



Short Communication

The Rusty-tailed Flycatcher (*Muscicapa ruficauda*; Aves: Muscicapidae) is a member of the genus *Ficedula*

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ABSTRACT

The phylogenetic relationships of the avian family Muscicapidae (Old World chats and flycatchers) have historically been enigmatic and remain an active area of study. Widespread instances of non-monophyly resulting from misleading morphological and behavioral similarities have merited numerous taxonomic revisions to the group. Here we report one such instance with regard to the Rusty-tailed Flycatcher *Muscicapa ruficauda*, which has recently been placed in the newly proposed monotypic genus *Ripleyia*, due to inferred sister relationship to the genus *Muscicapa* and related genera (Voelker et al., 2016a). This name was later replaced by *Ripleyornis*, as it was realized that *Ripleyia* is a junior homonym of a genus of Mollusca (Voelker et al., 2016b). Using a Bayesian phylogenetic assessment of the Muscicapidae with near-complete taxon sampling of the genus *Ficedula* for five loci, along with an acoustic comparison of *M. ruficauda* to a subset of other flycatcher species, we show that this species should be reassigned to the genus *Ficedula* and accordingly that the names *Ripleyia* and *Ripleyornis* are both junior synonyms of *Ficedula*.

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1. Introduction

The Rusty-tailed Flycatcher *Muscicapa ruficauda* (Swainson, 1838) is a small seasonally migratory passerine in the family Muscicapidae (Old World chats and flycatchers) that breeds in central Asia and the western Himalayas (Rasmussen and Anderton, 2005; Taylor and Clement, 2006). Unlike other members of the genus *Muscicapa*, whose songs are inconspicuous and rarely heard, *M. ruficauda* has a prominent song (Rasmussen and Anderton, 2005). Two recent phylogenetic studies that include this species find that it is not actually a member of the genus *Muscicapa* although they make opposing claims about the true relationship of the species to other members of the Muscicapidae (Price et al., 2014; Voelker et al., 2016a).

In the first study to sequence and utilize genetic data from *M. ruficauda*, Price et al. (2014) found that it was nested within the distantly related flycatcher genus *Ficedula* rather than in

Muscicapa. As this finding was not directly related to their main results, it was not discussed within the text outright but rather left to a supplemental figure (TreeBASE Study 15660; Price et al., 2014). A recent study of the phylogenetic affinities of the genus *Muscicapa* and allies by Voelker et al. (2016a) included data from a second *M. ruficauda* individual and found that the species was basal to the other taxa considered (36 of the 42 species that comprise the Muscicapini as defined by Sangster et al., 2010; Dickinson and Christidis, 2014). Based on this observation, Voelker et al. (2016a) proposed a new genus name for *M. ruficauda*: *Ripleyia*. This genus proposal was itself subsequently revised to *Ripleyornis* following the discovery that the former was a junior homonym for a genus of Mollusca (Voelker et al., 2016b).

Here, we evaluate the legitimacy of this new genus assignment by assessing the phylogenetic affinity of *M. ruficauda* utilizing genetic data from a near-complete sampling of the genus *Ficedula* (30 of 32 species) and broad coverage of the family Muscicapidae. We pair this phylogenetic assessment with a superficial acoustic comparison of the song of *M. ruficauda* to songs of Eurasian flycatchers in the genera *Ficedula* and *Muscicapa*.

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2. Material and methods

2.1. Taxon sampling

In order to determine the phylogenetic affinities of *Muscicapa ruficauda*, we utilize genetic data from two vouchered individuals (YPM 24522 and ZMMU R-130228; Table 1), near-complete taxon sampling of the genus *Ficedula* (30 of 32 recognized species), and two members of the genus *Muscicapa*. Moreover, to ensure broad family-level coverage, we include data from 14 species representing each of the major Muscipidae clades identified by Sangster et al. (2010). A single species of the Turdidae (sister family to Muscipidae; Alström et al., 2014) was used as an outgroup.

2.2. Phylogenetic analyses

We collected sequence data from five gene regions—two mitochondrial protein coding genes: cytochrome *b* (*cytb*) and NADH dehydrogenase II (*ND2*); and three nuclear introns: intron 2 of myoglobin (*myo*), introns 6 and 7 of ornithine decarboxylase (*ODC*), and intron 9 of phosphoenolpyruvate carboxylase (*PEPCK*). Data was primarily sourced from GenBank based on sequences generated by five published studies across the family Muscipidae (Outlaw and Voelker, 2006; Sangster et al., 2010; Zuccon and Ericson, 2010; Price et al., 2014; Moyle et al., 2015) after filtering out sequences identified by Moyle et al. (2015) as being incorrectly attributed (Table 1). Genetic data for the Black-and-orange Flycatcher *Ficedula nigrorufa* were generated for this study and have been submitted to GenBank (accession numbers in Table 1). All loci

Table 1

Sampling and GenBank numbers for phylogenetic analysis. Institution abbreviations for vouchered specimens are American Museum of Natural History (AMNH), Department of Zoology, University of Gothenburg (DZUG); Field Museum of Natural History (FMNH), University of Kansas Natural History Museum (KUNHM), Naturalis, Leiden (RMNH); Louisiana State University Museum of Natural Science (LSUMNS), Swedish Museum of Natural History (NRM), University of Washington Burke Museum (UWBM), Western Australian Museum (WAM), Yale Peabody Museum of Natural History (YPM), Zoological Museum, University of Copenhagen (ZMUC), and Zoological Museum of Moscow University (ZMMU). Unvouchered specimens indicate sampling locality if known. Congeneric surrogate sequences for nuclear locus *PEPCK* were used in five instances for non-*Ficedula* Muscipidae taxa.

Species	Common name	Sample information	<i>cytb</i>	<i>ND2</i>	Myoglobin	<i>ODC</i>	<i>PEPCK</i>
<i>Brachypteryx montana</i>	White-browed Shortwing	DZUG-U3 & NRM-6739	HM633264	GU358777	GU358707	GU358835	GU358908
<i>Copsychus fulvicatus</i>	Indian Robin	DZUG-U2149 & RMNH 145771	HM633377	GU358823	GU358764	GU358894	GU358920
<i>Cosyssa archeri</i>	Archer's Ground Robin	FMNH-385022 & DZUG-U60	FN546926	FN546894	HM633563	HM633703	
<i>Cyornis tickelliae</i>	Tickell's Blue Flycatcher	LSUMNS-20551	KJ456248	KJ455400	KJ454787	KJ455768	GU358925
<i>Enicurus leschenaulti</i>	White-crowned Forktail	DZUG-U46 & NRM-6682	HM633292	GU358794	GU358726	GU358855	GU325927
<i>Erithacus rubecula</i>	European Robin	NRM-976377	AY228058	DQ466861	AY228296	GU358857	GU358928
<i>Ficedula albicilla</i>	Taiga Flycatcher	KUNHM-10388	KJ930547	KJ909987	KJ931266	KJ931293	KJ931240
<i>Ficedula albicollis</i>	Collared Flycatcher		KF293721	KF293721		AF454254	
<i>Ficedula basilanica</i>	Little Slaty Flycatcher	KUNHM-18120	KJ930548	KJ909988	KJ931267	KJ931294	KJ931241
<i>Ficedula buruensis</i>	Cinnamon-chested Flycatcher	ZMUC-133499	DQ674481	GU358797	GU358729	GU358859	
<i>Ficedula crypta</i>	Cryptic Flycatcher	KUNHM-19200	KJ930549	KJ909989	KJ931268	KJ931295	KJ931242
<i>Ficedula disposita</i>	Furtive Flycatcher	KUNHM-25324	KJ930550	KJ909990	KJ931269	KJ931296	KJ931243
<i>Ficedula dumetoria</i>	Rufous-chested Flycatcher	KUNHM-15049	KJ930551	KJ909991	KJ931270	KJ931297	KJ931244
<i>Ficedula elisae</i>	Green-backed Flycatcher	U0311		KJ952174	KJ952137	KJ952034	
<i>Ficedula harterti</i>	Sumba Flycatcher	WAM-25182	DQ674488	DQ674461			
<i>Ficedula hodgsoni</i>	Pygmy Blue Flycatcher	LSUMZ-52616	KJ930546	KJ909986	KJ931265	KJ931292	KJ931239
<i>Ficedula hyperythra</i>	Snowy-browed Flycatcher	KUNHM-15255	KJ930569	KJ910002	KJ931282	KJ931308	KJ931256
<i>Ficedula hypoleuca</i>	European Pied Flycatcher	KUNHM-15444	KJ930552	KJ909993	KJ931272	KJ931299	KJ931246
<i>Ficedula luzoniensis</i>	Bundok Flycatcher	KUNHM-20911	KJ930562	KJ930622	KJ931286	KJ931312	KJ931260
<i>Ficedula mugimaki</i>	Mugimaki Flycatcher	KUNHM-12753	KJ930553	KJ909994	KJ931273	KJ931300	KJ931247
<i>Ficedula narcissina</i>	Narcissus Flycatcher	KUNHM-15129	KJ930554	KJ909995	KJ931274	KJ931301	KJ931248
<i>Ficedula nigrorufa</i>	Black-and-orange Flycatcher	AMNH SKIN-801349	KX230115		KX230116		
<i>Ficedula parva</i>	Red-breasted Flycatcher	NRM-996601	KJ362860	EU326786	GU358731	GU358861	GU358932
<i>Ficedula platanae</i>	Palawan Flycatcher	KUNHM-12605	KJ930555	KJ909996	KJ931275	KJ931302	KJ931249
<i>Ficedula rufigula</i>	Rufous-throated Flycatcher	AMNH DOT-24622	KJ930556	KJ909997	KJ931276	KJ931303	KJ931250
<i>Ficedula sapphira</i>	Sapphire Flycatcher	NRM-67529	KJ456276	GU358800	GU358732	GU358862	GU358933
<i>Ficedula semitorquata</i>	Semicollared Flycatcher	UWBM-61130	DQ674497	DQ674470			
<i>Ficedula sordida</i>	Slaty-backed Flycatcher		EF081346				
<i>Ficedula speculigera</i>	Atlas Pied Flycatcher		AJ299688				
<i>Ficedula strophliata</i>	Rufous-gorgeted Flycatcher	KUNHM-15267	KJ930557	KJ909998	KJ931277	KJ931304	KJ931251
<i>Ficedula subrubra</i>	Kashmir Flycatcher	Jammu & Kashmir, India	KJ456278	KJ455433	KJ454804	KJ455791	
<i>Ficedula superciliaris</i>	Ultramarine Flycatcher	Jammu & Kashmir, India	KJ456279	KJ455434	KJ454805	KJ455792	
<i>Ficedula timorensis</i>	Black-banded Flycatcher	WAM-22896	DQ674487	DQ674460			
<i>Ficedula tricolor</i>	Slaty-blue Flycatcher	KUNHM-11224	KJ930558	KJ909999	KJ931278	KJ931305	KJ931252
<i>Ficedula westermanni</i>	Little Pied Flycatcher	KUNHM-19122	KJ930559	KJ910000	KJ931279	KJ931306	KJ931253
<i>Ficedula zanthopygia</i>	Yellow-rumped Flycatcher	KUNHM-10282	KJ930560	KJ910001	KJ931280	KJ931307	KJ931254
<i>Luscinia svecica</i>	Bluethroat	DZUG-U33 & UWBM-74241	HM633323	KJ455487	HM633605	HM633741	GU358939
<i>Monticola solitarius</i>	Blue Rock Thrush	FMNH-358375 & NRM-6756	KJ456346	KJ455506	GU358742	GU358872	GU358942
<i>Muscicapa griseisticta</i>	Grey-streaked Flycatcher	DZUG-U292 & UWBM-44144	HM633336	HM633336	KU192869	KU192901	
<i>Muscicapa ruficauda</i>	Rusty-tailed Flycatcher	YPM 24522	KJ456351	KJ455514			
<i>Muscicapa ruficauda</i>	Rusty-tailed Flycatcher	ZMMU R-130228	KU192808	KU192873	KU192905		
<i>Muscicapa striata</i>	Spotted Flycatcher	NRM-6170	GU237091	GU237117	KU192908	GU358875	GU358945
<i>Myiomela leucura</i>	White-tailed Robin	NRM-6748	HM633275	GU358786	GU358718	GU358846	GU358918
<i>Niltava sundara</i>	Rufous-bellied Niltava	NRM-947301	KJ456364	KJ455526	GU358753	GU358883	GU358951
<i>Oenanthe deserti</i>	Desert Wheatear	NRM-6660	GU237095	GU237121	GU358754	GU358884	GU358952
<i>Phoenicurus phoenicurus</i>	Common Redstart	NRM-6219	GU237096	GU237122	GU358757	GU358887	GU358953
<i>Saxicola rubetra</i>	Whinchat	NRM-6186	GU237097	GU237123	GU358763	GU358893	GU358958
<i>Tarsiger cyanurus</i>	Oranged-flanked Bush Robin	NRM-6746	KJ024140	KJ024204	GU358768	GU358898	GU358963
<i>Turdus obscurus</i>	Eyebrowed Thrush	NRM-6480	EU154646	AY049511	EU154757	EU154872	GU358965

were aligned with MAFFT (<http://mafft.cbrc.jp/alignment/server/index.html>) and all autapomorphic insertions in single species were identified by eye and removed from alignments.

Bayesian phylogenetic analysis was carried out in the mpi version of MrBayes v. 3.2 (Ronquist et al., 2012). Sequence data was partitioned by locus, each with its own unlinked base frequencies and variable rate prior, and assigned the optimal-fit model of sequence evolution estimated using jModelTest v. 0.1.1 (Posada, 2008). The Eyebrowed Thrush *Turdus obscurus* (Turdidae) was defined as an outgroup. Four Metropolis-coupled MCMC chains with incremental heating temperature 0.1 or 0.05 were run for 10 million generations and sampled every 1000 generations.

Convergence to the stationary distribution of the single chains was inspected in Tracer v. 1.6 (Rambaut and Drummond, 2013) and the average standard deviation of split frequencies (ASDSF) of independent runs was below 0.05 for 10 million generations. The first 20% of generations were discarded as burn-in, and the consensus tree and posterior probabilities were calculated from the remaining samples (pooled from the two simultaneous runs). In order to evaluate concordance amongst gene trees for the placement of *Muscicapa ruficauda*, we repeated the above phylogenetic analyses with topology unlinked for the three loci with genetic data for *M. ruficauda*.

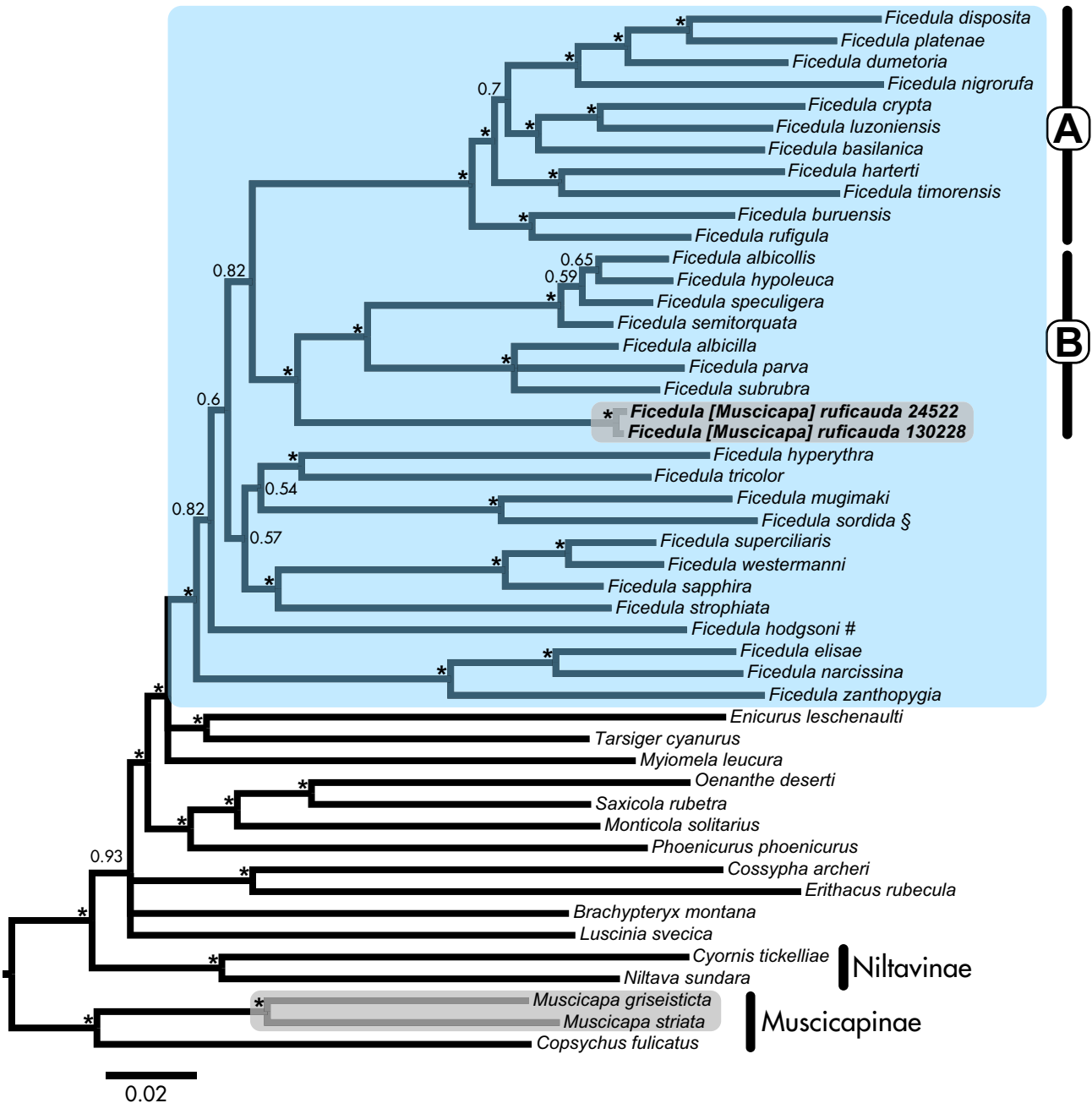


Fig. 1. Bayesian consensus tree from partitioned analysis of five loci (Table 1). Nodes with Bayesian posterior probability support ≥ 0.95 indicated by asterisks (*) and nodes with < 0.95 posterior support are shown. The Rusty-tailed Flycatcher '*Muscicapa*' *ruficauda* is shown in bold. The two samples of *M. ruficauda* and the two members of the genus *Muscicapa* sampled in this study are shaded in grey to highlight the phylogenetic distance between them. Clades discussed in the text with full posterior support are labelled (A–B). The genus *Ficedula* is boxed in blue. § The name of *Ficedula sordida* most widespread in the literature is *F. hodgsonii*; # *F. hodgsonii* is most commonly referred to as *Muscicapella hodgsonii* (cf. Zuccon, 2011).

2.3. Vocalizations

Songs of three *Muscicapa ruficauda* were obtained (one of our own from Kaghan valley, Khyber Pakhtunkhwa Province, Pakistan, and two others from Xeno-canto (www.xeno-canto.org): one more from Kaghan valley (XC19840) and the other from Himachal

Pradesh, India (XC288945). We have ample field experience with songs of nearly all continental Eurasian *Ficedula* and *Muscicapa* flycatchers. Most of the ones for which we lack personal field experience, as well as related Afrotropical flycatchers based on Voelker et al. (2016a), were sourced from Xeno-canto (www.xeno-canto.org) and AVoCet (<http://avocet.zoology.msu.edu>). Sonograms were

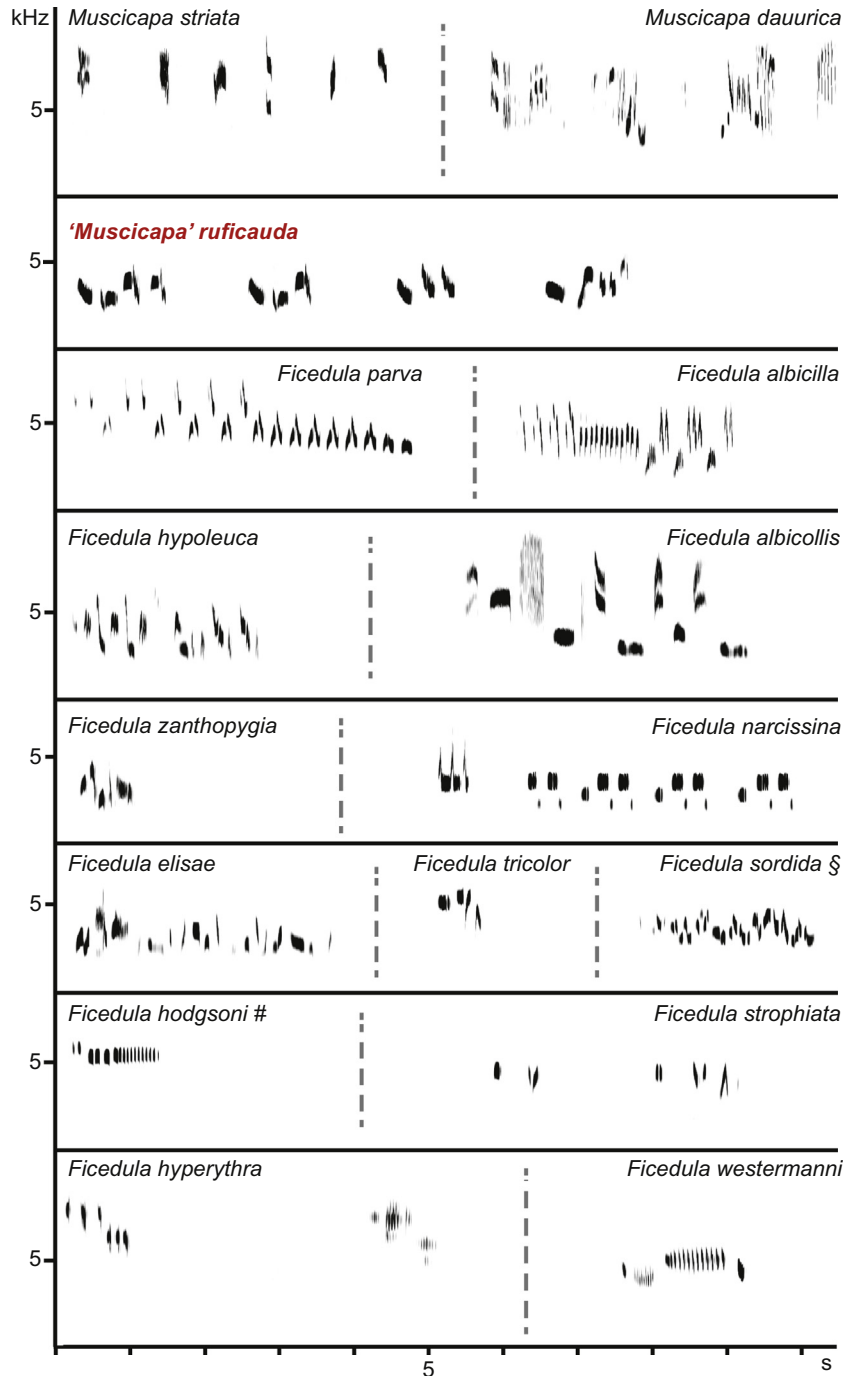


Fig. 2. Songs of *Muscicapa dauurica* Hokkaido, Japan, early June (XC286241); *Muscicapa striata* Västergötland, Sweden, early May (XC27532); '*Muscicapa*' *ruficauda*, Kaghan valley, Khyber Pakhtunkhwa Province, Pakistan, 2800 m, late May (XC307615); *Ficedula parva* Västergötland, Sweden, mid June (XC27480); *F. albicilla* Heilongjiang Province, China, mid June (XC307608); *F. hypoleuca* Västergötland, Sweden, early May (XC307609); *F. albicollis* Öland, Sweden, late May (XC27514); *F. zanthopygia* Heilongjiang, China, mid June (XC307619); *F. narcissina* Nagano prefecture, Japan, June (XC307646); *F. elisae* Shanxi, China, early June (XC307620); *F. tricolor* Sichuan Province, China, early June (XC307607); *F. sordida* (§ – formerly *F. hodgsonii*) Sichuan Province, China, mid June (XC307606); *F. hodgsoni* (# – formerly *Muscicapella hodgsoni*; cf. Zuccon, 2011) West Bengal, India, mid May (XC307614); *F. strophhiata* Sichuan Province, China, late May (XC307622); *F. hyperythra* Arunachal Pradesh, India, late May (XC307618); and *F. westermanni* West Bengal, India, mid May (XC307611). For '*Muscicapa*' *ruficauda* five consecutive strophes are shown (pauses between strophes have been artificially shortened, indicated by dots). The songs of *Muscicapa striata* and *M. dauurica* lack distinct strophes. For all *Ficedula* except *F. strophhiata* and *F. hyperythra* a single strophe is shown. For the two latter species two consecutive strophes are shown. All recordings by Per Alström, except *M. dauurica* (Peter Boesman), *M. striata*, *F. parva* and *F. albicollis* (Patrik Åberg) and *F. narcissina* (Urban Olsson).

created in Raven Pro 1.5 (Cornell Laboratory of Ornithology, Ithaca, USA) for visual inspection and visualisation of general characteristics in song structure. All of our own sound recordings used for sonograms have been deposited in Xeno-canto (cf. Fig. 2).

3. Results

3.1. Phylogenetic analyses

Evidence from our phylogenetic assessment of *Muscicapa ruficauda* strongly supports the placement of this species outside of the genus *Muscicapa*. Indeed, phylogenetic results from the partitioned data and individual gene trees in MrBayes strongly support (posterior probability 1.00) the finding of Price et al. (2014) that *M. ruficauda* is nested within the genus *Ficedula* (Fig. 1). Based on our near-complete sampling of this genus, we find that *M. ruficauda* is fully supported as sister to a Eurasian clade comprising the Collared Flycatcher *Ficedula albicollis*, European Pied Flycatcher *F. hypoleuca*, Semicollared Flycatcher *F. semitorquata*, Atlas Pied Flycatcher *F. speculigera*, Taiga Flycatcher *F. albicilla*, Kashmir Flycatcher *F. subrubra*, and Red-breasted Flycatcher *F. parva* (Fig. 1, clade B). The two *Ficedula* species missing from our analysis (Lompobattang Flycatcher *F. bonthaina* and Damar Flycatcher *F. henrici*) are Indonesian endemics and are unlikely to affect the phylogenetic affinities of *M. ruficauda*, as all other Indonesian-Philippine *Ficedula* species belong to an independent clade (Fig. 1, clade A).

3.2. Vocalizations

In our sample ($n = 3$ individuals), the song of *Muscicapa ruficauda* (Fig. 2) consisted of 3–6 (mean 3.9, $n = 18$ unique strophes) short, soft, whistled, rather low-pitched (mean bottom frequency 2279 kHz, mean top frequency 5026 kHz, $n = 18$ unique strophes) notes given in quick succession; the first note was usually at least slightly more drawn-out than the others. The strophes, which measured on average 1.0 s (0.7–1.4 s, $n = 18$ unique strophes) in length, were separated by pauses of 5–7 s (length varying, apparently depending on level of excitement). Strophes were sometimes repeated a few times, though often modified by dropping or adding one or two notes at the end.

Very few songs of *Muscicapa* were available in the databases (but many of calls). The song of the Brown Flycatcher *Muscicapa dauurica* is a thin, scratchy ramble of notes given at an irregular pace, without any distinct strophes, and that of the Spotted Flycatcher *Muscicapa striata* is weak and thin and sounds mostly like a stuttering series of call notes, without a clear structure (Fig. 2).

In contrast, most species of *Ficedula* have distinctive songs, with well-defined strophes consisting of a few to many notes, and distinct pauses between the strophes (Fig. 2). In most species, the pitch is fairly low and the songs have a whistled quality. The song of *F. hyperythra* is extremely high-pitched and thin but, as in the other congeners, it is clearly divided into strophes and pauses (Fig. 2).

4. Discussion

We find that *Muscicapa ruficauda* is well supported as a member of the genus *Ficedula* based on phylogenetic analysis, further supported by acoustic similarities. Our phylogenetic assessment of *M. ruficauda* within the context of the family Muscicapidae and near-complete sampling of the genus *Ficedula* are strongly in support of this species being a member of *Ficedula* (Fig. 1). This position is consistent with the previous findings of Price et al. (2014) based on a smaller sample of *Ficedula* species.

The song of *Muscicapa ruficauda* is more similar to songs of *Ficedula* than to *Muscicapa* flycatchers, both in structure and in tone. It is markedly different from the songs of other species of *Muscicapa*, which are renowned for being poor singers (e.g. Taylor and Clement, 2006), in agreement with our extensive field experience from the breeding grounds of most of the Asian species. It resembles songs of *Ficedula* flycatchers, which are generally proficient singers, in being regularly structured, with distinct multi-note strophes, which are repeated with some variation (representing a male's repertoire) following silent pauses. Although most *Ficedula* species have more complex songs than *M. ruficauda*, some have similarly simple or even simpler songs.

Songs in oscine birds are generally believed to have the potential to evolve rapidly, as indicated by the many closely related species with strongly differentiated songs (e.g. Alström and Ranft, 2003; Price, 2008). Although songs vary within *Ficedula* and overall similarity in any set of phenotypic traits is known to be an unreliable indicator of relationships, song characteristics support the genetic evidence that *Muscicapa ruficauda* is more closely related to *Ficedula* than to *Muscicapa*.

Muscicapa ruficauda has probably been misclassified due to its superficial plumage similarities to the *Muscicapa* flycatchers, especially the fact that it is sexually monomorphic, like all *Muscicapa* (and closely related taxa as indicated by Voelker et al., 2016a), whereas most *Ficedula* flycatchers display strong sexual plumage dimorphism. In addition to *M. ruficauda*, there are six other *Ficedula* species with sexual monomorphism or very slight dimorphism (Taylor and Clement, 2006) but these are all in clade A (Fig. 1).

5. Conclusions

Based on our results, the new genus name *Ripleyia* proposed by Voelker et al. (2016a) as well as the replacement name *Ripleyornis* (Voelker et al., 2016b) for *M. ruficauda* are artifacts of insufficient taxon sampling of the greater Muscicapidae. Accordingly, both *Ripleyia* and *Ripleyornis* are junior synonyms of *Ficedula*. In accordance with our findings, *M. ruficauda* should be included in the genus *Ficedula* and renamed as *Ficedula ruficauda*.

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