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Environmental correlates for the evolution of the leapfrog plumage pattern in Andean birds

Luis A. Sánchez-González[1], David A. Prieto-Torres[2], Ignacio Méndez[3]†, and Adolfo G. Navarro-Sigüenza[1]

[1]Museo de Zoología 'Alfonso L. Herrera', Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México D.F., México, [2]Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México, and [3] Instituto de Investigaciones en Matemáticas Aplicadas y en Sistemas (IIMAS), Universidad Nacional Autónoma de México, México D.F., México

Running heads
Left = Sánchez-González *et al*.
Right = Leapfrog plumage pattern evolution

Correspondence: L.A. Sánchez-González, Museo de Zoología 'Alfonso L. Herrera', Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apdo. Postal 70-399, México D.F., 04510, México. email: lasg@ciencias.unam.mx
† Deceased.

[H1] **ABSTRACT**

Definition of the leapfrog pattern: Two populations of a species, whose individuals are very similar in appearance, are geographically separated from each other by intervening populations of the same species whose individuals are very different from them in appearance (Remsen, 1984).

Background: Three distantly related Andean passerines (*Thlypopsis superciliaris*, *Myiothlypis coronata*, and some species in the genus *Atlapetes*) exhibit the leapfrog pattern in their plumage. Biotic and abiotic explanations have previously been discarded for these bird taxa.

Question: Are there environmental correlates that suggest causes for the evolution of the leapfrog plumage pattern in these birds?

Data description: We studied the leapfrog pattern in the plumage colours of the underparts (yellow and grey). We developed distribution models for the species and extracted raw environmental values for annual precipitation, annual temperature, and elevation for each.

Search method: We used discriminant analysis to estimate the probabilities of different plumage colours relative to the three selected environmental variables. In addition, we used a generalized linear model (GLM) via a multiple logistic regression fitted with a maximum likelihood approach. To better visualize the behaviour of our data in our GLM analyses, we used profiler plots to explore cross-sections of our response variables according to the two plumage colours in our selected taxa.

Conclusions: The plumage colours of the underparts are significantly correlated with the selected environment variables, suggesting that the leapfrog pattern may be influenced by specific combinations of temperature, precipitation, and/or elevation that occur in different Andean regions. Given that these environmental combinations may appear in isolated regions, convergent evolution may explain the presence of the leapfrog plumage pattern. Convergent evolution coupled with dispersal and/or secondary contact might lead to a better understanding of the evolution of leapfrog plumage patterns in distantly related Andean passerines.

Keywords: Andes, Bogert's rule, convergent evolution, ecogeographical rules, Gloger´s rule, passerines, plumage colours.

[H1] **INTRODUCTION**

Studies of plumage colour patterns in birds and processes influencing their evolution have mainly addressed topics such as interspecific and intraspecific communication, sexual selection, and physical properties of habitats (Marchetti, 1993; Price and Pavelka, 1996; Gomez and Théry, 2004; Price, 2006, Cuthill *et al*., 2017). Intra- and interspecific communication have been suggested to be an important factor in the evolution of plumage patterns, likely due to their role as a pre-mating barrier (reviewed in Price, 2008). Other factors include abiotic conditions, such as light intensity, humidity, and temperature; however, any specific evolutionary pressures in these factors remain elusive (Romano *et al*., 2018; Delhey *et al*., 2019). In addition, evolution of plumage is also mediated by the pleiotropic effects of genes controlling plumage coloration (Endler, 1993; Marchetti, 1993; Gomez and Théry, 2004; Cadena *et al*., 2011; Roulin and Ducrest 2011). In general, because plumage patterns are involved in species signalling, as well as other behavioural functions, evolution may result from antagonistic forces such as species recognition (facilitating communication) and crypsis (facilitating predator avoidance) (Gomez and Théry, 2004; Hill and McGraw, 2006; Bond, 2007; Cuthill *et al*., 2017).

[H2] **Characterization of patterns of colour variation in endotherms and their coincidence**

Characterization of patterns of colour variation in endotherms and their coincidence among distantly related taxa distributed in regions with similar climatic conditions, led to the development of Gloger's ecogeographic rule (Gloger, 1833; Zink and Remsen, 1986; Delhey, 2019; Delhey *et al*., 2019), which highlights the correlation between more humid and warm areas with saturated plumage colours. For ectotherms, Bogert's rule (also known as the thermal melanism hypothesis) postulates a saturation in colour running in the opposite direction (colours are darker in colder climates, due to advantages associated with the absorption of solar radiation (Bogert, 1949; Trullas *et al*., 2007). Although proposed for animal groups with different physiologies, recent studies have proposed that these two ecogeographical rules may be applied to animals in general (Delhey, 2019; Delhey *et al*.,2019; Romano *et al*., 2019). Other patterns of plumage differentiation, also probably related to climatic factors but with apparently random geographic distributions, are the 'checkerboard' (Diamond, 1973; Dumbacher and Fleischer, 2001) and 'leapfrog' patterns (Remsen, 1984). In the checkerboard pattern, closely

related taxa with similar plumage patterns are distributed apparently at random throughout suitable and continuous habitat (Dumbacher and Fleischer, 2001). The leapfrog pattern occurs when distinctive plumage types alternate along a linear string of populations within a single species (Remsen, 1984).

Leapfrog patterns were first documented in several Andean bird taxa with at least three described subspecies. Leapfrog patterns may be expressed either in simple traits (e.g. markings such as wing bars, crown stripes, or eyebrows), or in major suites of traits (i.e. whole plumage patterns). Long-distance dispersal or migratory processes were rejected as explanations for the evolution of the leapfrog pattern, as most species exhibiting it are highly sedentary (Remsen, 1984). Additional hypotheses, such as convergent or divergent evolution, centrifugal speciation, and inter-Andean corridors, were also discarded because geographic distributions of distinctive populations (those in between populations with similar plumage patterns) are scattered throughout the Andes, and do not show geographic coincidence with other populations manifesting a leapfrog pattern, so they appear randomly regardless of the geography or diversity of environments (see Figure 1 in Remsen, 1984), thus minimizing any possible role of environmental variables.

Some researchers have proposed a causal association between environmental factors and plumage in different geographic settings and bird taxa. Studies of owls in Europe and North America (Galeotti and Cesaris, 1996; Roulin and Randin, 2015) suggest they follow Gloger's rule, while other studies with passerines in Australia (Delhey, 2018) and barn owls worldwide (Romano *et al*., 2018) have found support for both Gloger's and Bogert's rule. These studies suggest that climatic factors may play a more important role in the evolution of plumage colour patterns than previously thought.

Based on evidence from other geographic settings, as well as the fact that similar or equal combinations of environmental variables may occur in isolated areas (Colwell and Rangel, 2009), we hypothesize that: (a) the leapfrog pattern in plumage is the result of convergent evolution, and secondary contact; and (b) Bogert's rule may apply at least in these taxa for which altitudinal replacements have been reported (as in *Atlapetes*). Here, using environmental data obtained from distributions generated by niche-based distribution models (Peterson *et al*., 2011), we searched for correlations between environmental features and the leapfrog variation pattern in the plumage of Andean passerine bird species from three genera (*Atlapetes*, *Thlypopsis*, and *Myiothlypis*). We discuss the role of environmental

features and suggest a biogeographic scenario for the origin and maintenance of the pattern in Andean forests of low to medium elevation.

[H1] MATERIALS AND METHODS

[H2] Taxon and trait selection

We based our analyses on Remsen's (1984) division of the leapfrog pattern into two different categories: (a) isolated colour patches (e.g. the presence of a white spot on the wing; hereafter, 'plumage markings'), or (b) a large proportion of the plumage (e.g. the underparts and/or upperparts; hereafter, 'plumage colour'). As plumage markings may have evolved for intra- and interspecific communication (Price, 2008), and are probably subject to different selection pressures that are not necessarily environmentally mediated, we included only taxa satisfying criterion (b), plumage colour. We selected three Andean passerine taxa [southwest Venezuela to central Bolivia (see Fjeldså and Krabbe, 1990)] that are largely restricted to the Humid Montane Forests (HMF), as defined elsewhere (Sánchez-González *et al*., 2008), although some (e.g. *Atlapetes* spp.) reach tropical lowlands (Table 1). We selected two widespread species, *Myiothlypis coronata* (Parulidae) and *Thlypopsis superciliaris* (Thraupidae), as well as a group of closely related species in the genus *Atlapetes* (Passeriformes: Passerellidae), including the yellow-plumaged *A. crassus*, *A. latinuchus*, *A. pallidinucha*, *A. terborghi*, *A. tricolor*, and *A. melanoleaemus*; as well as taxa with grey-underparts: *A. canigenis*, *A. leucopterus*, *A. nationi*, *A. rufigenis*, *A. seebohmi*, *A. schistaceus*, and *A. taczanowskii* (Table 1) (Sánchez-González *et al*., 2015).

[INSERT TABLE 1 ABOUT HERE]

The leapfrog pattern in all these sexually monomorphic taxa is characterized by the presence of plumage colours (yellow- and grey-plumaged taxa) that are mostly allopatric – or may show limited parapatry (Remsen, 1984). In *Atlapetes*, the leapfrog pattern also involves altitudinal replacements: yellow-plumaged birds are generally found at medium elevations, whereas grey-plumaged birds generally occupy lower and higher elevations (Remsen and Graves, 1995; Sánchez-González *et al*., 2015). Except for *M. coronata*, altitudinal distributions reveal a pattern in which grey-plumaged birds are generally found at higher elevations than yellow-plumaged birds (Table 1). In *Atlapetes*, yellow-plumaged (lower elevation) and grey-plumaged (higher elevation) taxa may be syntopic over a relatively narrow zone in some

cases; however, at sites where only one of the colours of a taxon is found, it may occupy the entire elevational gradient (Remsen and Graves, 1995).

Phylogenetic hypotheses proposed for *Atlapetes* have shown that yellow- and grey-plumaged taxa may be intermixed within clades (García-Moreno and Fjeldså, 1999; Sánchez-González *et al*., 2015). That discovery serves to reject earlier hypotheses about the monophyly of birds of similarly coloured plumage (Paynter, 1972, 1978). According to plumage reconstruction analyses, the most probable ancestral colour of underparts is yellow, which suggests that grey underparts are derived (Sánchez-González *et al*., 2015). In *T. superciliaris*, with a distribution from Colombia to Bolivia (Fjeldså and Krabbe, 1990), grey-plumaged populations inhabit Peruvian HMF (Fig. 1A), in between citrine-plumaged (hereafter, 'yellow-plumaged' for clarity) populations ranging both north and south (Remsen, 1984; Fjeldså and Krabbe, 1990). For *T. superciliaris*, the most recent phylogenetic hypothesis available (Burns *et al*., 2014) recovered a low-supported clade of mostly yellow- to orange-plumaged birds, suggesting again that the grey plumage may be evolutionarily derived. For *M. coronata*, yellow-plumaged birds are distributed throughout the Andes, except from eastern Ecuador to northwest Peru, where they are replaced by grey-plumaged birds (Fig. 1B). Recent phylogenetic hypotheses (see Lovette *et al*.,2010; Prieto-Torres *et al*., 2018) show that yellow-plumaged and grey-plumaged birds are sister taxa and belong to a clade in which most species have yellow underparts. That would also suggest that grey underparts may be evolutionarily derived.

[INSERT FIGURE 1 ABOUT HERE]

As colours exist on a continuum, comparisons of coloration may be difficult. Nevertheless, coloration forms classes easily recognizable to the human eye (Wang and Shaffer, 2008). Therefore, based on these clear differences, we established our comparisons between an achromatic (grey) and a saturated (yellow) plumage, as these have quite different reflectance values in the human visible spectrum (Burtt, 1986).

[H2] **Species distribution models**

Species distribution ranges are represented using either polygons or occurrence records. However, these approaches suffer from the effects of multi-level conflicts among scales and resolutions because polygons are spatially coarse and so are likely to include areas unsuitable for hosting populations or exclude other areas where populations do occur (see Peterson *et al*., 2018). In contrast, data-driven techniques such as species distribution modelling integrate

primary data on species occurrence with interpolated data from climate-station records that summarize environmental dimensions. In short, species distribution models (SDMs) allow for a more accurate delimitation of species ranges (see Mota-Vargas and Rojas-Soto, 2012).

For each species, we modelled climatic suitability areas for distribution using MaxEnt 3.4.1k (Phillips *et al*., 2006). This algorithm uses the maximum entropy principle to calculate the most likely distribution of focal species as a function of locality of occurrence and environmental variables given a sample of the background. This method follows from the idea that expected values for each feature (i.e. climatic variables) must be equal to the empirical average values of presence points of the species (Phillips *et al*., 2009; Elith *et al*., 2011; Merow *et al*., 2014). We know that MaxEnt performs better compared with other available methods when only presence data is available (Elith *et al*., 2006, 2011; Soberón and Nakamura, 2009). So, we used this approach to obtain our SDM. Further details on program procedures can be found elsewhere (e.g. Elith *et al*., 2006, 2011).

We obtained locality data from specimens in scientific collections available online (GBIF: https://www.gbif.org; also http://ornisnet.org; access numbers downloaded for each species record are given in evolutionary-ecology.com/data/3226Appendix.pdf), as well as from scientific publications (e.g. Remsen and Graves, 1995; Prieto-Torres *et al*., 2018). For each species, textual locality data were geographically referenced using published ornithological gazetteers (Paynter 1981, 1982, 1992, 1993, 1995; Stephens and Traylor, 1983), and online gazetteers (e.g. http://www.geonames.org; http://testbed.alexandria.ucsb.edu/gazclient/index.jsp). To reduce sampling bias and spatial autocorrelation on model performance (Boria *et al*., 2014), we removed records repeated in multiple sources, retaining only information for unique localities within a vicinity of ~3 km^2. Using the Birds of the World's website (birdsoftheworld.org/bow/home), we compared the spatial distribution of records with the geographic ranges of each species. (We removed all mismatched records.) Because low sample size in occurrence records may affect model performance (Peterson *et al*., 2011), we restricted our analyses to those taxa with ≥ 5 unique locality data points (i.e. single combinations of latitude-longitude). All geographic coordinates were transformed to decimal degrees, based on the WGS84 datum.

We used the 19 climatic variables in WorldClim 2.1 (Fick and Hijmans, 2017) and the Digital Elevation Model (DEM) from the Hydro 1K project (USGS, 2001) with a resolution of 30″ (~1 km^2 cell size). Even though topographic variables are not commonly used in SDM studies, we did include them because it has been shown (e.g. Mota-Vargas *et al*., 2013; Rheingantz *et*

al., 2014; Prieto-Torres and Pinilla-Buitrago, 2017) that they can be used as proxies for variables (e.g. micro-climate or edaphic conditions) correlated with species' physiological requirements. In addition, recent work on plumage and environmental variables have shown that elevation may play a significant role, especially in birds (Delhey, 2019; Delhey *et al*., 2019). We reduced collinearity (see Peterson *et al*., 2011) for each species by adopting two approaches that allowed us to select a subset of the original 20 variables to include in the modelling procedures. For the first approach, we selected variables using a Pearson's correlation coefficient ($r < 0.8$) and variance inflation factor (VIF) < 10, as implemented in the *corrplot* (Wei and Simko, 2017) and *usdm* (Naimi, 2015) R libraries. For the second approach, we derived a subset of six variables from the original set of 20 using a principal component analysis (PCA) (Dupin *et al*., 2011; Hanspach *et al*., 2011) to obtain different combinations of the environmental variables. We selected the better approach based on the statistics estimated in the *kuenm* R package (Cobos *et al*., 2019a, 2019b).

To generate species models, we created a model calibration area (M) based on the BAM diagram reflecting both the accessible historical areas and the restriction regions (e.g. dispersal barriers) for each species (see Soberón and Peterson, 2005; Barve *et al*., 2011). These individual calibration areas were defined based on the intersection of occurrence data with the WWF Terrestrial Ecoregions (Olson *et al*., 2001) and the biogeographic provinces of the Neotropics (Morrone, 2014). We assumed that these regions represent historical and ecological barriers to dispersal (e.g. rivers and valleys) for current populations of each species.

We developed models for species with 5–14 records ($n = 3$) using all presence data and default MaxEnt settings. We assessed these models with a jackknife test (Pearson *et al*., 2007) following instructions in the package tutorial, available at GitHub (https://github.com/jmbarrios/jackKnifeTest). Then, for species with >15 records, models were generated using the *kuenm* R package (Cobos *et al.*, 2019a), again available at GiHub (https://github.com/marlonecobos/kuenm), which performs a calibration protocol to assess model complexity (Merow *et al*., 2014). To do this, we ran models using 80% of the training records for model calibration and the other 20% for internal evaluation using the two selected sets of environmental variables (see above), 14 model response types (feature classes: L, Q, P, T, LQ, LP, LT, QP, QT, PT, LQP, LPT, QPT, LQPT), and 18 regularization multiplier values (RM = 0.5–8.0). For this latter step, we performed 500 iterations with 10 replicates. Then we chose the best models using the omission errors (Anderson *et al*., 2003), the partial

ROC test (Peterson *et al*., 2008), and the Akaike information criterion (AICc) (Merow *et al*., 2014; Muscarella *et al*., 2014) based on the original 20% of occurrence records selected for independent evaluation.

To generate the final distribution model for each species, we first calculated median values across replicates as a means of summarizing model predictions (Campbell *et al*., 2015). Then, to aid model validation and interpretation, we converted the continuous values of suitability from each model into a presence-absence map by setting a decision threshold equal to the 10% omission of the training occurrence data (i.e. a 10% false-negative rate). This approach allowed us to minimize the commission (overprediction) errors in the binary maps, thereby representing the realized niche (Soberón and Peterson, 2005) and a better recovery of species distributional areas (Escalante *et al*., 2013; Liu *et al*., 2013). Some of our selected species, however, present disjunct distributions even in well-surveyed areas with suitable habitats, likely representing true absences (Fjeldså and Krabbe, 1990; Stotz *et al*., 1996). Thus, to obtain the 'best hypothesis map' for each species for subsequent analysis, we applied the areographic method (see Rapoport, 1982; Mota-Vargas and Rojas-Soto, 2012), discarding those areas with high commission errors. For each species, we defined the average distance between the closest locality records as the radius of a circle drawn around each location point (Rapoport, 1982). These circles were used to clip and define the final distribution map for each species.

[H2] **Defining the average environmental conditions (ecological space) for each species**

From each final distribution map, we extracted average values of three environmental variables to represent the ecological space for each species across its geographic range. We used two bioclimatic variables (annual precipitation [Bio 12] and annual mean temperature [Bio 01]) because these have been defined as highly significant for HMF development (e.g. Ponce-Reyes *et al*., 2012; Rojas-Soto *et al*., 2012). Some authors have suggested an important role for elevation in the evolution and diversification of HMF avifaunas (Paynter, 1972, 1978; Terborgh, 1977; Remsen and Graves, 1995), and different species may show sharp elevational replacements (Paynter, 1972, 1978; Fjeldså and Krabbe, 1990; Remsen and Graves, 1995). So we also obtained elevation data (with a resolution of 250 m; available at srtm.csi.cgiar.org/) at the predicted presence cells for all species. We ran all procedures on ArcMap 10.2.2 (ESRI, 2010).

[H2] **Statistical analyses**

To estimate the probabilities of the presence of different plumage colours relative to the three selected environmental variables, we used a discriminant function analysis (DFA), which is a parametric technique that determines which quantitative variables best discriminate among two or more groups (Karr and James, 1975).

In addition, we analysed plumage colour patterns in relationship to elevation, annual precipitation, and annual temperature using a generalized linear model (GLM) via a multiple logistic regression (Lindenmayer *et al*., 1991; Nadeau *et al*., 1995; Manel *et al*., 1999; Franco *et al*., 2000; Luck, 2002). We fit the models using the maximum likelihood approach (McCullagh and Nelder, 1989; Cramer, 2003). Finally, to better visualize the behaviour of our data in the GLM analysis, we used profiler plots to explore cross-sections of each response variable as a function of the two plumage colours in our selected taxa.

[H1] **RESULTS**

The performance values of the two modelling approaches indicated that our species' distribution models were statistically better than random. Models developed for species with ≥ 15 occurrence records showed highly significant AUC ratios from the partial ROC test (ranging from 1.50 to 1.99; $P < 0.05$) and low omission errors (mean of 8.5 ± 4.2%, i.e. 4.4 ± 5.2 occurrence points), while the jackknife test showed statistically significant model inter-prediction ($P < 0.01$). Parameter settings (feature classes and regularization multiplier values) and performance values for each model are detailed in the Appendix. Final species models showed spatial distributional ranges from 1743 km^2 (*Atlapetes rufigenis*) to 162,183 km^2 (*A. latinuchus*). Final pixel numbers per taxon were: 180,972 for *T. superciliaris*, 595,078 for all *Atlapetes* species, and 249,883 for *M. coronata*.

Discriminant analyses showed the percentages of misclassified data points (and associated plumage colours) according to the three different environmental variables used (Appendix). *Atlapetes* had the highest percentage of misclassified points (44.65 %); *M. coronate* (29.47%) and *T. superciliaris* (28.05%) had similar percentages.

[INSERT TABLE 2 ABOUT HERE]

Results of the logistic regression models (Table 2) showed that the whole-model test for each taxon revealed significant values ($P < 0.0001$). However, the R^2 values were generally low, indicating that other factors not assessed are involved in plumage variation in

the studied species (see below). Thus, for *Atlapetes* spp., environmental variables explained only 7% of the variation in plumage; while for *T. superciliaris* and *M. coronata*, environmental variables explained 39% and 26%, respectively.

[INSERT FIGURE 2 ABOUT HERE]

We adjusted the prediction profilers (Fig. 2) for each taxon to equal probabilities (0.5 for each plumage colour). Plots for both *M. coronata* and *T. superciliaris* show that the probability of ecological conditions favouring grey plumage is low (up to 0.34 and 0.48, respectively), so such plumage is likely to be geographically restricted. For these two taxa, a grey plumage is more probable at medium elevations (between 1700 m and 2700 m) and medium temperatures (between 10°C and 18°C). Annual precipitation, however, showed a completely different picture: for *M. coronata*, a grey plumage is more probable at low and high rainfall (up to 1500 mm and more than 2500 mm respectively), while for *T. superciliaris*, a grey plumage is more probable between ~600 mm and 1600 mm. Finally, grey plumage in *Atlapetes* spp. seems to be due to an interaction of lower elevation (up to ~2000 m), lower temperatures (up to ~8°C), and both low and high precipitation regimes (between 0 mm and 1300 mm, and higher than 3600 mm); yellow plumage is likely at higher elevations (above 2000 m), higher temperatures (above 13.5°C), and medium precipitation values (between 1300 mm and 3600 mm).

[H1] DISCUSSION

Although previous explanations for the leapfrog pattern rejected the role of environmental variables (Remsen, 1984), our results suggest the presence of grey plumage and yellow plumage in the taxa studied here is likely related to environmental factors. In addition, these environmental factors appear to be congruent with two ecogeographic rules: Bogert's rule and Gloger's rule. In line with Bogert's rule, low to medium annual temperatures and elevations favoured grey plumage, possibly because of the thermoregulatory advantages of various pigmentations (Walsberg *et al*., 1978; Walsberg, 1983; Ward *et al*., 2002; Delhey *et al*., 2018; Romano *et al*., 2018). The three taxa, however, showed differing patterns in annual precipitation. In *M. coronata* and *Atlapetes* spp., medium rainfall values were associated with yellow plumage. In contrast, in *T. superciliaris* – and in line with Gloger's rule – lower rainfall values were associated with grey plumage.

These associations suggest that environmental factors may promote phenotypic changes, increasing the ability of organisms either to match the colour of the environment, or to optimize their performance in high-elevation habitats (Descimon, 1986). In addition, dark plumage better resists feather abrasion (Bonser, 1995) and bacterial degradation (Burtt and Ichida, 2004; Goldstein *et al*., 2004) in humid environments. Thus, we believe our results support the two ecogeographic rules in understanding the evolution of plumage along both latitudinal and altitudinal distributions of the taxa we studied.

Several factors appear to be involved in the evolution of the leapfrog plumage pattern in the Andes. Yes, precipitation and temperature may leave recognizable signatures on the plumage pattern that may be categorized as Gloger's or Bogert's ecogeographic rule, respectively (Delhey *et al*., 2018; Romano *et al*., 2018), but that does not rule out the involvement of other factors. For example, geographic context may play an important role. The species studied here live mostly in Andean cordilleras that run mainly in a north–south direction facing the cold Humboldt current along the Pacific coast. Thus, the western slopes display environmental conditions that are different from those on the much more humid eastern slopes (Chapman *et al*., 1926; Koepcke, 1961). Although there is also a region (from the southwest of Ecuador to the northwest of Peru; Fig. 1) in which both yellow *Thlypopsis* and grey *Myiothlypis* populations appear to be sympatric, the altitudinal distributions of these two taxa show the overlap to be rather narrow (Table 1), which suggests a significant role for precipitation in the evolution of these plumage colours (Fig. 2). As regards environmental conditions, these may be similar in geographically isolated regions [known as the Duality of Hutchinson (Hutchinson, 1975; Colwell and Rangel, 2009)], and apparently more geographically restricted (see Fick and Hijmans, 2017), at least for the species in our study.

A leapfrog pattern of plumage variation may respond also to historical and biotic factors. Clear biogeographic boundaries delimit the distribution of the montane avifauna across the Neotropical HMF (Krabbe, 2008; Sánchez-González *et al*., 2008); these barriers may have prevented dispersal across different regions and species. In addition to limited dispersal, ecological distribution in the absence of potential competitor species may play a role. In *Atlapetes* spp., the elevation-related distributions of yellow- and grey-plumaged species have been attributed to competitive exclusion (Paynter, 1978; Remsen, 1984; Remsen and Graves, 1995; but see Cadena and Loiselle, 2007), which may have occurred after secondary contact. In these cases, yellow-plumaged species are found in between grey-plumaged species. However, in the

absence of one of these phenotypes, the other may occupy the entire altitudinal gradient (Remsen and Graves, 1995).

Andean montane forests have experienced a long history of expansion, contraction, and elevational shifts in response to Pleistocene global climate changes (Wijninga, 1995; Jansson and Dynesius, 2002). Such shifts may have promoted the evolution of the leapfrog plumage pattern in underpart colours. In drier periods, HMF may have persisted in isolated, ecologically stable patches at different elevations (Fjeldså, 1995); in these, lineages may have persisted, leading to isolation and probably differentiation (Jansson and Dynesius, 2002). According to our analyses, a grey plumage is more probable at lower elevations, lower temperatures, and both low and high precipitation, while a yellow plumage is found mainly at medium to high elevations. Recent phylogenetic hypotheses have suggested strong diversification in both *Atlapetes* spp. (Sánchez-González *et al*., 2015) and *M. coronata* (Prieto-Torres *et al*., 2018) during the Pleistocene. Strong diversification would have supported differentiation in allopatric, environmentally stable areas, which would in turn have reinforced secondary contact and dispersal through ecologically suitable areas as the processes causing parapatric distributions in these taxa.

Secondary contact and dispersal of *Atlapetes* spp. may have shaped their actual distributions (Paynter, 1972, 1978; Remsen and Graves, 1995), given that some grey plumaged birds occupy the entire elevational gradient in the absence of yellow-plumaged birds (as does A. *canigenis* in southern Peru). The reverse also occurs: yellow-plumaged birds are found at higher elevations along the Andes where grey-plumaged forms are absent (Remsen and Graves, 1995). Prieto-Torres *et al*. (2018) invoke secondary contact as a likely explanation for parapatry in *M. coronata*.

The biogeographic dynamics of Andean forests may account for the effects of environmental variables in the recurrent evolution of these two plumage colours in these three Andean passerines. Natural selection acts on pigmentation, suggesting that evolution of plumage colours may be a response to changing environments (Endler, 1982; Galeotti *et al*., 2003). In addition, the geographic setting may allow for the development of similar environments in isolated regions (Colwell and Rangel, 2009), which initially may be the result of local adaptation (see Huey *et al*., 2000; Núñez-Zapata *et al*., 2018). Historical isolation due to the elevation required for the development of HMF (Brown and Kappelle, 2001), and the limited dispersal of isolates may promote and maintain variation in the leapfrog plumage. Thus, evolution of variation in the leapfrog plumage pattern does not require sympatry (Remsen, 1984). And its maintenance,

selection, and further fixation may evolve in allopatry [latitudinal or altitudinal (see Huey *et al*., 2000; Romano *et al*., 2018)].

Several factors are involved in evolution of the leapfrog pattern of plumage variation. Prominent among these is the development of suites of similar environmental variables in different isolated areas (Colwell and Rangel, 2009) – that is what our results suggest. However, the geographical setting, as well as historical and biotic factors, are also significant. It is likely the evolution of this plumage pattern requires the coming together of many environmental factors and that is why it is rarely reported (or recognized) outside Andean South America, although it does occur in New Guinea and Australia (Norman *et al*., 2002). Given that a number of factors are required to act in concert, the leapfrog pattern of plumage variation is likely the result of convergent evolution.

[H1] **AUTHORS' ORCID INFORMATION**

Luis A. Sánchez-González: https://orcid.org/0000-0002-8932-1657
David A. Prieto-Torres: https://orcid.org/0000-0002-0493-5941
Adolfo G. Navarro-Sigu¨enza: https://orcid.org/0000-0003-2652-7719

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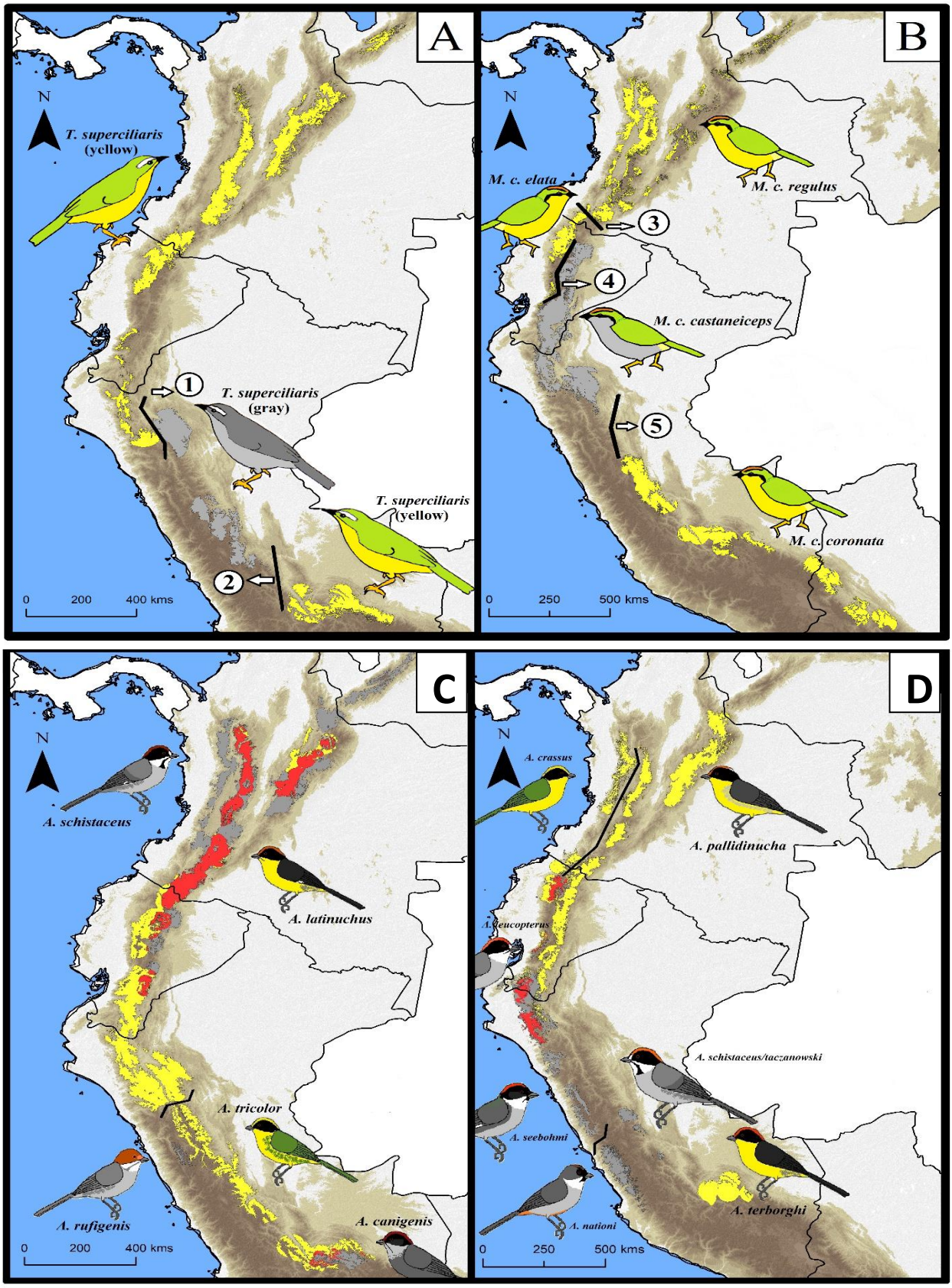
A
N
T. superciliaris (yellow)
1
T. superciliaris (gray)
T. superciliaris (yellow)
2
0 200 400 kms
B
N
M. c. elata
M. c. regulus
3
4
M. c. castaneiceps
5
M. c. coronata
0 250 500 kms
C
N
A. schistaceus
A. latinuchus
A. tricolor
A. rufigenis
A. canigenis
0 200 400 kms
D
N
A. crassus
A. pallidinucha
A. leucopterus
A. schistaceus/taczanowski
A. seebohmi
A. nationi
A. terborghi
0 250 500 kms

Fig. 1.

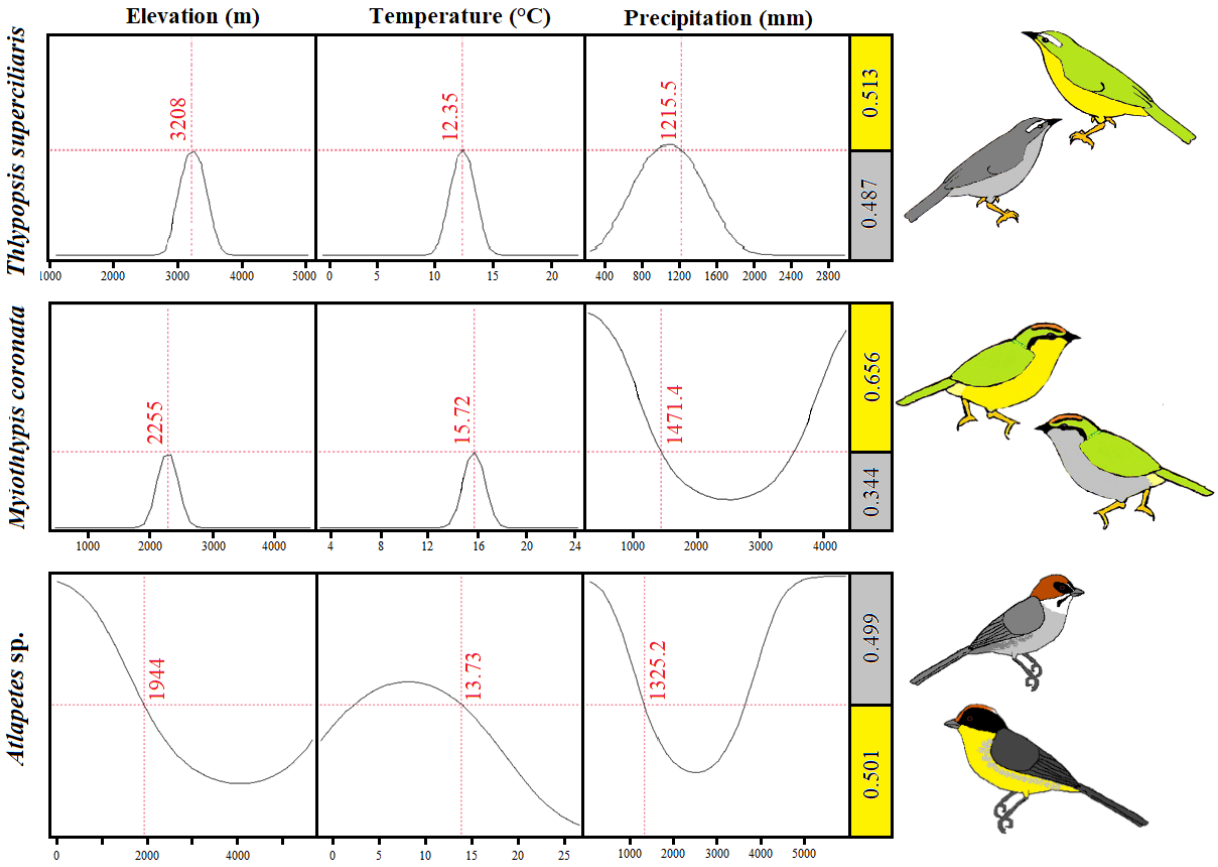
Elevation (m)
Temperature (°C)
Precipitation (mm)
Thlypopsis superciliaris
3208
12.35
1215.5
0.513
0.487
1000 2000 3000 4000 5000
0 5 10 15 20
400 800 1200 1600 2000 2400 2800
Myiothlypis coronata
2255
15.72
1471.4
0.656
0.344
1000 2000 3000 4000
4 8 12 16 20 24
1000 2000 3000 4000
Atlapetes sp.
1944
13.73
1325.2
0.499
0.501
0 2000 4000
0 5 10 15 20 25
1000 2000 3000 4000 5000

Fig. 2.

Fig. 1. Distribution of *Thlypopsis superciliaris* (A) and *Myiothlypis coronata* (B) showing the leapfrog pattern (yellow vs. grey plumage) along the Andes. Species of *Atlapetes* are shown in two panels (C and D), as there is no clear separation of colour by latitude, though there is in elevation. Red areas correspond to putative contact areas for different colour plumages. See text and Table 1 for details. Numbers 1–5 in panels (A) and (B) correspond to putative geographic barriers for the different studied species: (1) North Peruvian Low (NPL) and Huancabamba river valley, (2) Apurímac and Urubamba river valleys, (3) Patía and Caquetá river valleys, (4) Inter-Andean valleys in Ecuador, and (5) Huallaga river valley. Black lines in panels (C) and (D) correspond to barriers among *Atlapetes* species.

Fig. 2. Adjusted prediction profiles for each studied taxon based on equal probabilities for each plumage colour (0.5 for each plumage colour).

Table 1. Altitudinal range (metres above sea level) of the study taxa

Taxon	Elevational range
Thlypopsis	Grey-plumaged: 2200–3450 m
superciliaris	Yellow-plumaged: 1900–3350 m, mostly above 2100 m (all areas), locally to 3700 m (Ecuador), 2200–2900 m (west Andean slope in Peru)
Myiothlypis	Grey-plumaged: 1300–2500 m
coronata	Yellow-plumaged: 1300–2500 m, occasionally to 3100 m (Peru)
Atlapetes spp.	Grey-plumaged *A. rufigenis*: 2700–4600 m
	Grey-plumaged *A. schistaceus*: 2450–3700 m
	Grey-plumaged *A. taczanowskii*: 2500–3800 m
	Grey-plumaged *A. leucopterus*: 400–2000 m
	Grey-plumaged *A. canigenis*:2500–3500 m
	Grey-plumaged *A. seebohmi*: 1150–2800 m
	Grey-plumaged *A. nationi*: 2100–4000 m
	Yellow-plumaged *A. pallidinucha*: 2800–3600 m
	Yellow-plumaged *A. crassus*: 300–2000 m
	Yellow-plumaged *A. tricolor*: 1750–3050 m
	Yellow-plumaged *A. latinuchus*: 1600–2700 m
	Yellow-plumaged *A. terborghi*: 2500–3500 m

Table 2. Nominal logistic regression for the three Andean bird taxa analysed in this study

Thlypopsis superciliaris				
Model	Log-like	*df*	χ^2	Prob > χ^2
Difference	38659.325	9	77318.65	0.0001
R^2 (U)		**0.3927**		
Observations (or sum of weights)		**180972**		
Term	Estimate	SE	χ^2	Prob > χ^2
Intercept	–47.441877	0.4059733	13656	0.0001
Elevation	0.00911968	7.5187×10^{-5}	14712	0.0001
Temperature	1.69214749	0.0137443	15158	0.0001
Precipitation	–0.0014109	5.0121×10^{-5}	729.41	<0.0001
Myiothlypis coronata				
Model	Log-like	*df*	χ^2	Prob > χ^2
Difference	41264.71	9	82529.43	0.0001
R^2 (U)		**0.2632**		
Observations (or sum of weights)		**249883**		
Term	Estimate	SE	χ^2	Prob > χ^2
Intercept	23.2994564	0.2468197	8911.1	0.0001
Elevation	–0.00390201	0.0000461	7229.3	0.0001
Temperature	–0.7081781	0.0082563	7357.2	0.0001
Precipitation	–0.0025954	0.0000153	28747	0.0001
***Atlapetes* spp.**				
Model	Log-like	*df*	χ^2	Prob > χ^2
Difference	29084.7	9	58169.41	0.0001
R^2 (U)		**0.0731**		
Observations (or sum of weights)		**595078**		
Term	Estimate	SE	χ^2	Prob > χ^2
Intercept	4.05540017	0.0850976	2271.1	0.0001
Elevation	–0.0009075	0.0000164	3039.2	0.0001
Temperature	–0.1618165	0.0029137	3084.4	0.0001
Precipitation	–0.000163	0.0000063	649.75	<0.0001