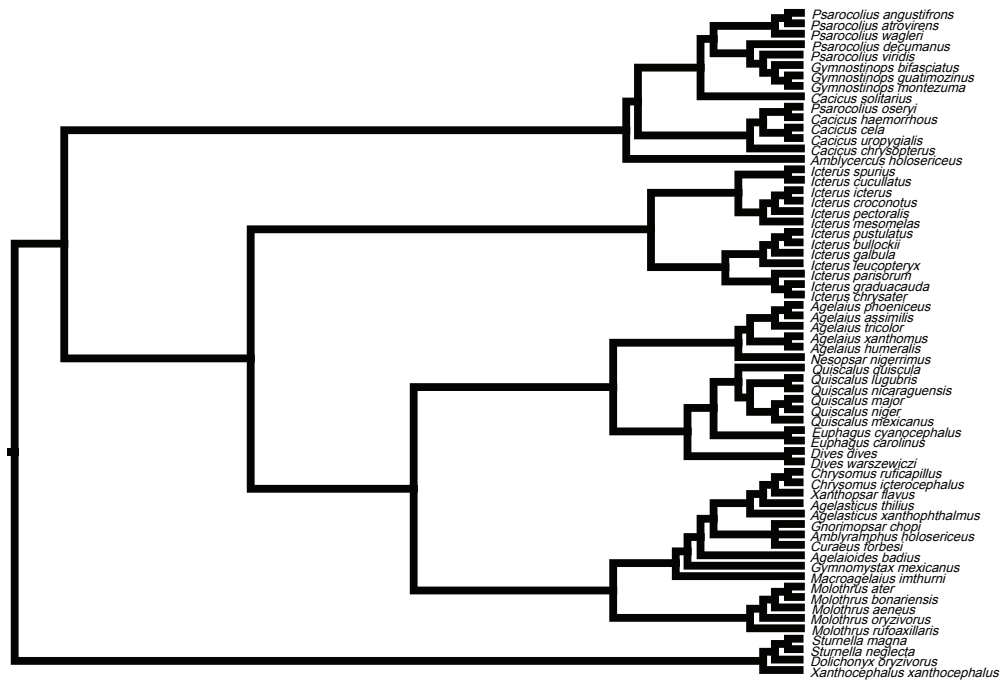
Figure A.12: Phylogenetic tree of blackbirds under gradual model of evolution. The tree is modified from Price *et al.* (2009) by removing *Icterus chrysocephalus* from the phylogeny as no data exists for this species in BirdLife International (2013).
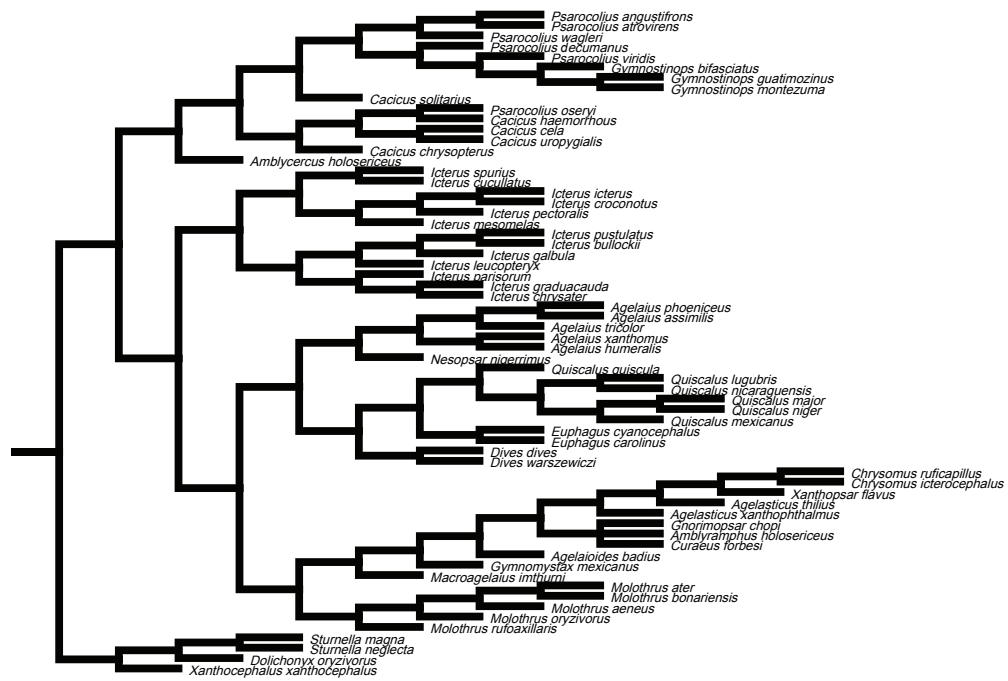
Figure A.13: Phylogenetic tree of blackbirds under punctuated model of evolution. See the caption in Figure A.12.