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Source: Bulletin of the British Ornithologists' Club, 140(3) : 351-358

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v140i3.2020.a8

New Guinea *Erythrura* parrotfinches: one species or two?

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Received 25 June 2020; revised 26 July 2020; published 21 September 2020

http://zoobank.org/urn:lsid:zoobank.org:pub:B742D56B-E1D8-46DC-A6A6-048CAE1FCFCA

Summary.—Two species of *Erythrura* parrotfinches, differing mainly in bill size, are described from the New Guinea highlands: Blue-faced Parrotfinch *E. trichroa* and Papuan Parrotfinch *E. papuana*. Morphological measurements from museum specimens support two non-overlapping groups, but mitochondrial DNA sequence data show negligible differences between the two species. These observations suggest that *E. trichroa* and *E. papuana* may form a single species in the highlands of New Guinea that exhibits a resource-based bill size polymorphism.

Two described species of *Erythrura* parrotfinches occur in the mountains of New Guinea: the widespread Blue-faced Parrotfinch *E. trichroa*, with subspecies *E. t. sigillifer* in New Guinea, nearby islands and northern Australia (Mayr 1931, Gill *et al*. 2020), and Papuan Parrotfinch *E. papuana*, endemic to New Guinea. These two species are similar in plumage but differ in morphology, with *E. papuana* being larger than *E. trichroa*, particularly in bill morphology (Fig. 1; Hartert 1900, Mayr 1931, Pratt & Beehler 2015). *E. trichroa* was described from specimens collected in the Caroline Islands (De Vis 1897, Mayr 1931) and is distributed from Sulawesi through Micronesia, Melanesia and northern Australia (Mayr 1931). Rothschild & Hartert (*in* Hartert 1900) described *E. papuana* as a subspecies of *E. trichroa* based on the similarity in plumage but larger size. Decades later, Hartert realised that two sympatric subspecies of *E. trichroa* had been described from New Guinea; 'This form [*E. t. papuana*] occurs in the same countries with the form described as *goodfellowi* by Grant, it can therefore not be a subspecies of *trichroa*' (Hartert 1930: 43). Hartert at this point elevated *E. t. papuana* to species level (*E. papuana*) and stated, 'We have thus a similar case as in the genus *Geospiza* on the Galapagos Islands, a large and a small form occurring together' (Hartert 1930: 43).

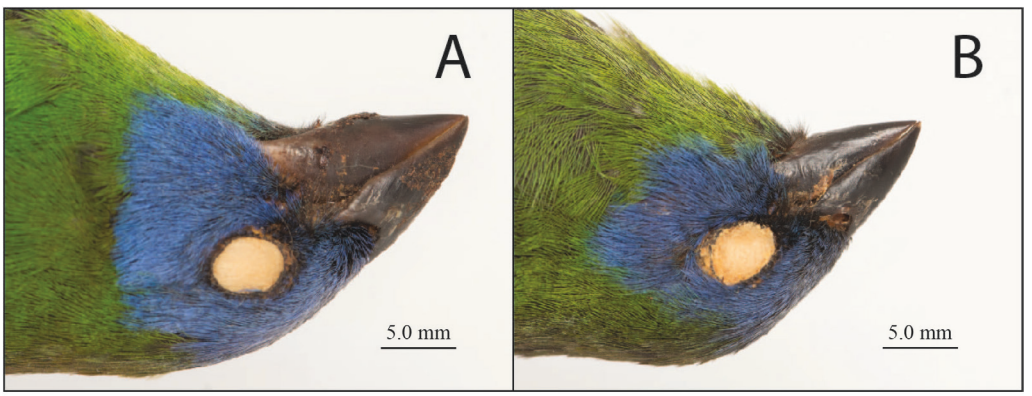

Figure 1. Comparison of bill size and shape between sympatric Papuan Parrotfinch *Erythrura papuana* (A) and Blue-faced Parrotfinch *E. trichroa* (B) from New Guinea (Lucas H. DeCicco)

ISSN-2513-9894 (Online)

Little is known about the ecology of these species, and some published information is contradictory, further confounding our understanding of *Erythrura* distributional ecology in New Guinea. Reported elevational ranges (750–3,000 m for *E. trichroa*, and 1,200–2,600 m for *E. papuana*; Pratt & Beehler 2015) indicate that the two species should occur broadly in sympatry (Rand & Gilliard 1967, Diamond & Marshall 1977, Pratt & Beehler 2015, Payne 2020; BWB pers. obs.). However, some authorities (e.g. Diamond 1972) have suggested that these species are locally allopatric with only occasional local sympatry, a pattern that 'can be described approximately as checkerboard allopatry' (Diamond 1972: 408). Diamond (1972) stated that there are no known differences in habitat, altitudinal or behavioural preferences between the species and suggested that these similarities did not permit local sympatry. However, Diamond & Marshall (1977) have noted that *E. papuana* feeds on figs and that in New Guinea *E. trichroa* forages on bamboo seeds. Rand & Gilliard (1967) reported *E. papuana* foraging with parrots on fruits in the canopy, a behaviour not reported in *E. trichroa* to our knowledge. *E. trichroa* is also found in high-elevation grassland / forest ecotones, where it forages on bamboo or grass seeds (BWB pers. obs.). Vocal differences between the species have not been assessed in detail and scant audio data are available for either species. Pratt & Beehler (2015) included brief descriptions of calls and songs of both species, suggesting minor differences in songs. Subtle sexual dimorphism has been suggested in the plumage of both species (e.g. Pratt & Beehler 2015) but bill size has not been reported to differ between the sexes. *E. trichroa* is more numerous than *E. papuana* (Diamond 1972, Pratt & Beehler 2015; BWB pers. obs.) and distributional patterns led Diamond (1972: 41) to suggest that '[p] resumably *E. papuana* is the older species in New Guinea and has been eliminated at all but a few localities by *E. trichroa*, a recent invader from the outside.'

For nearly a century, biologists have considered *E. papuana* and *E. trichroa* to be distinct species based on body and bill size differences (Hartert 1930). Hartert & Rothschild (*in* Hartert 1900) published a comparison of single wing measurements in the description of *E. t. papuana* and Hartert (1930) compared wing lengths and body masses between *E. trichroa* and *E. papuana* when he elevated the latter to species. Diamond (1972) provided three measurements (wing, exposed culmen, and mass) from 30 specimens of *E. trichroa* (17 male, 13 female) and 17 of *E. papuana* (nine male, four female, four unknown), and concluded that specimens of *E. papuana* were larger than all or almost all *E. trichroa* in those three characters. To our knowledge, there has been no further analysis regarding the differences in bill morphology between the two species.

In a recent phylogeny of the family Estrildidae, Olsson & Alström (2020) included mitochondrial DNA (mtDNA) sequences from single individuals of *E. trichroa* and *E. papuana*. These two samples shared a mitochondrial haplotype. However, they did not examine the specimens and explicitly noted '…one or more samples may have been misidentified' (Olsson & Alström 2020: 145–146).

While investigating patterns of genetic differentiation among allopatric populations of *E. trichroa* with a focus on the Solomon Islands (DeCicco *et al*. 2020), we became interested in the sympatric occurrence of the visually similar *E. trichroa* and *E. papuana* in New Guinea. Given their largely sympatric distributions and broadly recognised species status, we assumed that this pair would show divergence in mtDNA sequences. Further, we expected that these populations probably underwent allopatric speciation and are now in secondary contact, as suggested by Diamond (1972). Olsson & Alström (2020) provided a clear expectation to address with more sampling if these two species share similar or identical mtDNA sequences, or if the similarities they found were due to sample misidentification. We address these questions using morphological measurements to further characterise phenotypic differences and Sanger sequencing of mtDNA from a broader sampling to

ISSN-2513-9894 (Online)

investigate molecular divergence between the two taxa. Specifically, we ask: (1) Are the two species distinct in morphology as suggested by previous authors? (2) Are these species genetically distinct as would be expected based on Diamond's (1972) predictions? (3) Or, do these species share genetic similarities as suggested by Olsson & Alström (2020)?

Methods

We investigated molecular divergence in mtDNA between *E. trichroa* and *E. papuana* by sequencing subunit 2 of the *NADH* gene (*ND2*) from specimen-vouchered tissue samples of *E. trichroa* (*n* = 9) and *E. papuana* (*n* = 6) from New Guinea (Table 1). To provide perspective on molecular relationships between these two sympatric taxa, we also sequenced *E. trichroa* (*n* = 5) from the Solomon Islands and the closely related Red-eared Parrotfinch *E. coloria* (*n* = 2) from the Philippines (Table 1). We extracted genomic DNA from ethanol-preserved tissue samples using a Qiagen DNEasy® Blood and Tissue Kit following the manufacturer's protocol. We amplified *ND2* by polymerase chain reaction (PCR) using primers L5215 (Hackett 1996) and H6313 (Johnson & Sorenson 1998) in 25 uL reactions with OneTaq® HS Quick-Load® 2X Master Mix with Standard Buffer (M04885, New England Biolabs Inc.). The PCR conditions consisted of a 'touch-down' protocol: 95.0°C for 20 seconds; 95.0°C for 20 seconds, 60.0°C for 15 seconds, 70.0°C for 30 seconds repeated ten times; 95.0°C for 20 seconds, 56.0°C for 15 seconds, 70.0°C for 30 seconds repeated eight times; 95.0°C for 20 seconds, 50.0°C for 15 seconds, 70.0°C for 30 seconds repeated 35 times; 70.0°C for four minutes, and a holding temperature of 4.0°C. We sent the PCR amplicons to Genewiz for sequencing and visually inspected, cleaned and assembled these sequences in Geneious v8.1.9 (Biomatters). We aligned sequences using MUSCLE (Edgar 2004) implemented in Geneious, and calculated raw pair-wise genetic distances in R (R Core Team 2018) using the package SeqinR (Charif & Lobry 2007). We generated haplotype networks in PopART using the minimum spanning algorithm (Leigh & Bryant 2015).

We measured wing chord, bill length from the distal end of the nares to tip, and max. width of the mandible of 14 adult *E. trichroa* (seven male, six female and one unknown) and seven adult *E. papuana* (four male and three female) specimens collected in mainland New Guinea housed at the University of Kansas Natural History Museum, Lawrence (Table 1). We had partial overlap between our sampling of individuals for morphometric and genetic analysis (Table 1).

Results

E. trichroa and *E. papuana* from New Guinea were identical or very similar in *ND2* sequence, with on average 0.07% (range 0.00–0.20%) pair-wise uncorrected divergence among individuals. We noted similar levels of *ND2* sequence divergence in *E. trichroa* both within New Guinea populations at 0.04% (0.00–0.20%) divergence and between New Guinea and Solomons populations with 0.04% (0.00–0.20%) divergence. *E. coloria* was 1.12% divergent on average from *E. trichroa* (all populations combined) and 1.14% from *E. papuana*. We identified six unique haplotypes within our dataset (Fig. 2). *E. coloria* had one distinct haplotype removed from the others by at least 11 mutations. The remaining five haplotypes did not segregate by species or population. One main haplotype comprised individuals of *E. trichroa* (New Guinea and Solomons populations) and *E. papuana*. Single mutations separated the other four *ND2* haplotypes: one *E. trichroa* from New Guinea, one *E. trichroa* from the Solomons, one *E. papuana* from New Guinea, and a haplotype shared by one *E. trichroa* and one *E. papuana* both from New Guinea (Fig. 2).

ISSN-2513-9894 (Online)

TABLE 1
Parrotfinch (genus *Erythrura*) specimens used for genetic and morphometric analyses. Type of data taken from each specimen is denoted in the last column. All specimens are archived at the University of Kansas Natural History Museum, Lawrence.

Species	Specimen no.	Locality	Data type
E. coloria	KU 122191	Philippines, Mindanao	Genetic
E. coloria	KU 122152	Philippines, Mindanao	Genetic
E. papuana	KU 91959	Papua New Guinea, Eastern Highlands province	Morphometric
E. papuana	KU 96003	Papua New Guinea, Simbu province	Genetic/morphometric
E. papuana	KU 111653	Papua New Guinea, Madang province	Genetic/morphometric
E. papuana	KU 113245	Papua New Guinea, Central province	Genetic
E. papuana	KU 121546	Papua New Guinea, Eastern Highlands province	Morphometric
E. papuana	KU 121598	Papua New Guinea, Central province	Genetic/morphometric
E. papuana	KU 121599	Papua New Guinea, Central province	Genetic/morphometric
E. papuana	KU 121600	Papua New Guinea, Central province	Genetic/morphometric
E. trichroa	KU 43646	Papua New Guinea, Morobe province	Morphometric
E. trichroa	KU 93596	Papua New Guinea, Morobe province	Morphometric
E. trichroa	KU 96004	Papua New Guinea, Simbu province	Genetic/morphometric
E. trichroa	KU 111462	Papua New Guinea, Madang province	Genetic
E. trichroa	KU 111654	Papua New Guinea, Madang province	Morphometric
E. trichroa	KU 111655	Papua New Guinea, Madang province	Morphometric
E. trichroa	KU 111656	Papua New Guinea, Madang province	Genetic/morphometric
E. trichroa	KU 111658	Papua New Guinea, Eastern Highlands province	Genetic/morphometric
E. trichroa	KU 111659	Papua New Guinea, Eastern Highlands province	Morphometric
E. trichroa	KU 114201	Papua New Guinea, West Sepik province	Genetic/morphometric
E. trichroa	KU 114203	Papua New Guinea, West Sepik province	Genetic/morphometric
E. trichroa	KU 114229	Papua New Guinea, Eastern Highlands province	Morphometric
E. trichroa	KU 114284	Papua New Guinea, Eastern Highlands province	Genetic/morphometric
E. trichroa	KU 114285	Papua New Guinea, Central province	Morphometric
E. trichroa	KU 114770	Papua New Guinea, Eastern Highlands province	Genetic
E. trichroa	KU 114838	Papua New Guinea, Central province	Genetic
E. trichroa	KU 121568	Papua New Guinea, Madang province	Morphometric
E. trichroa	KU 131742	Solomon Islands, Malaita	Genetic
E. trichroa	KU 132030	Solomon Islands, Guadalcanal	Genetic
E. trichroa	KU 132039	Solomon Islands, Guadalcanal	Genetic
E. trichroa	KU 133546	Solomon Islands, Makira	Genetic
E. trichroa	KU 133569	Solomon Islands, Makira	Genetic

In contrast, we found no overlap between *E. trichroa* and *E. papuana* in multiple morphological measurements (Fig. 3): mean wing chord = 60.6 mm (range 57.8–63.5) for *E. trichroa* and mean = 65.7 mm (64.3–68.1) for *E. papuana*; bill length from distal end of nares to tip mean = 9.1 mm (8.6–9.6 mm) for *E. trichroa* and mean = 10.4 mm (10.0–10.9 m) for *E. papuana*; and max. width of mandible mean = 7.4 mm (7.1–7.8 mm) for *E. trichroa* and

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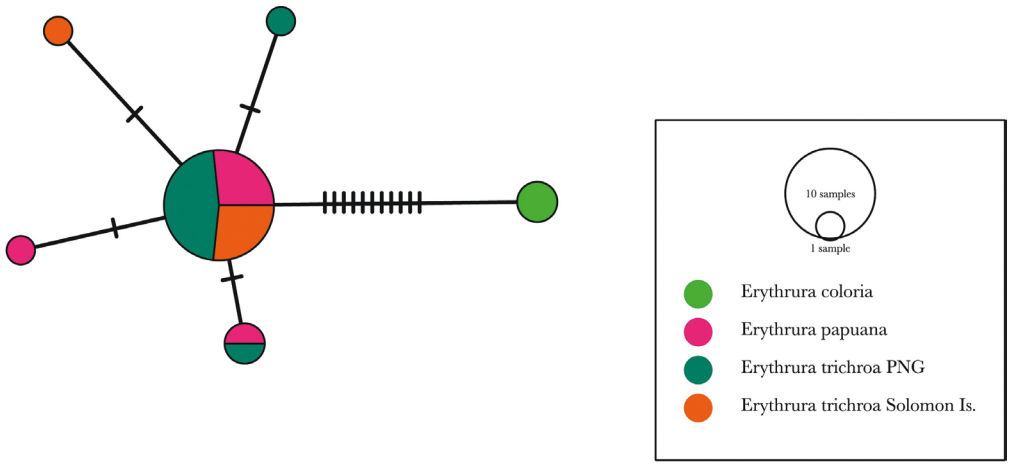

Figure 2. Haplotype network showing genetic relationships among Red-eared Parrotfinch *Erythrura coloria*, Blue-faced Parrotfinch *E. trichroa* and Papuan Parrotfinch *E. papuana*.

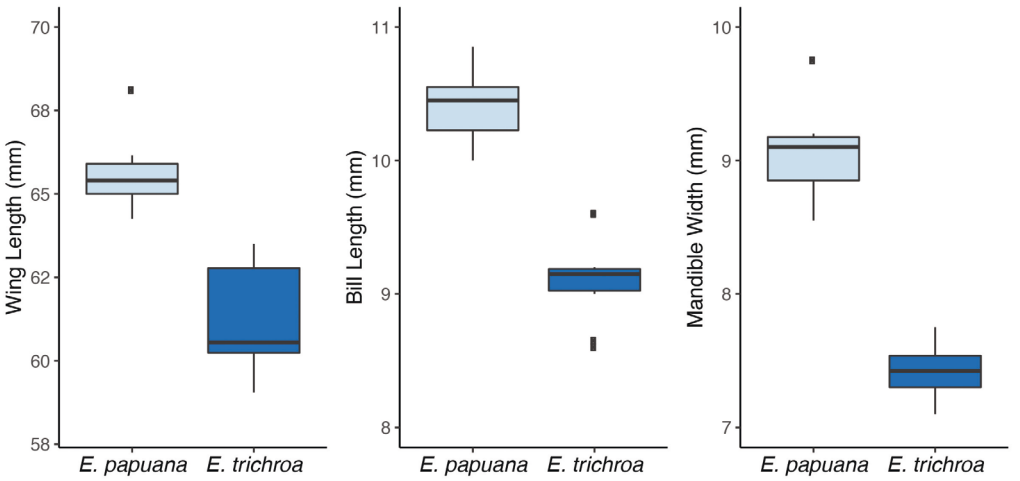

Figure 3. Comparison between Papuan Parrotfinch *Erythrura papuana* and Blue-faced Parrotfinch *E. trichroa* in three morphological measurements. Table 1 lists the specimens used for these comparisons.

mean = 9.1 mm (8.6–9.8) for *E. papuana*. To determine if bill size scaled roughly with body size, we standardised bill measurements by the wing measurement of each species (e.g., mean bill length of *E. trichroa* / mean wing chord of *E. trichroa*). In both bill length and width *E. papuana* had a proportionately slightly larger bill (mean bill length / mean wing chord = 0.15 for *E. trichroa* and 0.16 for *E. papuana*, mean bill width / mean wing chord = 0.12 for *E. trichroa* and 0.14 for *E. papuana*). Larger datasets and more comprehensive bill measurements will be needed to assess shape and proportional differences in greater detail. Based on our sampling, bill size did not differ markedly by sex (i.e., mean bill length was the same for male and female *E. trichroa*). Our morphological results agree with those reported in Diamond (1972) and corroborate that these named species differ in morphology despite sharing identical or near-identical mitochondrial *ND2* sequences. We conclude that these two species do indeed form morphologically distinct groups despite a lack of divergence in mtDNA.

ISSN-2513-9894 (Online)

Discussion

Here we provide the first thorough assessment of genetic differences between *E. trichroa* and *E. papuana* in New Guinea, and we corroborate previously identified morphological differences with additional measurements such as mandible width, which is an important indicator of dietary differences in seed-eating birds (e.g. Smith 1987). We did not assess plumage variation due to small sample sizes. Diamond (1972) suggested that the extent of blue in the face varied slightly between *E. trichroa* and *E. papuana*, but this characteristic also varies within species due to age and sex (e.g. Pratt & Beehler 2015).

Our findings identify morphological differences in the presence of identical mtDNA haplotypes. Several potential explanations for this pattern exist, but fall broadly under three general themes: (1) morphological differences arose in allopatry with either limited genetic divergence or gene flow upon secondary sympatry, (2) sympatric or ecological speciation is occurring with strong selection on different phenotypes, or (3) these two phenotypes represent a single panmictic population with a phenotypic polymorphism. We lack nuclear sequence data to test for concordance with our mitochondrial data. If nuclear sequence data disagree with the mitochondrial data we present, the first hypothesis could easily account for this pattern through gene flow and mitochondrial capture from one species to the other (e.g. Hird & Sullivan 2009, Irwin *et al*. 2009, Ferreira *et al*. 2018). Expanded geographic sampling, particularly from western populations of *E. papuana* in the Bird's Head region of New Guinea will be necessary to fully explore this hypothesis. Non-sex-linked bill polymorphism is exceedingly rare in birds and has been studied in detail only in the African finch genus *Pyrenestes*, which exhibits a resource-based polymorphism within a panmictic population. Extensive research on the *Pyrenestes* system (e.g. Smith 1990a, 1993, 1997, Clabaut *et al*. 2009, vonHoldt *et al*. 2018) revealed that three distinct phenotypes, differing primarily in bill morphology, have evolved due to resource-driven disruptive selection within a panmictic population. Further, the genetic regions controlling these bill morphs have been identified (vonHoldt *et al*. 2018). Bill morphology disparity between the small- and large-billed morphs was found to be controlled by a single genomic region but the morphology of the mega-billed morph was controlled by a different region (vonHoldt *et al*. 2018). In this example, bill size in the small and large morphs did not scale with body size, but bill and body size was larger in the mega-billed morph (Smith 1990b). Therefore, the fact that bill size scales roughly to body size in the *Erythrura* species pair does not strongly disagree with what we know of bill polymorphism in birds. It is possible that the proposed dietary differences between *E. trichroa* and *E. papuana* in New Guinea (bamboo seeds vs. figs) represent the ecological divergence that permitted the evolution of these two forms. Compared to other islands on which *E. trichroa* occurs, New Guinea is the largest and most biologically rich, including high flora diversity and a comparatively complex and diverse avifauna. Populations of *E. trichroa* on the nearby large islands of New Britain and New Ireland, where *E. papuana* does not occur, warrant further morphological investigation.

Additional research on this system is needed to determine if morphological variation in New Guinea parrotfinches represents an example of two species undergoing sympatric speciation, two species in secondary contact following allopatric divergence, or a single species exhibiting a resource-based polymorphism. We will obtain genomic sequence data to test whether the patterns of mtDNA similarity we found here extend across the nuclear genome. We will also expand our morphometric dataset by measuring New Guinea *Erythrura* specimens housed at additional institutions. *E. trichroa* and *E. papuana* in New Guinea provide a novel system for investigating the complicated relationship between

ISSN-2513-9894 (Online)

genetic and morphological divergence, and future studies should reveal the underlying mechanisms that have resulted in the patterns we present here.

Acknowledgements

We thank all those that led or assisted in the field work that resulted in the specimens and tissue samples used in this research. Georgia Kaipu of the National Research Institute kindly facilitated research visas and numerous provincial approvals for collection of the research specimens used in this study. Dr Andrew Motu, Jim Anamiato and Bulisa Iova of the PNG National Museum supported and participated in the biodiversity inventories that made this work possible. Comments by three anonymous reviewers and copy-edits by Guy Kirwan improved this manuscript greatly. This work was supported in part by the National Science Foundation (DEB-1557053 to RGM).

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ISSN-2513-9894 (Online)