



Frontispiece: New tanager described in this issue by Lane et al. Male above, female below. Watercolor by Daniel F. Lane.

RESEARCH ARTICLE

A new genus and species of tanager (Passeriformes, Thraupidae) from the lower Yungas of western Bolivia and southern PeruDaniel F. Lane,^{1,*} Miguel Angel Aponte Justiniano,² Ryan S. Terrill,^{1,a} Frank E. Rheindt,^{3,b} Luke B. Klicka,^{4,c} Gary H. Rosenberg,⁵ C. Jonathan Schmitt,^{6,d} and Kevin J. Burns⁴¹ LSU Museum of Natural Sciences, Baton Rouge, Louisiana, USA² Museo de Historia Natural de Noel Kempff Mercado, Santa Cruz, Bolivia³ Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA⁴ Department of Biology, San Diego State University, San Diego, California, USA⁵ Avian Journeys, Tucson, Arizona, USA⁶ Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA^a Current address: Moore Laboratory of Zoology, Occidental College, Los Angeles, California, USA^b Current address: Department of Biological Sciences, National University of Singapore, Singapore^c Current address: School of Arts & Sciences, Peru State College, Peru, Nebraska, USA^d Current address: Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA*Corresponding author: dlane@lsu.edu

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ABSTRACT

We describe a colorful and distinctive new species of tanager from the lower slopes of the Andes of southeastern Peru and western Bolivia. The species was first noted from southeastern Peru in 2000, but little of its natural history was uncovered until the 2011 discovery of a breeding population in deciduous forest in an intermontane valley, the Machariapo valley, in Bolivia. This species appears to be an intratropical migrant, breeding in deciduous forest during the rainy season (November–March) and spending the dry season dispersed along the lower slopes of the Andes, apparently favoring *Guadua* bamboo-dominated habitats in both seasons. Phylogenetic evidence suggests this tanager is embedded within a clade of thraupids that includes *Ramphocelus*, *Coryphospingus*, *Loriotus*, *Tachyphonus*, and related genera in the subfamily Tachyphoninae. Within this subfamily, the new species falls in a clade with two monotypic genera, *Eucometis penicillata* (Gray-headed Tanager) and *Trichothraupis melanops* (Black-goggled Tanager). There is strong support for a sister relationship between the new tanager and *T. melanops*, but because all three species in this clade are highly distinctive phenotypically, we propose erecting a new genus and species name for the new tanager.

Keywords: bamboo specialist, intratropical migrant, Neotropics, oscine passerine, South America

LAY SUMMARY

- We discovered a new species of tanager, from the foothills of the Andes mountains in Peru and Bolivia, which we name the Inti Tanager. The name “Inti” is the Quechua (a language indigenous to the region) word that means “sun,” referring to the bright yellow color of the bird.
- Unlike most new bird species discovered recently, which typically differ only subtly from their closest relatives, this species is so different in appearance and genetics that we also described a new genus just for it.
- The tanager family, to which the new species belongs, is one of the largest bird families in the world (with about 377 species), restricted almost entirely to the American tropics and including many beautifully colorful species.
- We uncovered a surprising piece of natural history about the Inti Tanager: it migrates from its breeding grounds in a little-explored valley in Bolivia to “winter” along the lower slopes of the Andes in Peru. Such migration within the tropics is rare within the tanagers.
- That this unique, bright yellow bird could have gone unnoticed by ornithologists until recently attests to the remoteness of the areas where it lives and to the importance of continued biological surveys off-the-grid in South America.

Un genero y especie de tangara (Passeriformes, Thraupidae) nueva de las Yungas bajas del oeste de Bolivia y el sur del Perú

RESUMEN

Describimos una nueva especie de tangara, colorida y distintiva, de las colinas bajas de los Andes del sureste de Perú y del oeste de Bolivia. La especie fue registrada por primera vez en el sureste peruano en el año 2000, pero poco de su historia natural fue develada hasta el año 2011, cuando se descubrió de una población reproductiva en bosques caducifolios en un valle intermontano (valle del Machariapo) en Bolivia. Parece que esta especie es un migrante intratropical, que se reproduce en bosques caducifolios durante la temporada de lluvias (noviembre-marzo) y pasa la temporada seca, dispersa a lo largo de las colinas bajas de los Andes, aparentemente prefiriendo los hábitats dominados por el bambú *Guadua*, en ambas estaciones. La evidencia filogenética sugiere que esta tangara está dentro de un clado de tráupidos que incluye a *Ramphocelus*, *Coryphospingus*, *Loriotus*, *Tachyphonus* y géneros relacionados en la subfamilia Tachyphoninae. Dentro de esta subfamilia, la nueva especie pertenece a un clado con dos géneros monotípicos, *Eucometis penicillata* y *Trichothraupis melanops*. Existe un fuerte soporte para una relación hermana entre esta nueva tangara y *T. melanops*, pero debido a que las tres especies dentro de este clado son fenotípicamente muy diferentes, proponemos erigir un nuevo género y nombre de especie para la nueva tangara.

Palabras clave: Sudamerica, Neotropicos, paserino oscino, migrante intratropical, especialista en bambú

INTRODUCTION

In 1964, John O'Neill's discovery of *Wetmorethraupis sterrhopteron* (Lowery and O'Neill 1964) grabbed the ornithological community's attention, demonstrating that not only new species, but new genera, of birds remained yet to be discovered in the Neotropics. Since that time, several other new tanagers (Thraupidae) have been discovered in Peru and elsewhere in South America, including the new genus, *Nephelornis* (Lowery and Tallman 1976). Most of these discoveries, post 1964, have been made in previously unexplored isolated mountain ranges along the Amazonian slope of the Andes or lowland interfluvia. However, the discovery of a new genus and species of tanager from one of the ornithologically best-studied sites in Peru, the Kosñipata road that links the city of Cusco to the Río Alto Madre de Dios and borders Manu National Park, upends this pattern spectacularly. This region has been a popular destination for ecotourism for several decades and has also been the target of museum-based faunal surveys (Patterson et al. 1998, Patterson et al. 2006, Walker et al. 2006). Thus, DFL and GHR were entirely unprepared when they first spotted a distinctive passerine, appearing entirely yellow with a black supercilium and pink thraupid-like bill, along the Kosñipata road at ~1,400 m on 10 October 2000, while guiding a bird-watching tour. Our first impression was that it recalled the color pattern of a certain species of *Oriolus*! We obtained little documentation of the bird during this first encounter other than a brief (~9 s) sound recording (by GHR: ML 258172441) and a pencil sketch (by DFL), and were unable to draw the attention of our group to the bird before it disappeared over a ridgetop. Despite subsequent attempts at the same locality, both with and without tour groups, we were unable to relocate the mysterious bird again until 7 October 2003, when, while guiding another tour, DFL and GHR visited the same locality and again heard and saw the bird—this time

directing our clients' attention to it and obtaining better voice recordings (ML 238361). The next observation was 9 June 2004, when, accompanied by Huw Lloyd, Abraham Urbay T., and Barry Walker, DFL finally obtained a specimen (deposited at the Museo de la Universidad Mayor de San Marcos or MUSM), and additional sound recordings (ML 238417), of the unknown thraupid at the same site. Limited information on the species' natural history and (particularly) a lack of material with which to ascertain phylogenetic relationships prevented immediate action after this specimen was collected.

On 10 December 2011, FER discovered a breeding population of the new tanager in semi-deciduous forest to the northwest of a large patch of semi-natural savanna near the town of Apolo, La Paz department, Bolivia. FER first observed the species after playing back an unknown vocalization he heard commonly in the hills at this site. Upon seeing it, he immediately recognized it as the new tanager from Kosñipata, reporting the discovery to DFL shortly thereafter. Between 22 and 27 December 2012, DFL, FER, CJS, RST, and Herman Lijerón returned to this area, making recordings, natural history observations, and collecting a series of specimens. RST, MAAJ, Glenn Seeholzer, and Herman Lieron returned to this site again on 11–18 December 2013, obtaining more natural history observations. DFL, MAAJ, Miguel Angel Montenegro, and Herman Lijerón returned again to this site between 23–29 January 2019 to obtain yet more natural history information, and another small series of specimens.

Our initial impressions of this bird suggested that it might be a tanager (Thraupidae); however, that family has undergone major taxonomic upheaval in recent decades, absorbing many species previously placed in Emberizidae, Parulidae, and Cardinalidae, and shedding former members into Fringillidae, Cardinalidae, or altogether new families (e.g. Burns 1997, Burns et al. 2014, Burns et al. 2016)! In light of these taxonomic revelations, “tanagers” are no longer

easily identified by morphological characters that we now recognize as cases of convergence with other groups of nine-primaried oscine passerines. As a result of this morphological ambiguity, we relied on DNA sequences to place this species into the avian tree of life, assigning it to a family and recovering its phylogenetic relationships. The results of our phylogenetic investigation provided us with the necessary justification to erect a new genus within the larger phylogenetic framework of thraupids for this distinctive new taxon.

METHODS

Phylogenetics: Taxon- and Character-Sampling

This study fit into a larger phylogenetic project in KJB's lab involving all of Thraupidae and related nine-primaried passerines (e.g., Burns et al. 2014). Comparisons of DNA sequences from that project with DNA sequences of the new species indicate that it is indeed a tanager. Tanagers are a large radiation well known for their diverse bill morphologies, colors, behaviors, vocal abilities, and ecologies (Isler and Isler 1987, Hilty 2011, Mason and Burns 2015, Title and Burns 2015, Shultz and Burns 2017, Demery et al. 2021, Vinciguerra and Burns 2021). Taxonomic ideas about what species belong to the family have changed radically in the last several decades, with traditional taxonomies recognizing 242 species (e.g., Storer 1970), but current taxonomies (e.g., Clements et al. 2019) recognizing 377 species, placing Thraupidae as one of the most speciose family of birds globally. This diversity is classified into 111 genera (of which, 34 are monotypic) and 15 subfamilies (Burns et al. 2014, 2016), and our initial analyses show the new species belongs in the subfamily Tachyphoniinae. Therefore, additional analyses and taxon sampling presented in this paper focus on members of this subfamily. To investigate the relationship of the new species to other tanagers, we used Sanger sequencing approaches as well as genome-level data obtained from ultraconserved elements (UCEs). For Sanger sequencing, we used 4 different gene regions to infer phylogenetic relationships. Two of these are mtDNA gene regions: cytochrome *b* (*cyt b*) and nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2). The other two are nuclear loci: recombination-activating gene (RAG1) and ninth intron of the Z-linked aconitase 1 (ACO1-19). All 4 of these have been useful in resolving relationships among tanagers (Burns and Racicot 2009, Shultz and Burns 2013, Burns et al. 2014). Taxon sampling for all analyses is presented in Table 1, and taxonomy follows Clements et al. (2019), with a few exceptions. Given the lack of monophyly of *Tachyphonus* found in previous studies (Burns and Racicot 2009, Burns et al. 2014) and reconfirmed in the present study, we use the generic names *Loriotus* (Piacentini et al. 2019) as well as *Chrysocorypha* and *Maschalethraupis* (Burns et al. 2016) for some species traditionally considered part of *Tachyphonus*, despite

reluctance of some taxonomic authorities to accept these names (e.g., Remsen et al. 2020). In addition, *Ramphocelus passerinii* and *R. costaricensis* were included as separate species in our analyses but are recognized as one species in Clements et al. (2019). Outgroup sampling included 30 of the 31 species of Tachyphoniinae (Table 1); tissues of *Conothraupis mesoleuca* are unavailable. For *cyt b*, we used 2 individuals of the new species and 30 species of Tachyphoniinae. For ND2, we included 14 individuals of the new species, as well as 29 of Tachyphoniinae. For the nuclear loci, we included 1 individual of the new species and a subset of the remaining species. Taxon sampling for UCE analyses was guided by the Sanger analyses and included 1 of the new individuals and 4 outgroups. For Sanger sequencing, DNA sequences of the new species are available in GenBank (accession numbers: MZ713258–MZ713271 and MZ813087–MZ813090); GenBank numbers of previously sequenced species are available in Burns et al. (2014). For UCE data, all raw sequence reads are archived on the NCBI Sequence Read Archive (BioProject Number PRJNA750076).

Sanger Phylogenetic Inference

We used standard protocols (Mauck and Burns 2009, Barker et al. 2013) to extract, amplify and sequence genomic DNA. We initially aligned sequences for the 4 gene regions in Clustal X (Larkin 2007) using a large data set of nearly all tanagers using default settings. We altered the gap opening and extension costs to test the strength of alignment. We removed gaps in the alignment that did not correspond to insertions for the species studied here. We verified proper translation of protein-coding genes (*cyt b*, ND2, RAG1) using MESQUITE v.2.72 (Maddison and Maddison 2010).

We inferred phylogenies with Bayesian methods as implemented in BEAST v1.8.1 (Drummond and Rambaut 2007) using default parameters. Analyses were run for a concatenated dataset and the individual gene regions. The intron (ACO1-19) was analyzed as a single partition, but the 3 exons (*cyt b*, ND2, RAG1) were all partitioned by codon position. We used jModelTest v0.1.1 (Posada 2008) and PartitionFinder (Lanfear et al. 2012) to identify the best-fit model of evolution for each gene using Akaike's information criterion. BEAST input files were created in BEAUti v1.8.1 (Drummond and Rambaut 2007), and then BEAST analyses were run for 10 million generations, sampling every 1,000 generations. The first 1 million (10%) generations were discarded as burn-in for all BEAST analyses after examination for stationarity with Tracer v1.5 (Rambaut and Drummond 2007).

Ancestral polymorphism and incomplete lineage sorting can result in gene tree incongruence among species (Pamilo and Nei 1988). Coalescent-based species tree analyses account for gene tree heterogeneity while estimating the relationships among species. Therefore, we

also used *BEAST v.1.8.1 (Drummond and Rambaut 2007), a Bayesian method that uses a coalescent model to infer a species tree, to examine relationships among species. The *BEAST assessment included all of these markers (ND2, *cyt b*, ACO1-I9, and RAG1) together. In the analysis, the 2 mtDNA markers (ND2 and *cyt b*) were considered a single gene because the mitochondrial genome is inherited as one locus. The mtDNA markers and RAG1 were partitioned by codon, allowing substitution rate parameters and base frequencies to vary among codon positions. However, the non-coding region (ACO1-I9) was considered a single partition. The molecular clock, substitution models, and trees were all unlinked for the 3 independent loci (ACO1-I9, RAG1, mtDNA) with a relaxed, uncorrelated lognormal clock implemented. The input file was created with BEAUti, and the *BEAST analysis was run for 100 million generations sampled every 10,000 generations. We then used Tracer v1.5 (Rambaut and Drummond 2007) to assess convergence and parameter stabilization between duplicate runs.

Ultraconserved Element (UCE) Phylogenetic Inference

Total genomic DNA was extracted using QIAGEN DNeasy Blood and Tissue kits (San Francisco, CA) following standard protocol. DNA concentrations were determined with a Qubit 2.0 fluorometer. Extractions were normalized to 25 ng μL^{-1} and samples were sheared to a target fragment length of 500 base pairs (bp) on a Bioruptor (Diagenode). We performed library prep (end repair, A-tailing, and adapter ligation) using a Kapa BioSciences KAPA library prep kit. Libraries were dual-indexed libraries with iTru adapters (Glenn et al. 2019) and pooled in groups of 8 that included 62.5 ng DNA of each library. Sequence capture and post-enrichment amplification followed standard protocols (Faircloth et al. 2012) using the Mycroarray MYbaits kit for Tetrapods UCE 5K version 1, which targets 5,060 UCE loci. Libraries were combined into a single pool at equimolar ratios and sequenced using an Illumina HiSeq 3000 (PE100) by Rapid Genomics (Gainesville, FL).

We de-multiplexed and removed low-quality bases and adapter sequences for raw UCE reads using Illumiprocessor v2.0 (Lohse et al. 2012, Del Fabbro et al. 2013, Faircloth 2013, Bolger et al. 2014). We assembled cleaned reads into contigs using the program TRINITY (Grabherr et al. 2011) and then extracted contigs that matched UCE loci for each sample using the Python package *phyluce* (Faircloth 2016). Further data processing within *phyluce* included the alignment of UCE loci with MAFFT (Katoh and Standley, 2013) permitting missing nucleotides on the margins of the alignment if data were present for 65% of samples included in the dataset. Then we used Gblocks (Castresana 2000, Talavera and Castresana 2007) to trim alignments internally using default settings. We retained UCE loci present in at least 80% of the samples, resulting in 4,881 loci that were used for phylogenetic analyses.

A maximum-likelihood phylogeny was estimated with RAxML v8 (Stamatakis 2014) using the 80% complete dataset of concatenated UCE loci and a GTR + GAMMA model of sequence evolution. In phylogenetic scenarios with 2 or more short successive internodes known as the “anomaly zone” (Degnan and Salter 2005, Degnan and Rosenberg 2006), the most common gene tree will conflict with the species tree. In such a situation, concatenated datasets will converge on an incorrect topology. Therefore, we estimated species tree topologies using SVDquartets (Chifman and Kubato 2014) and ASTRAL (Mirarab et al. 2014), both of which are gene tree-based coalescent methods. We completed SVDquartets within PAUP* (Swofford 1998) and sampled all possible quartets. The quartet trees were amalgamated into a species tree using the *Quartet FM* algorithm (Reaz et al. 2014) and node support was determined by 500 bootstrap replicates. For ASTRAL, we examined individual gene trees estimated with RAxML v8.1.3 within a multispecies coalescent model, and node support was established from quartet frequencies (Sayyari and Mirarab 2016).

Niche Modeling Methods

We produced hypothetical models of the distribution of this species using GPS points taken from the specimens collected in Bolivia and Peru. Because these models are based on few, highly clustered points, they did not meet traditional requirements for a species distribution model, and should be considered hypothetical range maps, not objective distribution models. We generated absence points in several locations in La Paz department in other habitat types, including grasslands (Apolo Valley and Atén), lower montane humid forest (north of Atén), and a gradient from humid montane to upper montane forest along the La Paz–Apolo road. Because this species was very responsive to playback in the Machariapo Valley in the breeding season, RST generated absence points by playing the song of the new species for at least five minutes and listening and watching for response. To model the distribution of this species, we employed the Maxent algorithm in the package *dismo* (Hijmans 2017) in R (R Core Team 2019) using 19 WorldClim variables (Hijmans et al. 2005) separately for the Machariapo valley (“breeding”) and Kosñipata (“nonbreeding”) sites, with accessible area set below 1,400 m (roughly the upper elevation cutoff for the species at both seasons), and outside the dry, grassy Apolo Valley. The absence points were relatively few, and so were supplemented with pseudoabsence points generated randomly within 100 km of each point. The presence points were too tightly clustered to be thinned, and so these models are highly affected by spatial autocorrelation. To calculate range size, we calculated the area covered by 50% predicted climate suitability in square kilometers (km^2) for the breeding and nonbreeding ranges, separately.

TABLE 1. Voucher number of sequences used in this study. Museum abbreviations: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; LSUMZ, Louisiana State University Museum of Natural Science Collection of Genetic Resources; MBM, University of Nevada Las Vegas, Barrick Museum of Natural History; MNK, Museo de Historia Natural Noel Kempff Mercado; STRI, Smithsonian Tropical Research Institute; USNM, National Museum of Natural History (Smithsonian Institution); UWBM, University of Washington, Burke Museum.

Species	Mitochondrial data	Nuclear data	UCE data
<i>Chrysocorypha delatarii</i>	LSUMZ B11710	LSUMZ B11710	n/a
<i>Conothraupis speculigera</i>	LSUMZ B5127	LSUMZ B5127	n/a
<i>Coryphospingus cucullatus</i>	ND2: UMMZ 235435, cyt b: FMNH 334587	FMNH 334587	FMNH 334587
<i>Coryphospingus pileatus</i>	FMNH 392719	n/a	n/a
<i>Creurgops dentatus</i>	LSUMZ B580	LSUMZ B580	n/a
<i>Creurgops verticalis</i>	LSUMZ B7974	LSUMZ B7974	n/a
<i>Eucometis penicillata</i>	LSUMZ B6551	LSUMZ B6551	LSUMZ B6551
<i>Lanio aurantius</i>	MBM 8738	n/a	n/a
<i>Lanio fulvus</i>	LSUMZ B2694	LSUMZ B2694	n/a
<i>Lanio leucothorax</i>	STRI JTW572	n/a	n/a
<i>Lanio versicolor</i>	LSUMZ B1014	n/a	n/a
<i>Loriotus cristatus</i>	LSUMZ B9548	LSUMZ B9548	LSUMZ B9548
<i>Loriotus luctuosus</i>	LSUMZ B2279	n/a	n/a
<i>Loriotus rufiventer</i>	LSUMZ B3629	LSUMZ B3629	n/a
<i>Maschalethraupis surinamus</i>	LSUMZ B4795	LSUMZ B4795	n/a
<i>Ramphocelus bresilius</i>	cyt b only: no voucher, see Hackett (1996)	n/a	n/a
<i>Ramphocelus carbo</i>	ND2: FMNH 430084, cyt b: LSUMZ B4988	FMNH 430084	n/a
<i>Ramphocelus costaricensis</i>	LSUMZ B16144	n/a	n/a
<i>Ramphocelus dimidiatus</i>	LSUMZ B16559	n/a	n/a
<i>Ramphocelus flammigerus</i>	ND2: USNM 607943, cyt b: USNM B01238	n/a	n/a
<i>Ramphocelus melanogaster</i>	LSUMZ B44693	n/a	n/a
<i>Ramphocelus nigrogularis</i>	ND2: FMNH 323781 (ND2), cyt b: LSUMZ B2850	n/a	n/a
<i>Ramphocelus passerinii</i>	MBM 8627	n/a	n/a
<i>Ramphocelus sanguinolentus</i>	FMNH 343376	FMNH 343376	n/a
<i>Rhodospingus cruentus</i>	LSUMZ B5184	LSUMZ B5184	n/a
<i>Tachyphonus coronatus</i>	AMNH DOT 2452	AMNH DOT 2452	n/a
<i>Tachyphonus phoenicius</i>	AMNH DOT 4797	n/a	n/a
<i>Tachyphonus rufus</i>	LSUMZ B6668	n/a	n/a
<i>Trichothraupis melanops</i>	AMNH DOT 2464	UWBM 70274	AMNH DOT 2464
<i>Volatinia jacarina</i>	FMNH 394403	FMNH 392749	n/a
New species	ND2: LSUMZ 195912, 195915, 195916 195921, 195922, 195924, 195925 MNK 6360-6366 cyt b: LSU 195921, MNK 6365	LSUMZ 195921	LSUMZ 195915

RESULTS

Phylogenetic Results

All phylogenetic analyses (Figures 1 and 2) consistently identified the new species as belonging to a strongly supported clade containing two other species, *Eucometis penicillata* and *Trichothraupis melanops*. Both these species have long been recognized as distinct, each belonging to its own monotypic genus. All 3 species have short, bushy crests, and are largely understory denizens that may occasionally join mixed-species flocks, but otherwise have little in common. The individual gene trees differ in the phylogenetic placement of the new species with respect to *Eucometis* and *Trichothraupis* (Figure 1). ND2 and cyt b place the new species as most closely related to *Trichothraupis*, ACO1-19

places it as most closely related to *Eucometis*, and RAG1 identifies a clade containing *Eucometis* and *Trichothraupis* as sister to the new species. Analyses combining these genes also differed, with the concatenated analyses agreeing with the mitochondrial trees in placing the new species and *Trichothraupis* as closest relatives. In contrast, the *BEAST tree agreed with the RAG1 tree, with *Eucometis* and *Trichothraupis* forming a clade that is the sister clade to the new species. However, none of these analyses showed strong support for the placement of the new species within the three species clade.

For ND2, we sequenced multiple individuals, and these were all similar in sequence. Only 5 haplotypes were found, with a maximum difference of 0.2% (2 bp). One haplotype was shared among 5 individuals, 1 among 3 individuals,

the other 3 haplotypes were unique. As expected, based on the tree structure, *Eucometis*, *Trichothraupis*, and the new species showed similar levels of genetic divergence among each other. For example, uncorrected distance for ND2 for each pairwise comparison is ~10% (*Eucometis* vs. *Trichothraupis* = 9.9%, *Trichothraupis* vs. new species = 9.9%, *Eucometis* vs. new species = 10.1%).

UCE analyses more definitively identified the relationships of the three species with respect to each other (Figure 2). All three analyses using the UCE data (RAxML, SDVQuartets, and ASTRAL) show the new species is most closely related to *Trichothraupis*. Support for this relationship is strong, with 100% bootstrap support for RAxML and SDVQuartets and 1.0 posterior probability for ASTRAL. This relationship was also identified in the mitochondrial trees and in the concatenated analyses. Given the large amount of data included in the UCE tree, and its agreement with some of the analyses based on single genes, we feel that the new species is likely most closely related to *Trichothraupis*. However, the branch connecting the clade containing the new species and *Trichothraupis* is short, indicating the two species likely diverged from each other shortly after their common ancestor diverged from *Eucometis*.

Unlike the genetic data, the morphology and plumage of the 3 species do not provide a clear picture of the evolutionary relationships among them. The new species and *Eucometis* share similar yellow-colored dorsal and ventral plumage, and some populations of *E. penicillata* have a pink bill, although not as bright and eye-catching as the color of the new species' bill. All 3 species have a short crest; in *Eucometis* the crest is gray, and in the new species and *Trichothraupis*, the crest is yellow/orange. Besides this, and pronounced sexual dimorphism in plumage, we know of no other traits (plumage, bill color, song, morphology) that the new species and *Trichothraupis* share to the exclusion of *Eucometis*. In addition, the new species has many unique features among tanagers (described below) including its bill color.

Given the results of this phylogenetic analysis, and the distinctiveness in plumage and voice, we here erect a new genus:

***Heliothraupis*, Lane, Burns, Klicka, and Price-Waldman, gen. nov.**

Type species: *Heliothraupis oneilli* (see below).

Diagnosis of genus. A nine-primaried oscine; coloration, general size and shape, and voice eliminate most families within this group except Thraupidae and Cardinalidae. Similar in size to larger members of these two families. Sexually dimorphic, with males exhibiting a short bushy crest that can be raised or flattened against the crown, this feature lacking in females (Figure 3). Unlike other members of the Thraupidae, the bright coloration of the feathers of the crest includes feathers of the forehead all the way to the base of

the maxilla. The yellow on the underwing coverts and inner webs of the inner remiges is unique among thraupids. Tail rounded, slightly graduated, longer than most members of Thraupidae (similar to *Schistochlamys* spp.) with 12 rectrices (Figure 3). Both sexes are yellow overall with a bright salmon orange bill, unique among the Tachyphoniinae clade within the thraupids. The bill is not conical but considerably longer than deep (11.2 mm vs. 7.3 mm; Table 2), similar in shape to that of *Piranga*, including the presence of a weakly defined "tooth" about mid-way along the cutting edge of the maxilla (Figure 3). Bill depth at nares ~1 mm greater than bill width at nares (Table 2). Rictal bristles are present, but are not long, growing from the lores and sparingly around base of mandible laterally and between the rami. Tarsi are scutellate-laminipantar, as is common among most nine-primaried oscines (Rand 1959; Figure 3). Primary extension averages ~1/5 of total wing length (Table 2). The cardinalid "tanagers" (*Piranga*, *Chlorothraupis*, *Habia*) famously were only discovered not to be members of Thraupidae using molecular methods (Burns 1997). Thus, we cannot provide strong morphological characters to separate *Heliothraupis* from cardinalid "tanagers," but their relationships are resolved by molecular means. Osteological characters will be presented elsewhere.

Etymology. The genus *Heliothraupis* is derived from classic Greek *helios*, meaning "sun" (due to the bright yellow plumage of this species) and *thraupis* meaning "finch" or "small bird," but in current usage usually referring to tanagers.

We consider *Heliothraupis* to be monotypic, and describe its sole species here:

***Heliothraupis oneilli*, Lane, Aponte, Rheindt, Rosenberg, Schmitt, and Terrill, sp. nov.**

English name: Inti Tanager

Spanish name: Tangara Inti

Holotype. MNK-AV 6350; BOLIVIA: dept. La Paz; Prov. Franz Tamayo, loc. ANMI. Madidi, valle del Machariapo, ca. 33 km NW Apolo, 14°26.4'S, 68°31.9'W, elevation 960 m. Male. Tissue sample: LSUMZ B-95316. 27 January 2019. Collected and prepared by Miguel Angel Aponte Justiniano, field catalog number 1189. Associated sound recordings: (ML 238445).

Diagnosis of species. The combination of several distinct plumage characters is unique within the family (see Frontispiece). The brilliant yellow plumage with the contrasting black supercilium and pinkish bill of the male is more likely to remind one of an African or Asian *Oriolus* oriole (e.g., *Oriolus auratus*, African Golden Oriole, *Oriolus chinensis*, Black-naped Oriole, or *Oriolus tenuirostris*, Slender-billed Oriole) before any Neotropical species comes to mind! The burnt orange crest is similar to that of *Tachyphonus delatrii*. This crest differs from that of male *Trichothraupis melanops* in that it is never hidden

by the lateral crown feathers. The mostly yellow female is less distinctive, perhaps most likely confused with a juvenile *Schistochlamys melanopsis* (Black-faced Tanager), or a female *Piranga olivacea* (Scarlet Tanager), *P. flava* (Hepatic Tanager), or *P. rubra* (Summer Tanager), but is brighter yellow than any of these, with a proportionately longer tail than *Piranga*, and with at least some bright orange or pink on the bill.

Description of holotype. Plumage colors were scored using [Munsell \(no date\)](#), judged under a mixture of natural and fluorescent lighting. Forehead and crown are burnt orange closest to 7YR 6/12; the crown feathers behind the center of the crown are longer, forming a short, shaggy crest. A line of blackish feathering extends from the nares, the lores, just over the eyes, and along the sides of the crown above the auriculars, ending at the rear of the auriculars. The feathering between the eye and the rictus, as well as the lower half of the orbital feathering are yellow, closest to 2.5Y 8.5/12. Auriculars are a greenish-yellow closest to 5Y 7/12. Body feathers from nape to upper tail coverts are a uniform olive closest to 7.5Y 5/8. Lesser, median, and greater secondary and primary wing coverts also closest to 7.5Y 5/8; small feathers along leading edge of wing from “wrist” to base of outermost primary yellow, closest to 5Y 8.5/12. Rectrices and remiges are also olive, darkest near feather shaft (closest to 7.5Y 4/6), becoming paler towards margins (remix margins visible on closed wing), closest to 7.5Y 5/8, inner tips of primaries darkest, closest to 5Y 3/4. Axillaries and underwing coverts yellow, closest to 5Y 8.5/12. Undersides of primaries dusky (closest to 5Y 4/2), innermost portion of inner web becoming most contrastingly yellow (closest to 5Y 8/8). Primaries 8-4 emarginated ([Figure 3](#)). Malar, chin, throat, and center of breast saffron yellow, closest to 2.5Y 8/16, becoming a medium yellow (closest to 5Y 8.5/14) on belly and undertail coverts. Sides of breast and flanks olive-yellow, closest to 5Y 6/10. Label information: Weight 21.8 g; Length 18 cm; Wingspan 26.5 cm; Bill orange; Tarsi, toes yellowish brown; No wing, tail, or body molt; Medium fat; Left testis 7 x 5 mm; Skull 100% ossified; Stomach contained seeds and insect remains; Collected by mist net; Voice recorded by MAA and also on 25 January by DFL (ML 238445).

Paratypes. MUSM 30068, LSUMZ 195912, 195915, 195916, 195921, 195922, 195925, 195925, B-95315, MKN-AV 6349, 6360, 6361, 6362, 6363, 6364, 6365, 6366.

Description of paratypes. In addition to the holotype, another 16 paratype specimens of *Heliothraupis* exist. Fifteen of these are also males, 14 from within 10 km of the type locality, and collected between 22 and 26 December 2012 and 25–28 January 2019. One male, the first specimen that was collected on 9 June 2004, is from the Kosñipata road in Peru (MUSM 30068). None of these males differ noticeably from the holotype in plumage coloration or pattern. Although the crowns of some individuals appear very

slightly scaled with darker orange tips to the crest feathers, others have more saturated orange-yellow on the center of the breast and undertail coverts. Of the 14 males taken in December, only 2 exhibited any molt: LSUMZ 195916 had all rectrices sheathed (presumably adventitious replacement). Of the 3 birds taken in January, 2 exhibited molt. MNK.AV. 6349 had asymmetrical wing (primaries 6 on both wings, and secondaries 2, 3 on left wing and 3 on the right wing sheathed) and tail (left rectrices 3, 4, right rectrices 2, 3 sheathed) molt and moderate body molt, and LSUMZ B-95315 had only asymmetrical tail molt (left rectrix 3, right 3–6 sheathed). An additional bird observed and photographed on 22–24 January 2019 had all rectrices sheathed. The Peruvian specimen (MUSM 30068), collected on 9 June 2004, had rectrices that were heavily worn, both primaries 6 and secondaries 1 sheathed, and it showed trace body molt; we conclude that the bird was beginning definitive prebasic molt.

We only collected 1 female, (LSUMZ 195925), taken 25 December 2012 from one of the southernmost and highest-elevation territories we encountered in 2012 (BOLIVIA: dpto La Paz, Machariapo Valley, 14°36'S, 68°27'W, 1,100 m), which differed from the males primarily in head and breast plumage. The forehead to nape of the female is olive, concolor with the remaining dorsal plumage, closest to 7.5Y 5/8. The lores and anterior portion of the orbit feathering are a pale greenish-cream closest to 7.5Y 8/8. Rear portion of orbit a pale yellow 5Y 8/8. The auriculars, rear portion of the supercilium, malar, and sides of neck are yellow-olive (5Y 7/10). Chin and throat a pale medium yellow (5Y 8.5/10). A weakly defined broad ochraceous-yellow band across the breast is closest to 2.5Y 7/12 with weak olive streaks, particularly towards sides of breast (closest to 7.5Y 7/12). Label information: Weight 29.1 g. Wingspan 251 mm. Iris dark brown. Mandible orange with dusky splotch. Maxilla dusky with orange around tomium and nares. Tarsi and toes gray. Shot in tropical deciduous forest with scrub (mate of LSUMZ 195924). Unshelled egg in oviduct 23 x 16 mm. No bursa of Fabricius. Skull 100% ossified. No molt. Stomach contained arthropod parts. We only observed one other female, on 26 December 2012, near the locality of the female specimen, which it resembled, except in having an entirely pinkish-orange bill.

Specimens examined. All known specimens of *H. oneilli* were reviewed and measured, as well as male specimens of several related taxa for comparison ([Table 2](#)): *Trichothraupis melanops*: LSUMZ 96899, LSUMZ 196420, LSUMZ 169146. *Eucometis penicillata pallida*: LSUMZ 167782, LSUMZ 167783. *Eucometis penicillata stictothorax*: LSUMZ 138840. *Eucometis penicillata albicollis*: LSUMZ 125305, LSUMZ 183845, LSUMZ 183846. *Eucometis penicillata penicillata*: LSUMZ 83563, LSUMZ 173154, LSUMZ 110917. *Loriotus (Tachyphonus) cristatus*: LSUMZ 133848, LSUMZ 133844, LSUMZ

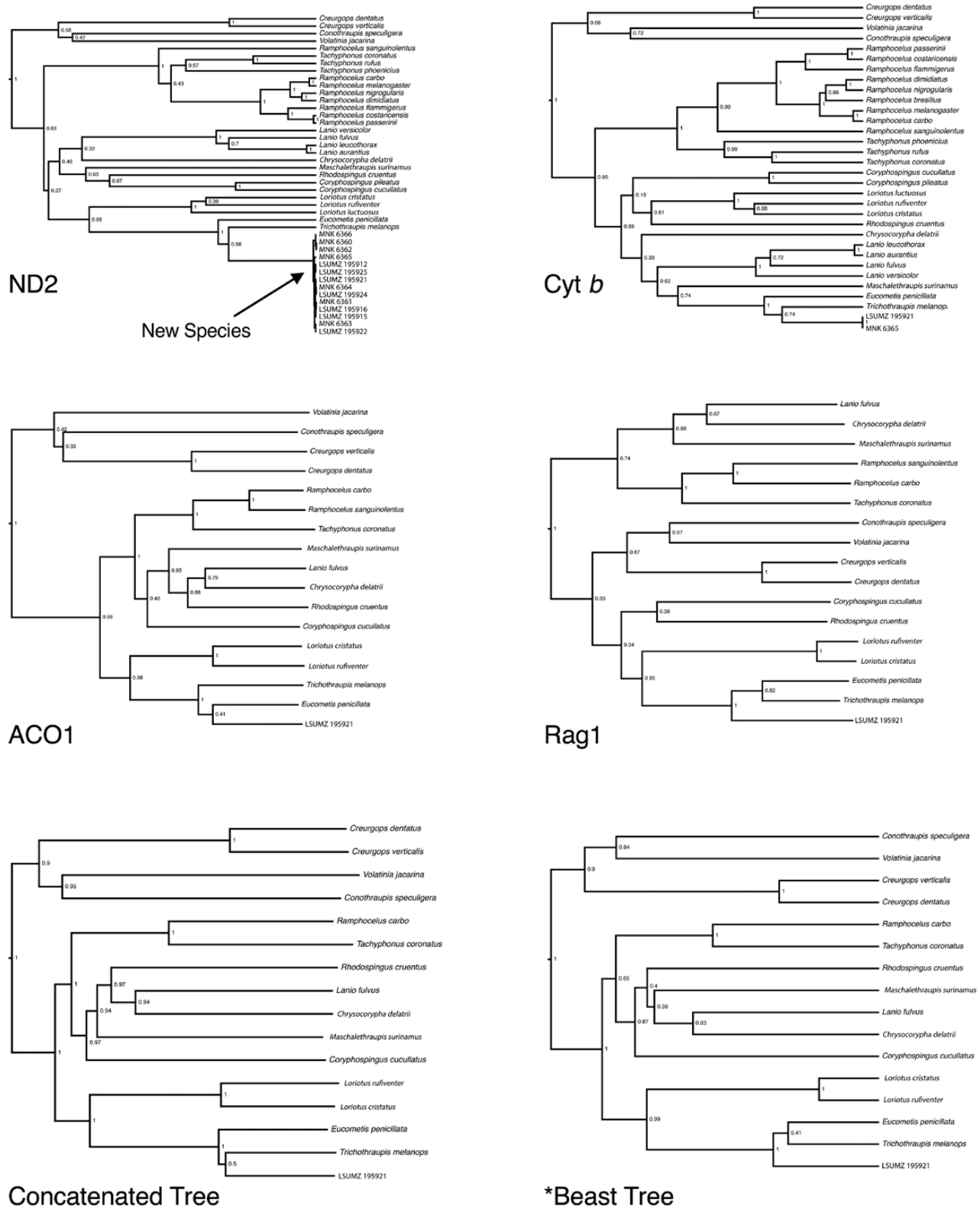


FIGURE 1. Phylogenetic analyses of the new species and relatives using separate gene trees (ND2, *cyt b*, ACO1, and Rag1) and combined analyses (Concatenated, *Beast). Support values (posterior probabilities) are shown at each node. All trees strongly support the placement of the new species in a clade with *Eucometis penicillata* and *Trichothraupis melanops*. However, the trees disagree on the relationships of these taxa relative to each other, and none of the trees show strong support for relationships among these three taxa, emphasizing the distinctness of these three species relative to each other.

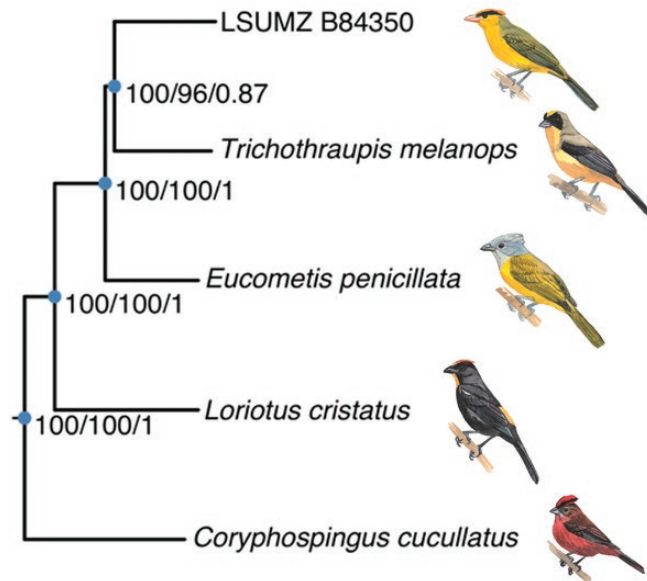


FIGURE 2. Phylogenetic analyses of the new species and close relatives based on UCE loci. Support values for each node shown for RAxML, SVDQuartets, and ASTRAL. There is strong support for a clade containing the new species, *Trichothraupis melanops*, and *Eucometis penicillata*. Within this clade, *T. melanops* is identified as the closest living relative to the new species. Although strongly supported, the branch connecting the clade comprising the new species and *T. melanops* is short. Thumbnail illustrations of the birds by DFL.

133849. *Loriothus (Tachyphonus) rufiventer*: LSUMZ 117481, LSUMZ 116170, LSUMZ 191773.

Etymology. The species name *oneilli* is to honor our mentor, friend, and colleague, John P. O'Neill, whose efforts started the LSUMNS's South American program, and who played an important role in directing much of the fieldwork over a period of over 40 years. John has shared his knowledge, kindness, generosity, and good humor with several generations of students at LSU, as well as with the greater birding and ornithological communities, particularly in Peru, and this has made him a beloved and treasured member of each. He is renowned for his ability to choose likely sites worthy of ornithological exploration, a skill that has been rewarded with his authorship of the descriptions of 15 new species (including 3 new genera) of birds. John has been an active element in the development of domestic ornithological study in Peru, a country that has become a second home to him, not least of which for being one of the progenitors of the field guide *Birds of Peru*, and assuring a Spanish edition was published in addition to English. He also provided financial and logistical support to the ornithological departments of MUSM and CORBIDI at key periods of the respective development of both Peruvian institutions and has participated tirelessly in efforts to engage young Peruvians in ornithological fieldwork. He embodies the spirit of inclusiveness

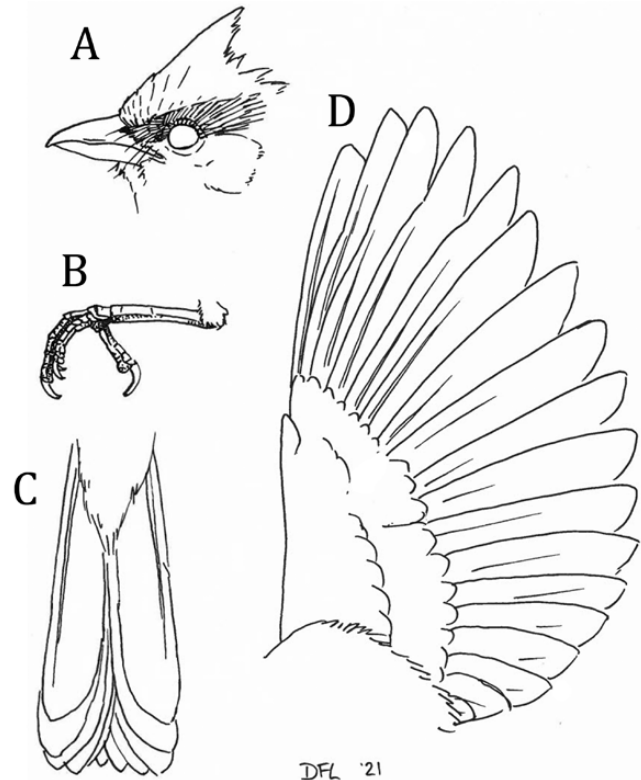


FIGURE 3. Line drawings of external morphological characters of *Heliotraupis*, based on LSUMZ 195912. (A) Bill structure, (B) outside view of left leg, (C) underside of tail, and (D) dorsal view of open right wing. Drawing by DFL.

and views each person who has worked alongside him in the process of conducting fieldwork as an equal, from the local camp assistants to fellow biologists to politicians and donors. The Peruvian government formally recognized his contributions to the development of ornithology and ecotourism in Peru through the 2008 Distinguished Service Merit Award. We cannot express how much John has meant to us as an inspiration in our own careers. Our proposed common name "*Inti*" is derived from the Quechua and Aymara word for "Sun" and thus parallels the genus name.

Distribution and habitat. As of this writing, documented reports of *H. oneilli* have only been made along the Kosñipata road, Cusco department, Peru, and the Machariapo Valley to the northwest of Apolo, La Paz department, Bolivia (Figure 4). In La Paz, the species appears to favor short (4 m canopy) to moderate-stature (~20 m canopy) deciduous and semi-deciduous woodland between approximately 750–1500 m elevation. Most individuals were present on ridges where the vegetation was shorter and drier. The canopy of these woodlands was dominated by *Anadenanthera colubrina*, *Schinopsis brasiliensis* (Parker and Bailey 1991), and a tall columnar cactus, probably *Cereus stenogonus*

TABLE 2. Specimen measurements. These measurements are means (mm) with standard deviation in parentheses unless otherwise stated. Specimens examined are listed in main text.

Taxon	Sex (n)	Weight (g)	Culmen	Bill width	Bill depth	Wing length	Primary extension	Tail length	Tarsus length
<i>Heliothraupis oneilli</i>	F (1)	29.1	11	5.9	7.6	77.5	14	71.5	18.4
<i>Heliothraupis oneilli</i>	M (17)	23.3 (1.15)	11.2 (0.40)	6.3 (0.31)	7.3 (0.24)	82.9 (2.66)	15.1 (1.53)	74.7 (2.68)	19.4 (1.00)
<i>Trichothraupis melanops</i>	M (3)	23.2 (0.67)	9.2 (1.63)	6.6 (0.37)	6.5 (0.33)	83.2 (1.02)	18 (1.39)	68.4 (0.92)	20 (0.58)
<i>Eucometis penicillata pallida</i>	M (2)	26.9, 24.7	9.9, 9.5	6.3, 6	6.7, 6.5	80.2, 84.9	14.8, 16	64.2, 67.9	22.2, 20.5
<i>Eucometis penicillata strictothorax</i>	M (1)	30	10.3	6.7	7.2	83.2	13.6	72.7	20.9
<i>Eucometis penicillata albicollis</i>	M (3)	26.4 (1.25)	11.8 (0.79)	7.4 (0.36)	6.87 (0.39)	85.7 (1.47)	13.3 (0.74)	76.2 (0.66)	20 (0.26)
<i>Eucometis penicillata penicillata</i>	M (3)	33.5 (1.5)	10.8 (0.50)	7.6 (0.16)	7.3 (0.29)	84.6 (1.38)	14.4 (1.73)	75 (2.70)	19.9 (0.58)
<i>Loriotus cristatus</i>	M (3)	22.9 (0.85)	11.6 (0.53)	6.5 (0.22)	6.8 (0.24)	82.8 (2.83)	15 (2.07)	70.8 (2.98)	18.3 (0.12)
<i>Loriotus rufiventer</i>	M (3)	20.7 (2.33)	10.3 (0)	6.0 (0.26)	6.4 (0.16)	73.3 (2.47)	12.9 (0.97)	61.8 (1.77)	18.4 (0.62)

(<https://www.inaturalist.org/observations/38163969>; <https://www.inaturalist.org/observations/38163964>), as well as the shorter and more slender *Cereus yungasensis* (<https://www.inaturalist.org/observations/20039659>; <https://www.inaturalist.org/observations/38164825>); ground cover was not particularly thick, but it included a spiny terrestrial bromeliad and in places a carpet of small-stature bamboo-like grass species, *Pharus lappulaceus* (<https://www.inaturalist.org/observations/31035377>). Densities of *Heliothraupis* in this habitat were remarkably high, and in December 2012, we detected a minimum of 12 singing males along ~2 km (linear distance) of deciduous ridgeline habitat at about 700–900 m elevation. Some individuals were encountered on the floor of the adjacent valley (50–100 m below the tops of the ridges) where the canopy was taller and the diversity of vegetation was greater and with a denser understory, but, at least in some cases, it is likely that the birds that descended to the valley floor from more typical ridge habitat did so in response to voice playback. In mid-December 2013, RST revisited territories where we had collected males in 2012. In each instance, the territory was occupied by a new male, which further indicates the high breeding density of this species in the Machariapo valley. At higher elevations (>1,000 m), where the edaphic conditions appeared drier, the species was present in shorter-stature (4–7 m canopy) woodland, including disturbed roadside growth, with a much denser understory with some isolated taller trees (reaching 10 m). An unidentified bamboo species (<https://www.inaturalist.org/observations/20039775>) formed dense patches in this woodland, and we noticed singing male *Heliothraupis* over these patches. In 2012, there was a seeding event with the low-stature bamboo-like *Pharus lappulaceus* in the valley, illustrated by the presence of *Sporophila schistacea* (Slate-colored Seedeater), a nomadic bamboo specialist that breeds during such seeding events (Parker 1982, Neudorf and Blanchfield 1994). In 2019, most territories of *Heliothraupis* were concentrated where there was significant growth of either this or another low-stature bamboo-like grass, tentatively identified as *Lasiacis maculata* (<https://www.inaturalist.org/observations/20029720>). A species of *Guadua* bamboo (<https://www.inaturalist.org/observations/38163982>) was present in the highest-elevation territory of *Heliothraupis*, at ~1,500 m. We infer that the species may require these bamboos or bamboo-like grasses as an important feature in its breeding habitat in these semi-deciduous forests. More thorough characterizations of the edaphic conditions and flora of the region can be found in Parker and Bailey (1991), Perry et al. (1997), Kessler and Helme (1999), and Cayola et al. (2005).

Observations along the Kosñipata road, Peru, have been between about 1,000 and 1,400 m elevation, at the change from “lower montane rainforest” to “cloud forest” elevation bands and the vegetation contains elements

of both (Terborgh 1985). The immediate area in which *Heliothraupis* has been seen is largely what appears to be second-growth (post-landslide?) humid forest with a broken canopy and high *Guadua* bamboo component. In 2000, the *Guadua* bamboo was seeding over much of the area in which we made our first *Heliothraupis* observation, and again, *Sporophila schistacea* was present. This *Guadua* bamboo was dying back and being replaced by vines and other second growth by 2003, only returning to become a major component of the habitat locally by about 2011 or so (DFL, personal observation).

We know of sightings of *H. oneilli* in the Kosñipata valley from 9 June, 30 July, 9 August, 3 September, 7 and 10 October, dates that span the heart of the dry season locally (Pepe Rojas, Julian Heavyside, personal communication). Several visits by DFL to this locality in early November to search for *H. oneilli* (including in 2003, only two weeks after an encounter) were fruitless. Thus, the scanty evidence so far suggests that the species is only present along the Kosñipata road as a low-density non-breeder during the dry season and migrates elsewhere to breed. Observations from the Machariapo valley, Bolivia, span from 9 October 2018 (Rich Hoyer, personal communication), 19–22 November 2017 (Herman van Oosten, personal communication, 24 January 2018), 20 November (Diego Calderon, personal communication), to the latest sighting in the area (and coincidentally, the first verified observation of the species, although unidentified at the time!) on 13 March 1993 (Mark Pearman, personal communication, 2 May 2019). In both 2012 and 2013, we observed males taking up residence on territories where either no singing male had been detected for several days, or where the previous male had been collected in mid to late December, indicating either recent arrival from nonbreeding grounds or an indicator of a high instance of “floater” males looking for vacancies to fill.

Niche Modeling Results

We found that the model predicted that this species occurs through the deciduous forest of the Machariapo Valley in the breeding season, and along the lower *Yungas* (humid montane forests) of southern Peru in the nonbreeding season (Figure 4). Of course, more documented observations of this bird at new localities will improve our understanding of its true breeding and nonbreeding distributions. In general, temperature seasonality and minimum temperature of the coldest month, and precipitation of the driest month best informed the breeding range. This preliminary model predicts that ~2,500 km² fall within 50% climatic suitability for the breeding range for this species, and ~26,000 km² of habitat falls within 50% climatic suitability for the nonbreeding range.

Behavioral observations. All evidence suggests that *Heliothraupis* is mainly insectivorous but will feed on

fruits opportunistically, similar to related *E. penicillata* and *Trichothraupis melanops* (Isler and Isler 1987). A few foraging maneuvers were observed, mostly of the 2003 and 2004 Peruvian individuals, probing into nodes of *Guadua* bamboo and gleaning from foliage in the canopy of medium and tall-stature trees (DFL and H. Lloyd, personal observation). In these observations, the individuals appeared to forage in low bamboo (<4 m off ground) but climbed into the canopy to sing. At least in the initial Peruvian observation in October 2000, the species briefly joined and followed a mixed-species insectivore flock, but in most subsequent observations in Peru, and all observations in Bolivia, it did not associate with mixed flocks, despite their presence nearby. Stomach contents from the Kosñipata specimen are strictly arthropods: an orthopteran (nymph stage grasshopper 15 mm in length), various hymenopterans, and various unidentified arthropod parts.

In La Paz, Bolivia, we mostly detected males by their loud and distinct song given from subcanopy perches. On 23 December 2012, DFL encountered one silent male within 4 m of the floor, under a singing male. It is not clear if the silent bird was foraging or perhaps a “floater” passing through furtively in search of an available territory. DFL observed a different singing male on 24 December 2012 doing a reach-out maneuver between songs, plucking an arachnid from a branch, beating it, and ingesting it. On 24 January 2019, DFL video recorded (ML 488583) a male beating a 4–5 cm long “stick grasshopper” (family Proscopiidae; <https://www.inaturalist.org/observations/20029957>), and then swallowing it whole. DFL also observed males eating the fruit of the slender columnar cactus *Cereus yungasensis* (<https://www.inaturalist.org/observations/20039794>), taking mouthfuls of the white flesh from fruit that had burst open. All of the December 2012 Bolivian specimens’ stomachs were reported to contain arthropods or “insect parts,” but the January 2019 specimens included arthropods and seeds, presumably primarily from *Cereus yungasensis*.

The following observations were made by Herman van Oosten (personal communication, 24 January 2018) on 20 November 2017 in the Machariapo valley: “Apparently, the female also sings the same song as the male. [At] about 0910 [hrs] I observed the female with a small twig/root so she was building a nest... With the twig, she flew into the spineless bamboo in the undergrowth while the male was within tens of meters from her. That same day I observed the male with a large grasshopper but he disappeared for a few seconds, then showed up again with the female, sitting cheek to cheek but just behind leaves unfortunately. They flew off and seconds later we saw the female with a large grasshopper—we had the impression it was the same insect so perhaps the male fed the female?”

Although the initial observation in October 2000 along the Kosñipata road suggested that *H. oneilli* may

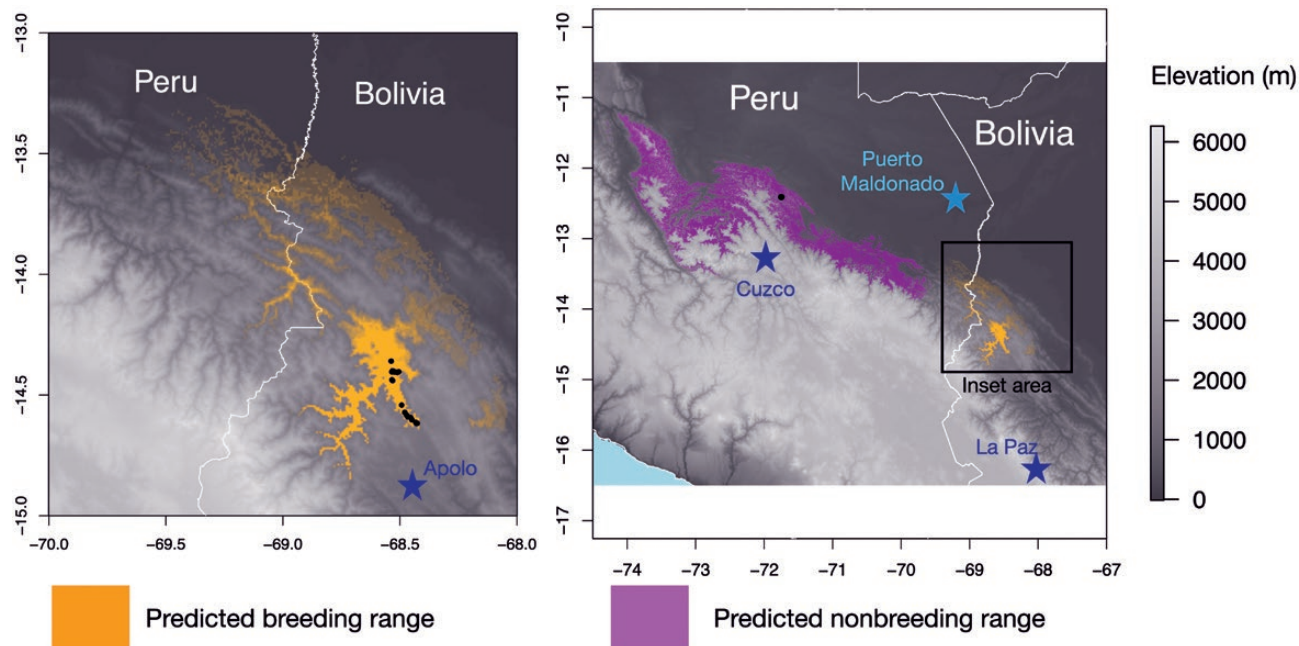


FIGURE 4. Confirmed localities of *Heliotrochilus oneilli* plotted as black dots and predicted distribution based on our modeling, using parameters set at 50% suitability, with the predicted breeding range (in gold) and predicted nonbreeding range (in purple) plotted on a false color map of elevation of the eastern slope of the Andes in western Bolivia and Southern Perú. From the confirmed observations reported, we believe that this species breeds in high densities in a small region (~2,500 km²), and then disperses to a much larger zone (~26,000 km²) in the nonbreeding season, resulting in considerably lower population density at that time.

occasionally join mixed-species flocks—as do the related species *Trichothraupis melanops* and members of *Tachyphonus* and *Loriotus*, as well as cis-Andean populations of *E. penicillata*, but strangely not trans-Andean *E. penicillata* subspecies *pallida*, *spodocephala*, *stictothorax*, *cristata*, and *affinis* (Isler and Isler 1987, Valley and Dyer 2018)—we have not noticed *H. oneilli* regularly joining such flocks on other occasions, despite being in their vicinity. Thus, we consider *H. oneilli* to be only an occasional or opportunistic flock follower. Similarly, we have not noticed *H. oneilli* following army ant swarms, a regular activity of its close relative *Eucometis* (Isler and Isler 1987). However, given its secretive behavior and difficulty in detection when not singing, it is possible that the species may engage in one or both of these social activities more commonly than presently known.

Voice. Despite its colorful plumage, *H. oneilli* seems to be quite retiring and would go unnoticed if not for its loud and distinctive song. Typically, this song is given from higher perches—between about 4 and 15 m off the ground—in the mid-story and subcanopy, particularly from the upper slopes or crests of ridges. This song is loud, carries quite far, tends to be given late into the morning, after the main dawn chorus is over, and well into the heat of the day after most other birds have quieted down. In humid montane or disturbed habitats, such as those where *H. oneilli* has been found along the Kosñipata

road, its song could potentially be confused with that of *Vireo leucophrys* (Brown-capped Vireo) or *Geothlypis aequinoctialis* (Masked Yellowthroat), respectively, but is not easily confused with any syntopic species in its breeding habitat. We recorded a fair amount of variation in song (Figure 5A–I) among neighboring individuals within a locality at the breeding site, potentially suggesting low philopatry among males. It appears, however, that any given male has only one song in its repertoire, exhibiting very limited within-individual variation. The simple, repetitive structure of the song is rather unlike the elaborate songs of *Eucometis* and *Trichothraupis*, although Andean populations of the latter seem less inclined to sing compared to those of the Atlantic Forest of southern Brazil, and their songs are effectively unrepresented in sound archives (DFL, personal observation). We have cataloged our recordings of *H. oneilli* at Macaulay Library [ML 258172441 (2000), ML 238361 (2003), 238417 (2004), 238433, 238434, 238435, 238436, 238437, 238438, 238439, 277328041, 277329101, 277329111, 277329891, 277329961, 277330281, 277330531, 277330541, 277331301 (2012), 238440, 238441, 238442, 238443, 238444, 238445, 238446, 238447, 238448 (2019)].

Based on our recordings, *H. oneilli* gives only a few calls, the most common sounding rather similar: one is a high, wiry “psit” (Figure 5J) or drawn out “pseet,” (Figure 5K and L), the latter also acting as the flight call. These

vocalizations are distinctive within the range and habitat of the species and may be the best way to locate a non-singing bird. A highly agitated individual, after some playback, gave a short descending series of wiry notes introduced by the “pseet” call (Figure 5M).

DISCUSSION

From the timeline of sightings from the Kosñipata area and the Machariapo valley, we conclude that *H. oneilli* is an intratropical migrant, which apparently is a rare behavior among Thraupidae. It appears to migrate away from the Machariapo valley area, as several surveys by competent observers during other seasons have failed to find this bird (Parker and Bailey 1991, Pearman 1993 [but see above], Perry et al. 1997). The high density of singing males during our Machariapo visits in November 2011 and December of 2012 and 2013 suggests that birds are in early stages of their reproductive cycle at that time. In our January 2019 visit we did not detect as many singing males which we suspect reflects a later stage in reproduction, which may be supported by the active molt of flight feathers, a phenomenon that typically occurs after breeding among many Neotropical passerines (Johnson et al 2012).

In the Thraupidae, excluding some members of *Sporophila*, we only know of *Asemospiza (Tiaris) obscura* (Dull-colored Grassquit; Bates 2006) and *Conothraupis speculigera* (Black-and-white Tanager) to be similarly migratory. *Conothraupis speculigera* also breeds in semi-deciduous woodlands in the Tumbesian and Marañon regions of southwestern Ecuador and northwestern Peru, spending its nonbreeding season mostly on the eastern slope of the Peruvian Andes between about 250 and 700 m (O’Neill 1966, Witt 2005, Lobo-y-Henriques et al. 2012, Harvey et al. 2014). The first movements of *H. oneilli* from nonbreeding to breeding areas probably are in October, with most males on territory by November. Nesting is well underway by late December, as suggested by the female specimen (LSUMZ 195925) with ova in her oviduct; most likely, the difficulty of finding other females was because they were actively incubating. By late January, males are starting to show molt, and we deduce that nesting is almost complete by this time, with birds perhaps departing the semi-deciduous forest between March and June. We note that females appear to be exceptionally difficult to observe and that perhaps post-breeding males fall silent and also become similarly difficult to observe. We are unaware of any observations of fledglings or independent juveniles. If the species remains mostly in bamboo understory when not singing, then its skulking behavior and dense habitat may explain the difficulty in encountering silent birds.

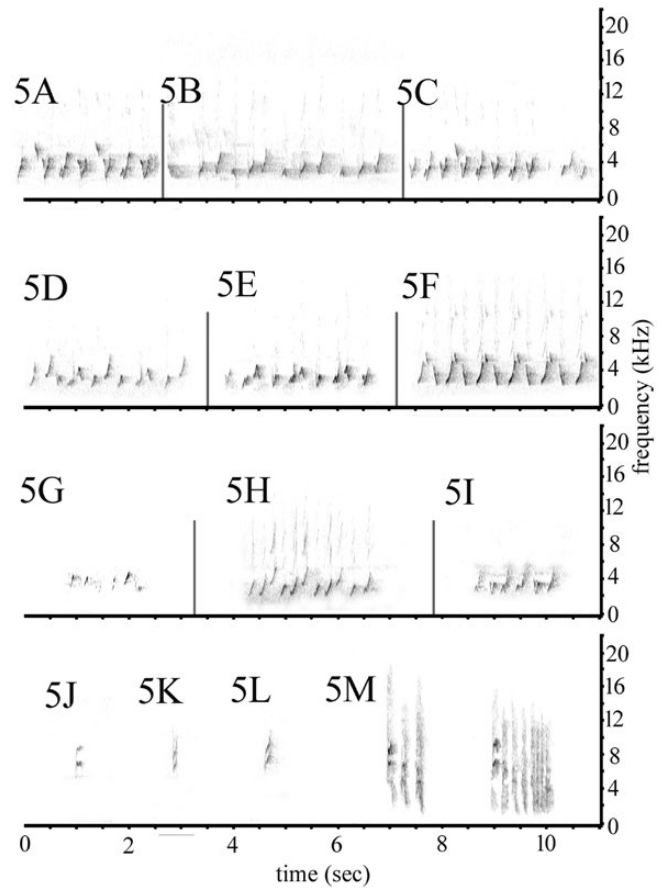


FIGURE 5. Spectrograms of vocalizations of *Heliothraupis oneilli*. The x-axis represents time in seconds, the y-axis represents frequency in kilohertz. All recordings are by DFL unless otherwise noted; “ML #####” refers to the catalog number at Macaulay Library (available at <https://macaulaylibrary.org/asset/#####>). First, songs from 6 individuals from La Paz, Bolivia, to show variation among individuals within a population: (A) 22 December 2012. ML 238433. (B) 24 December 2012. ML 238435. (C) 23 December 2012. ML 238434. (D) 24 January 2019. ML 238442. (E) 24 January 2019. ML 238443. (F) 26 January 2019. ML 238446. The following are songs from three different individuals from the Kosñipata road in Cusco, Peru, to show variation at that site: (G) 10 October 2000. Recorded by GHR, ML 258172441. (H) 7 October 2003. ML 238361. (I) 9 June 2004. ML 238417. Finally, examples of the common calls of *Heliothraupis oneilli*: (J) 24 January 2019. ML 238443. (K) 7 October 2003. ML 238361. (L) 24 January 2019. ML 238442. (M) 26 December 2012. ML 238437.

Given the high correlation of bamboo or bamboo-like grasses in both breeding and nonbreeding habitats where we have observed *H. oneilli*, we believe that the species is tied to the matrix structure of bamboo-dominated habitats. Furthermore, stands of bamboo may replicate the low-stature vine tangles typical of tropical deciduous forest habitats in some way and thus may be an attractive micro-habitat in otherwise humid foothill forest in the dry season, much as may be the case for *Conothraupis speculigera* in

southwestern Amazonia (O'Neill 1966, Witt 2005, Harvey et al. 2014).

Based on our distributional models, we predict that *H. oneilli* may be largely restricted in breeding distribution to the deciduous Machariapo/Tuichi valley system in La Paz, Bolivia, but we recommend efforts to encounter it in habitats nearby, for example in the foothills along the north side of the Apolo plateau and nearby valleys of Puno, Peru. Preliminary visits to Puno at the appropriate season by observers familiar with the species have had no success in detecting it so far (G. Seeholzer et al., personal communication). Similarly, it would be of interest to try to find the center of the species' nonbreeding distribution. We suspect that the *Guadua*-rich slopes of Santuario Nacional Megantoni and the nearby Urubamba valley, Cusco department, Peru, where the river exits the Andes, may be an important area for the species, but there are no observations yet to confirm this. Nevertheless, the species appears to be found in regions that have been relatively little disturbed by human activity, and in fact huge regions of the Andean foothills between Cusco and La Paz are relatively inaccessible. Indeed, many are within national parks and other protected lands that have little or no access, suggesting that anthropogenic changes to population sizes may be minimal at present. However, recent efforts, financed by China, to put a road through Parque Nacional Madidi to connect Apolo to Rurrenabaque in La Paz, Bolivia, could result in an influx of human colonizers, and then the deciduous forests of the Machariapo valley, in particular, could be at risk of clearing as a result. Our modeling efforts (Figure 4) are largely conjectural, and although our model of potential breeding and nonbreeding distributions were estimated at approximately 2,500 km² and 26,000 km², respectively, these could be quite generous and used parameters set at >50% suitability. If we dropped the suitability percentage of breeding distribution to >75%, the area would be ~1,175 km², and at >90% suitability, only 547 km². Given the amount of speculation here, we hesitate to offer a conservation status but rather suggest that *H. oneilli* be considered Data Deficient until surveys can better determine population size, trends, and distribution.

We hope that future researchers will uncover more natural history information about *H. oneilli*. Of particular interest will be its nesting habits, its microhabitat requirements, population densities over the course of the year, seasonality in movements, and whether it is philopatric in breeding and nonbreeding areas. In addition, further comparisons between *H. oneilli* and other members of the Tachyphoniinae with respect to comparative evolutionary biology (e.g., plumage coloration, song evolution, habitat selection, and seasonal movements) would be important to assess. That such a distinctive

species has “slipped under the radar” for as long as it has is quite a testament to how difficult it is to encounter and observe.

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Data depository: All sequences from this study have been deposited in GenBank (accession numbers: MZ713258–MZ713271 and MZ813087–MZ813090) and BioProject Number PRJNA750076. Sound recordings and videos have been deposited to Macaulay Library (see reference numbers in text).

LITERATURE CITED

- Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette (2013). Going to extremes: Contrasting rates of diversification in a recent radiation of New World passerine birds. *Systematic Biology* 62:298–320.
- Bates, J. M. (2006). The seasonal movements of southern populations of Dull-colored Grassquit (*Tiaris obscura obscura*). *Bulletin of the British Ornithologists' Club* 126:50–53.
- Bolger, A. M., M. Lohse, and B. Usadel (2014). Trimmomatic: A flexible trimmer for Illumina Sequence Data. *Bioinformatics* 30:2114–2120.
- Burns, K. J. (1997). Molecular systematics of tanagers (Thraupinae): Evolution and biogeography of a diverse radiation of Neotropical birds. *Molecular Phylogenetics and Evolution* 8:334–348.
- Burns, K. J., and R. A. Racicot (2009). Molecular phylogenetics of a clade of lowland tanagers: Implications for avian participation in the great American interchange. *The Auk* 126:635–648.
- Burns, K. J., A. J. Schultz, P. O. Tittle, N. A. Mason, F. K. Barker, J. Klicka, S. M. Lanyon, and I. J. Lovette (2014). Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution* 75:41–77.
- Burns, K. J., P. Unitt, and N. A. Mason (2016). A genus-level classification of the family Thraupidae (Class Aves: Order Passeriformes). *Zootaxa* 4088:329–354.
- Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17:540–552.
- Cayola, L., A. Fuentes, and P. M. Jørgensen (2005). Estructura y composición florística de un bosque seco subandino yungueño en el valle del Tuichi, Área Natural de Manejo Integrado Madidi, La Paz (Bolivia). *Ecología en Bolivia* 40:396–417.
- Chifman, J., and L. Kubatko. (2014). Quartet inference from SNP data under the coalescent model. *Bioinformatics* 30:3317–3324.
- Clements, J. F., T. S. Schulenberg, M. J. Iliff, S. M. Billerman, T. A. Fredericks, B. L. Sullivan, and C. L. Wood (2019). The eBird/Clements Checklist of Birds of the World: v2019. <https://www.birds.cornell.edu/clementschecklist/download/>
- Del Fabbro, C., S. Scalabrin, M. Morgante, and F. M. Giorgi (2013). An extensive evaluation of read trimming effects on Illumina NGS data analysis. *PLoS One* 8:e85024.
- Degnan, J. H., and L. A. Salter. (2005). Gene tree distributions under the coalescent process. *Evolution* 59:24–37.
- Degnan, J. H., and N. A. Rosenberg. (2006). Discordance of species trees with their most likely gene trees. *PLOS Genetics* 2:e68.
- Demery, A.-J. C., K. J. Burns, and N. A. Mason (2021). Bill size, bill shape, and body size constrain bird song evolution on a macroevolutionary scale. *Ornithology* 138:ukab011. <https://doi.org/10.1093/ornithology/ukab011>
- Drummond, A. J., and A. Rambaut (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7:214.
- Faircloth, B. C. (2013). illumiprocessor: A trimmomatic wrapper for parallel adapter and quality trimming. <http://dx.doi.org/10.6079/J9ILL>.
- Faircloth, B. C. (2016). PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 32:786–788.
- Faircloth, B. C., J. E. McCormack, N. G. Crawford, M. G. Harvey, R. T. Brumfield, and T. C. Glenn (2012). Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology* 61:717–726.
- Glenn, T. C., R. A. Nilsen, T. J. Kieran, J. G. Sanders, N. J. Bayona-Vásquez, J. W. Finger, T. W. Pierson, K. E. Bentley, S. L. Hoffberg, Louha S., F. J. Garcia-De Leon, M. A. del Rio Portilla, et al. (2019). Adapterama I: Universal stubs and primers for 384 unique dual-indexed or 147,456 combinatorically indexed Illumina libraries (iTru & iNext). *PeerJ* 7:e7755
- Grabherr, M. G., B. J. Haas, M. Yassour, J. Z. Levin, D. A. Thompson, I. Amit, X. Adiconis, L. Fan, R. Raychowdhury, Q. Zeng et al. (2011). Trinity: Reconstructing a full-length transcriptome without a genome from RNA-Seq data. *Nature Biotechnology* 29:644–652.
- Hackett, S. J. (1996). Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). *Molecular Phylogenetics and Evolution* 5:368–382.
- Harvey, M. G., D. F. Lane, J. Hite, R. S. Terrill, S. Figueroa R., B. T. Smith, J. Klicka, and W. Vargas C. (2014). Notes on bird species in bamboo in northern Madre de Dios, Peru, including the first Peruvian record of Acre Tody-Tyrant (*Hemitriccus cohnhafti*). *Occasional Papers of the Louisiana State University Museum of Natural Science* 81:1–38.
- Hijmans, R. J., S. Cameron, J. Parra, P. Jones, A. Jarvis, and K. Richardson (2005). WorldClim, version 1.3. University of California, Berkeley, CA, USA. <https://www.worldclim.org/data/worldclim21.html>
- Hijmans, R. J., S. Phillips, J. Leathwick, J. Elith, and M. R. J. Hijmans (2017). Package “dismo”. *Circles* 9:1–68.
- Hilty, S. L. (2011). Family Thraupidae (tanagers). In *Handbook of the Birds of the World*, vol. 16 (J. del Hoyo, A. Elliott, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain. pp. 46–329

- Isler, M. L., and P. R. Isler (1987). *The Tanagers: Natural History, Distribution, and Identification*. Smithsonian Institution Press, Washington, D.C., USA.
- Johnson, E. I., P. C. Stouffer, and R. O. Beirregaard, Jr. (2012). The phenology of molt, breeding and their overlap in central Amazonian birds. *Journal of Avian Biology* 43:141–154.
- Katoh, K., and D. M. Standley (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30:772–780.
- Kessler, M., and M. Helme (1999). Floristic diversity and phytogeography of the central Tuichi Valley, and isolated dry forest locality in the Bolivian Andes. *Candollea* 54:341–366.
- Lanfear, R., B. Calcott, S. Y. W. Ho, and S. Guindon (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29:1695–1701.
- Larkin, M. A. (2007). ClustalW and ClustalX version 2.0. *Bioinformatics* 23:2947–2948.
- Lobo-y-Henriques, J. C., Y. J. Bates, and D. Willard (2012). First record for the Black-and-white Tanager (*Conothraupis speculigera*) in Colombia. *Conservación Colombiana* 17:45–51.
- Lohse, M., A. M. Bolger, A. Nagel, A. R. Fernie, J. E. Lunn, M. Stitt, and B. Usadel. (2012). RobiNA: a user-friendly, integrated software solution for RNA-Seq-based transcriptomics. *Nucleic Acids Research* 40:622–627.
- Lowery, G. H., Jr., and J. P. O'Neill (1964). A new genus and species of tanager from Peru. *The Auk* 81:125–131.
- Lowery, G. H., Jr., and D. A. Tallman (1976). A new genus and species of nine-primaried oscine of uncertain affinities from Peru. *The Auk* 93:415–428.
- Maddison, W., and D. Maddison (2010). MESQUITE: A modular system for evolutionary analysis, version 2.6. mesquiteproject.org
- Mason, N. A., and K. J. Burns (2015). The effect of habitat and body size on the evolution of vocal displays in Thraupidae (tanagers), the largest family of songbirds. *Biological Journal of the Linnean Society* 114:538–551.
- Mauck, W. M., and K. J. Burns (2009). Phylogeny, biogeography, and recurrent evolution of divergent bill types in the nectar-stealing flowerpiercers (Thraupini: *Diglossa* and *Diglossopsis*). *Biological Journal of the Linnean Society* 98:14–28.
- Mirarab, S., R. Reaz, M. S. Bayzid, T. Zimmermann, M. S. Swenson, and T. Warnow. (2014). ASTRAL: genome-scale coalescent-based species tree estimation. *Bioinformatics* 30:i541–i548.
- Munsell. [No date]. *The Munsell book of color*. Gretag Macbeth LLC; New Britain, NY, USA.
- Neudorf, D. L., and P. J. Blanchfield (1994). The Slate-colored Seedeater (*Sporophila schistacea*): A bamboo specialist? *Ornitología Neotropical* 5:129–132.
- O'Neill, J. P. (1966). Notes on the distribution of *Conothraupis speculigera* (Gould). *The Condor* 68:598–600.
- Pamilo, P., and M. Nei (1988). Relationships between gene trees and species trees. *Molecular Biology and Evolution* 5:568–583.
- Parker, T. A., III (1982). Observations of some unusual rainforest and marsh birds of southeastern Peru. *The Wilson Bulletin* 94:477–493.
- Parker, T. A., III, and B. Bailey (Editors) (1991). *A Biological Assessment of the Alto Madidi Region and Adjacent Areas of Northwest Bolivia*, May 18–June 15, 1990. RAP Working Papers 1, Conservation International, Washington, D.C., USA.
- Patterson, B. D., D. F. Stotz, and S. Solari (2006). Mammals and birds of the Manu Biosphere Reserve. *Fieldiana Zoology* 2006:110. [https://doi.org/10.3158/0015-0754\(2006\)110\[1:MABOTM\]2.0.CO;2](https://doi.org/10.3158/0015-0754(2006)110[1:MABOTM]2.0.CO;2)
- Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco (1998). Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593–607.
- Pearman, M. (1993). The avifauna of the Río Machariapo dry forest, northern depto. La Paz, Bolivia: A preliminary investigation. *Bird Conservation International* 3:105–117.
- Perry, A., M. Kessler, and N. Helme (1997). Birds of the central Río Tuichi Valley, with emphasis on dry forest, Parque Nacional Madidi, depto. La Paz, Bolivia. In *Studies in Neotropical Ornithology Honoring Ted Parker* (J. V. Remsen, Jr., Editor). American Ornithologist's Union, Washington (DC).
- Piacentini, V., P. Unitt, and K. J. Burns (2019). Two overlooked generic synonyms in the Thraupidae (Aves: Passeriformes). *Zootaxa* 4608 (3): 593–594.
- Posada, D. (2008). JModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25:1253–1256.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rambaut, A., and A. Drummond (2007). Tracer, v1.5. <http://tree.bio.ed.ac.uk/software/tracer/>
- Rand, A. L. (1959). Tarsal scutellation of song birds as a taxonomic character. *The Wilson Bulletin* 71:274–277.
- Reaz, R., M. S. Bayzid, and M. S. Rahman. (2014). Accurate phylogenetic tree reconstruction from quartets: A heuristic approach. *PLoS One* 9:e104008.
- Remsen, J. V., Jr., J. I. Areta, E. Bonaccorso, S. Claramunt, A. Jaramillo, J. F. Pacheco, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer (2020). A classification of the bird species of South America. American Ornithological Society. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm>
- Sayyari E., and S. Mirarab. (2016). Fast coalescent-based computation of local branch support from quartet frequencies. *Molecular Biology and Evolution* 33:1654–1668.
- Shultz, A. J., and K. J. Burns (2013). Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. *Molecular Phylogenetics and Evolution* 66:112–125.
- Shultz, A. J., and K. J. Burns. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution* 71:1061–1074.
- Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313.
- Storer, R. W. (1970). Subfamilies Thraupinae and Tersiniinae. In *Check-List of Birds of the World*, vol. 13 (R. A. Paynter, Jr., Editor). Museum of Comparative Zoology, Cambridge, MA, USA. pp. 246–409.
- Swofford, D. L. (1998). PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer, Sunderland, MA.
- Talavera, G., and J. Castresana (2007). Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56:564–577.
- Terborgh, J. (1985). The role of ecotones in the distribution of Andean birds. *Ecology* 66:1237–1246.

- Title, P. O., and K. J. Burns (2015). Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. *Ecology Letters* 18:433–440.
- Vallely, A. C., and D. Dyer (2018). *Birds of Central America*, Princeton University Press, Princeton, NJ, USA.
- Vinciguerra, N. T., and K. J. Burns (2021). Species diversification and ecomorphological evolution in the radiation of tanagers (Passeriformes: Thraupidae). *Biological Journal of the Linnean Society* 133:3. <https://doi.org/10.1093/biolinnean/blab042>
- Walker, B., D. F. Stotz, T. Pequeño, and J. W. Fitzpatrick (2006). Birds of the Manu Biosphere Reserve. In *Mammals and Birds of the Manu Biosphere Reserve, Peru* (Patterson, B. D., D. F. Stotz, and S. Solari, Editors). Field Museum of Natural History, Chicago, IL, USA. *Fieldiana Zoology* 2006:110. pp. 23–49.
- Witt, C. C. (2005). Syntopic breeding suggests mimicry of the Black-and-white Seedeater (*Sporophila luctuosa*) by the Black-and-white Tanager (*Conothraupis speculigera*). *Ornitologia Neotropical* 16:387–396.