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thamnofilídeos da Tribo Formicivorini (Aves,
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Resumo

A comunicação animal transmite informações usando diferentes tipos de sinais sensoriais que possuem propósitos específicos (e.g. cortejo, defesa territorial, manutenção de grupos unidos e minimização da predação) e estão suscetíveis a pressões do habitat (Hipótese de Condução Sensorial - HCS). Em aves, alguns estudos de sinais acústicos e visuais demonstraram que a estrutura do canto está associada com a capacidade de transmissão do som em diferentes habitats e alguns aspectos de plumagem (e.g. coloração, brilho e padrão) parecem variar de acordo com as condições de iluminação do ambiente. Além dos efeitos de habitat, outros fatores como limitação energética, risco de predação e de parasitismo podem limitar o investimento em mais de um tipo de sinal sensorial. Devido a esse alto custo, foi proposta a existência de uma demanda conflitante (*trade-off*) evolutiva entre os diferentes tipos de sinais sensoriais denominada Hipótese de Transferência (HT) ou de “*Trade-off*”. Os poucos estudos que testaram a HT em aves apresentaram resultados contrastantes, sendo corroborada apenas em dois trabalhos. Além disso, há uma baixa quantidade de trabalhos que consideraram as condições de habitat como covariáveis. Assim, nós avaliamos a HT entre os sinais acústicos e visuais, considerando simultaneamente os efeitos potenciais das condições de habitat (HCS) em um diverso grupo de aves subóscines neotropicais, comumente conhecidas como papa-formigas (Thamnophilidae). Especificamente, nós integramos a filogenia em escala genômica da tribo Formicivorini (36 espécies) com dados vocais, de plumagem, ecológicos e comportamentais utilizando uma abordagem comparativa filogenética para testar simultaneamente a HT, a HCS e também considerando a influência do comportamento de formação de bandos mistos na diversidade da estrutura dos sinais acústicos e visuais. Enquanto que demandas conflitantes significativas entre algumas medidas

de plumagem e de canto foram encontradas em ambos os sexos (e.g. luminância dorsal contra declive de frequência) corroborando a HT, uma tendência oposta não significativa foi encontrada entre o dimorfismo sexual de plumagem e canto. Todas essas relações são influenciadas por condições de habitat e comportamento como covariáveis, corroborando a HCS e a influência do comportamento de bandos mistos na evolução da estrutura dos sinais acústicos e visuais.

Palavras-chave: Hipótese de condução sensorial, hipótese de transferência, Formicivorini, plumagem, canto.

Abstract

Animal communication transmits information using different sensory signals that have particular purposes (e.g. courtship, territorial defense, maintaining groups together and minimizing predation) and are susceptible to habitat pressures (Sensory Drive Hypothesis - SDH). In birds, some studies on acoustic and visual signals showed that song structure is associated with sound transmission capacity in different habitats and some plumage features (e.g. color, brightness and pattern) seem to vary according to light conditions of the environment. In addition to habitat effects, other factors such as energetic limits, predation, and parasitism risk can limit the investment in more than one type of sensory signal. Due to this high cost, it was proposed the existence of an evolutionary trade-off between the different types of sensory signals termed Transfer (TH) or Trade-off hypothesis. Few studies that have tested the TH in birds showed contrasting results, being corroborated only in two studies. Also, there is a low in the number of studies that have considered habitat conditions as covariates (SDH). Here, we assess the TH between acoustic and visual signals, while simultaneously considering potential effects of habitat conditions (SDH) in a diverse group of Neotropical suboscine birds, commonly known as antbirds (Thamnophilidae). Specifically, we integrated a genome-scale phylogeny of the tribe Formicivorini (36 species) with vocal, plumage, ecological, and behavioral data within a phylogenetic comparative framework to simultaneously test the TH and SDH while assessing the influence of mixed-species flocking foraging behavior on the structural diversity of acoustic and visual signals. Whereas in both sexes we found significant trade-offs between some plumage and vocal traits (e.g. dorsal luminance versus frequency slope), providing support for the TH, we found a non-significant opposite trend between plumage and vocal sexual dimorphism. All these relationships are

influenced by habitat conditions and behavioral traits as covariates, corroborating the SDH and mixed-species flocking behavior influence in the evolution of visual and acoustic signals.

Keywords: Sensory drive hypothesis, transfer hypothesis, Formicivorini, plumage, song.

General Introduction

Animal Communication and sensory signals

Animal communication transmits information using different types of sensory signals (e.g. visual, auditory, olfactory and contact). These signals have different communication purposes such as courtship, territorial defense, maintaining groups together and minimizing predation. However, the efficacy of the signal transmission from an emitter to a receiver is subject to habitat pressures (Endler, 1992; Endler, 1993).

According to the Sensory Drive Hypothesis (SDH), habitat physical conditions can “drive” the evolution of sensory signals in particular directions (Endler, 1992). In birds, the SDH has been tested in acoustic and visual signals for a variety of groups. Regarding acoustic signals, some studies showed that song structure is related to sound transmission capacity in different habitats. Whereas some studies found a relationship between habitat and song frequency traits (e.g. Morton, 1975; Slabbekoorn and Smith, 2002; Seddon, 2005; Kirschel *et al.*, 2009; Mason and Burns, 2015), in other studies habitat was correlated only with temporal components of song structure (e.g. Badyaev and Leaf, 1997; Derryberry *et al.*, 2018). With respect to visual signals, some plumage aspects such as color, brightness, and pattern seem to vary according to light conditions of the environment in order to provide maximum contrast against the background (e.g. Marchetti, 1993; Endler and Thery, 1996; McNaught and Owens, 2002; Gomez and Théry, 2004; Shultz and Burns 2013; Shultz and Burns 2017). Closed habitat birds have brighter and more complex color patterns than birds from open habitat (Marchetti, 1993). In the forests, canopy birds have brighter coloration and more diverse color patterns than understory birds (Gomez and Théry, 2004; Shultz and Burns 2017).

In addition to habitat effects, other factors such as energetic limits, predation and parasitism risk can limit the investment in more than one type of sensory signal (Endler, 1993; Partan and Marler, 1999; Partan and Marler, 2005). Due to this high cost, it was proposed the existence of an evolutionary trade-off between the different types of sensory signals in organisms (Darwin, 1871), termed Transfer (Gilliard, 1956) (TH) or Trade-off hypothesis (Repentigny *et al.*, 2000). Few studies have tested the TH in birds and they showed diverse results. Two studies found a trade-off between song complexity and plumage elaboration in cardueline finches (Badyaev and Weckworth, 2002) and in new world warblers (Laverde-R., 2017), whereas four studies did not find any trade-off between these signals in trogons (Ornelas *et al.*, 2009), tanagers (Mason *et al.*, 2014), estrildid finches (Gomes *et al.*, 2017) and old-world orioles (Matysioková *et al.*, 2017). Four other studies found a positive correlation between these signals in North American wood warblers (Shutler and Weatherhead, 1990), 123 species of North American oscines (Repentigny *et al.*, 2000), Asian barbets (Gonzalez-Voyer *et al.*, 2013) and 1023 species of songbirds (Webb *et al.*, 2016). These conflicting results might result from methodological differences or because this hypothesis is simply not held in all groups. Furthermore, only a few studies tested the TH considering the habitat conditions as a covariate (Gonzalez-Voyer *et al.*, 2013; Mason *et al.*, 2014; Laverde-R., 2017; Gomes *et al.*, 2017). Therefore, the fundamental research goal of the proposed research was to assess the existence of a trade-off between acoustic and visual signals (TH), while simultaneously considering potential effects of habitat conditions (SDH) in a diverse group of Neotropical birds.

Family Thamnophilidae

The Thamnophilidae is a large family of insectivorous passerine birds which contains about 230 species and is supported by recent molecular studies (Irestedt *et al.*, 2004; Moyle *et al.*, 2009; Bravo *et al.*, 2012; Bravo *et al.*, 2014). They are diurnal birds that exhibit great morphological, ecological, and behavioral diversity. The family members are commonly known as antbirds due to a common foraging behavior of following swarms of army-ants in order to prey arthropods flushed by these ants (Willis and Oniki, 1978). The family distribution is Neotropical and the vast majority inhabits lowland and foothill humid forests (Zimmer and Isler, 2016). The greatest diversity is found in the Amazon Basin, where 40-45 species may occur syntopically in various places in Bolivia, Peru, Brazil and Colombia (e.g. Terborgh *et al.*, 1990). However, the species diversity falls off with increasing elevation in mountain regions, with none occurring above 3000 m. Most of the species are arboreal, occupying all forest strata, i.e. from the ground to the canopy (Zimmer and Isler, 2016).

Antbird songs are relatively simple and usually consist of series of simple notes delivered in a stereotyped pattern, referred to as loudsong by Willis (Willis 1967; Zimmer and Isler 2016). Despite their simplicity, loudsong composition exhibits a great variety of ways in which notes are shaped and combined. Loudsongs are vocalized in different contexts, but usually they seem to be used in maintaining pairs together, and in territorial defense. Most of the thamnophilid species have males and females with similar patterned loudsongs. Both sexes can have near identical loudsongs, just varying in the pitch. Females of some species have higher-pitched loudsongs than males, whereas other females have loudsong in the same pitch as the male, or at a lower pitch (Zimmer and Isler 2016). Moreover, all vocalizations in the Thamnophilidae family are assumed to be innate or genetically determined and independent of learning or cultural evolution

(Touchton *et al.*, 2014). Thus, they have an important role in the maintenance of species integrity and are of extreme importance for diagnosing species (Isler *et al.*, 1998).

The thamnophilid plumages does not have great color variation, but most have attractive patterns in black and white or rufous, buff or brown tones. Many species also have spotted and streaked patterns that can cover all body or just specific regions like throat, belly, crown, nape and back (Figure 1). Sexual dimorphism is pronounced in almost all family. Whereas males usually have combinations of grey, black and white; females often have brown, rufous and buff tones (Zimmer and Isler, 2016).

Figure 1. Some antbird species showing the plumage and sexual dimorphism diversity in the family. 1. *Epinecrophylla ornata*, 2. *Terenura maculata*, 3. *Myrmotherula cherriei*, 4. *Myrmotherula grisea*, 5. *Formicivora grisea*, 6. *Pyriglena leuconota*, 7. *Rhegmatorhina hoffmannsi*, 8. *Taraba major*, 9. *Cymbilaimus lineatus*, 10. *Microrhopias quixensis*. Images were extracted from the *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona.

Although their diet is basically composed of arthropods, antbirds exhibit a wide variety of foraging behaviors. Many antbird species participate in mixed-species foraging flocks. These flocks are formed of different species that unite and move together during foraging in the tropical forests in order to enhance foraging and decrease chances of predation (Powell, 1979). These flocks are formed by several closely related species and occur throughout the year (Powell, 1979; Munn, 1985). Another common behavior is observed in the dead-leaf users. Many thamnophilids species specialize in foraging dead leaves that falls from the canopy and are trapped by vines and other vegetation most in the understory, creating an arboreal leaf litter, which provides hiding places for many arthropods (Remsen and Parker, 1984). Lastly, the most noted foraging behavior present in the family consists of following army-ants. A number of antbirds have specialized in following swarms raiders in order to prey many arthropods that are trapped or flushed by these carnivorous ants (Willis and Oniki, 1978). All described foraging behaviors when present in a species can be obligatory or occasional.

Tribe Formicivorini

The family is subdivided in three subfamilies: Eucrepomidae, Myrmornithinae, and Thamnophilinae (Bravo *et al.*, 2012). The latter contains most of the species in the family and is organized in five tribes: Microrhopiini, Formicivorini, Thamnophilini, Pyriglenini e Pithyini (Moyle *et al.*, 2009). One of the strongly supported groups in the family by recent molecular studies is the tribe Formicivorini, which contains 36 species, commonly known as antwrens (Bravo *et al.*, 2012; Bravo *et al.*, 2014, Remsen *et al.*, 2018). They are small birds that inhabit a wide diversity of habitats and exhibit contrasting patterns of foraging behavior, acoustic, and visual signals. They are primarily distributed in lowland

forests and different species are associated with different habitats (e.g. flooded forests, white sand forests) and foraging strata (e.g. understory, canopy). Foraging behavior is also variable, some species engage in obligate or facultative mixed-species flocking behavior, whereas others forage solitary or in small family groups (Bravo *et al.*, 2014; Zimmer and Isler, 2016).

Acoustic and visual signals are variable in the group. Their songs show little to no sexual dimorphism and they are composed by a series of single notes that ranges in number of notes, duration, intensity, frequency, and composition. Song and note structure can vary geographically in some species. Regarding plumage, antwrens are sexually dimorphic. They exhibit small color variation, but have high variation in plumage patterns, ranging from plain colors to spots and streaks around their body regions (e.g. throat, wings, dorsal and ventral region) (Zimmer and Isler, 2016). Some species have white or pale gray flanks that contrasts with dark body feathers. Another pattern present in a few antwrens is a bright white interscapular patch in the center of the back. The species with these different patterns of flanks and interscapular usually display it, suggesting an important role in communication.

It is expected that the interaction between ecology and behavior influences the structure of acoustic and sensory signals. For instance, because mixed-species flocking behavior depends on inter and intraspecific communication among group members (Powell, 1979), it could be predicted that species engaging in this behavior exhibit more structured sensory signals.

Therefore, the combination of a variation in acoustic and visual signals, occupied habitats and mixed-species flocking behavior make the tribe Formicivorini an ideal group to test the TH, and a possible influence

of habitat (SDH) and mixed-species flocking behavior in the structure of these signals.

Justification

The tribe Formicivorini is an ideal group for this study because it has a great diversity in habitat preferences, foraging behavior and inter/intraspecific interaction levels that can generate a variety of communication possibilities. However, the way these traits may be influencing the visual and acoustic communication in the evolutionary context of the group is still unknown. Therefore, this study aimed at unravelling how habitat (SDH) and foraging behavior can influence the structure of acoustic and visual signals, and elucidate whether there is an evolutionary trade-off between these sensory signals (TH). Besides contributing to our understanding of the evolution of acoustic and visual signals in the Formicivorini, it will also shed light on the TH while accounting for possible effects posed by habitat (SDH) and behavioral traits.

General conclusions

In the present study, we integrated a genome-scale phylogeny of the tribe Formicivorini with vocal, plumage, ecological, and behavioral data following a phylogenetic comparative framework in order to comprehend the evolution of acoustic and visual signals in the diverse Formicivorini clade.

We found significant trade-offs between some acoustic and visual signals (TH) in both sexes. In males, antwrens with a brighter dorsal region have a lower number of note types in a song and a lower frequency range per song duration. While in females, antwrens with a brighter dorsal region have a lower frequency range per song duration and those with a more complex patterned dorsal region and wing coverts more contrasted have a lower frequency range per song duration and a lower note diversity. These significant trade-offs are under a force of selection towards an adaptive optimum in males and in almost all cases in females.

When we tested the relationship between sexual dimorphism in plumage and song traits, we found an opposite trend. A non-significant positive correlation was found, thus refuting the TH and evidencing a trend that the greater the plumage dimorphism, the greater the vocal dimorphism. The observed pattern was under an absence of selection forces and suggests a redundancy on the sensory signals system communication or a multimodal communication system in which each sensory signal communicate different information in the antwrens taxa with high sexual dimorphism, while the antwrens with low sexual dimorphism may have evolved other ways to recognize each other that were not assessed in this study (e.g. calls, duets, stereotyped body motion displays).

All these described relationships (either the trade-offs between some plumage and vocal traits or the positive correlation between sexual dimorphism in plumage and song traits) are influenced by at least one ecological trait (i.e. habitat exposure or foraging strata) or with mixed-species flocking behavior as covariates, corroborating the SDH and mixed-species flocking behavior influence on visual and acoustic signals structure. Although we have not been able to determine more precisely how these covariates limits these plumage and song traits, they seem to have an important role in shaping the acoustic and visual signals structure evolution.

The present study had an important role in comprehending how the plumage and song evolved in the tribe Formicivorini and which traits are influencing the observed pattern. Also, it shed light on the poorly studied TH that have mixed evidences in the literature, it accounted for the habitat effects on both acoustic and visual signals and a possible influence of foraging behavior. We suggest that further studies investigating the TH should consider habitats effects and other possible important behavioral traits as covariates in their study models. Also, a family level study with all antbirds incorporating other possible important habitat and behavior traits is recommended to access if the observed patterns are maintained in a larger scale.

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