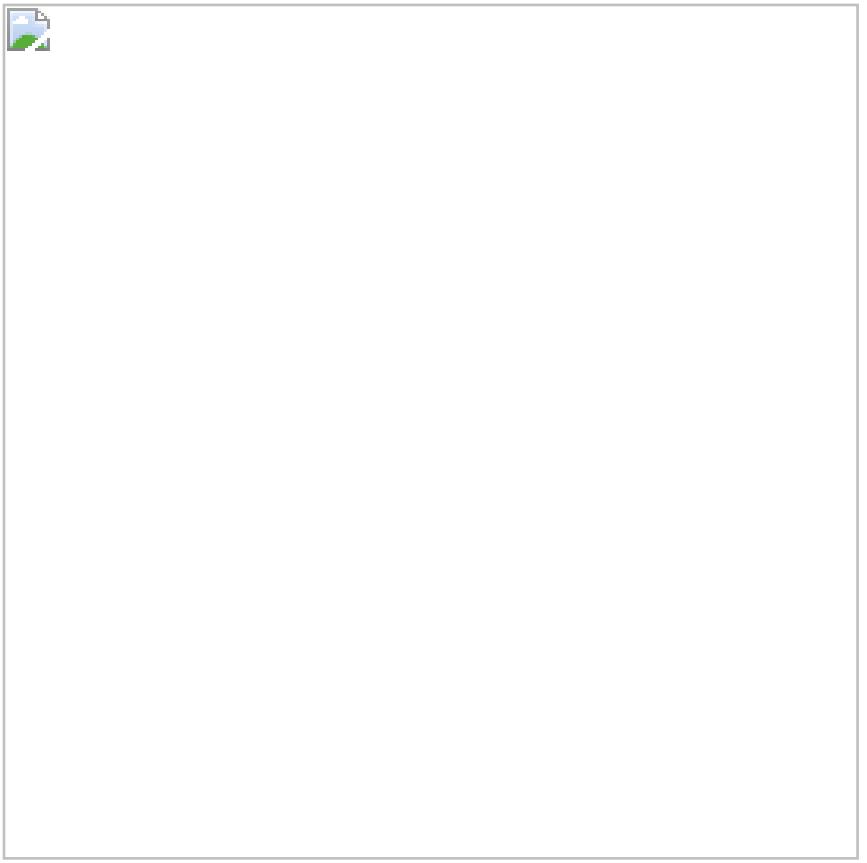

On the taxonomic status of Burmese Collared Dove Streptopelia (decaocto) xanthocycla

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On the taxonomic status of Burmese Collared Dove *Streptopelia* (*decaocto*) *xanthocycla*

by Hein van Grouw, Germán Hernández-Alonso*, Nuno F. Martins & M. Thomas P. Gilbert*

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http://zoobank.org/urn:lsid:zoobank.org:pub:837F85CB-63A9-428D-8FBB-10E98FD5D9E6

Summary.—Although described as a subspecies of Eurasian Collared Dove *Streptopelia decaocto*, the isolated Burmese population *S. d. xanthocycla* is considered to be a species by some authors, based on presumed morphological differences between the two taxa. To resolve the issue, a whole-genome resequencing-based study was conducted. The results show that Burmese *xanthocycla* can indeed be considered a separate species, and therefore that Eurasian Collared Dove is monotypic. As no type material exists for the Burmese Collared Dove, a neotype is designated for *xanthocycla* to clarify its taxonomy.

'I do not for a moment think the bird will be found worthy of specific rank, ...'
Newman (1906: 324)

In the past, many different subspecies were described for Eurasian Collared Dove *Streptopelia decaocto* (van Grouw 2022), often based on vague and inconsistent morphological characteristics. All but one are nowadays generally synonymised under *S. d. decaocto* (Fig. 1). Only the population isolated in Myanmar (former Burma)[1]—*xanthocycla*—is still accepted as a distinctive subspecies different from populations in Europe and elsewhere in Asia (Baptista *et al*. 1997, Dickinson & Remsen 2013). Besides being slightly darker overall, it has a distinctive yellow instead of greyish-white orbital ring (Fig. 2). However, based on these differences, del Hoyo & Collar (2014) split Burmese Collared Dove as a species, despite the lack of any supporting molecular evidence.

Although Oates (1883: 293) already mentioned 'eyelids and skin of face yellow', prior to the early 20th century no one else had drawn attention to the fact that Burmese birds differed in this respect from Indian ones. It was Newman (1906) who fully recognised the difference, based on a live bird in London Zoological Gardens, which he described as a new subspecies of Eurasian Collared Dove, *Turtur decaocto xanthocyclus*, for its yellow orbital ring. In October 1896 the zoo had received three individuals, presumably from the Minbu and/or Mague districts of upper Burma. One, a male, survived almost ten years in the zoo but when, around 1904, Newman's attention was drawn to it, the other two had already died. Unfortunately, despite his request that the bird be preserved as a specimen after its death, the skin was not retained as, apparently, the cadaver was heavily damaged by rats post-mortem (Newman 1906), so the holotype of *xanthocycla* no longer exists.

Minor plumage differences between *decaocto* and *xanthocycla* exist, but some populations of the former (notably those in India and Sri Lanka) are generally darker than their European

* These authors contributed equally to the manuscript.

[1] The type locality is 'Minbu or Mague District in Upper Burma, situated on the Irawady about Lat. 20' (Newman 1906), but *xanthocycla* is endemic to the Irrawaddy Valley of central and southern Myanmar, where it occurs in the dry-zone lowlands, in scrub, cultivation and open country. Some authors (e.g. Gibbs *et al*. 2001, Dickinson & Remsen 2013) have also mentioned its presence in parts of China, but we have found no evidence for that, and presumed records seem to refer to nominate *decaocto* instead.

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Figure 1 (left). Eurasian Collared Dove *Streptopelia decaocto*, South Holland, the Netherlands, 12 January 2021 (© Alois van Mingeroet)

Figure 2 (right). Burmese Collared Dove *Streptopelia xanthocycla*, Bagan, Mandalay District, Myanmar, 15 November 2013 (© Otto Samwald)

Figure 3. From left to right Eurasian Collared Dove *Streptopelia decaocto*, Sri Lanka (NHMUK 1946.28.232), Burmese Collared Dove *S. xanthocycla*, Myanmar (NHMUK 1948.80.3337) and Eurasian Collared Dove, Serbia (NHMUK 1969.3.1); although Sri Lankan (and Indian) Eurasian Collared Doves are slightly smaller than Burmese Collared Dove, their dark upperparts are almost identical, whilst European (and Chinese) Eurasian Collared Doves are paler than Burmese Collared Dove but they are similar in size or even larger (see Table 1) and the white tail tip can be even larger (Jonathan Jackson, © Trustees of the Natural History Museum, London)

counterparts, and thus look more like *xanthocycla* (Fig. 3). Also, *decaocto* can exhibit a slight yellowish hue to the orbital ring (Swinhoe 1870: 446; HvG pers. obs.). The tail of *xanthocycla* is considered longer than in *decaocto*, with the result that the outer rectrices were believed to show equivalently more white (del Hoyo & Collar 2014: 162). The *decaocto* specimens used in the comparison originated from north-east India (N. J. Collar *in litt*. 2024) and are indeed smaller and slightly shorter tailed, but Eurasian Collared Doves in China and Europe are similar in size to *xanthocycla* or even longer tailed. Tail length, therefore, in Burmese doves

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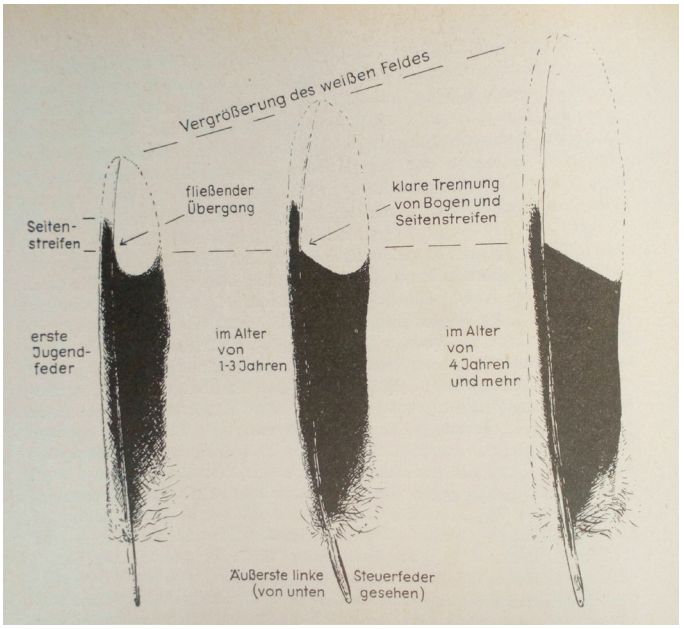

Figure 4. Fig. 1 in Lachner (1965), demonstrating the increase with age in the amount of white in the outer tail feathers in male Eurasian Collared Dove *Streptopelia decaocto*; in doves four years or older (right) the black in the outer web is strongly reduced whereas the white part and the feather as a whole have significantly increased in length (Hein van Grouw)

Figure 5. Outer tail feathers moulted in four successive years by a male Eurasian Collared Dove *Streptopelia decaocto*, hatched in 1998 and captive bred by HvG; the increase in length and the amount of white as the bird got older is clear (Hein van Grouw)

does not average longer than that of *decaocto* throughout its range (see Table 1). Also, in adult Eurasian Collared Doves, especially males, the tail grows longer over the first four years of life (Lachner 1965; HvG pers. obs.), so that males four years and older have significantly longer tails than those in their first to third years (Figs. 4–5). Also, it is the white tip that increases in length, resulting in the outer tail feathers showing equivalently more white as the

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TABLE 1
Measurements of Burmese Collared Dove *Streptopelia xanthocycla* and different populations of Eurasian Collared Dove *S. decaocto*.

Streptopelia xanthocycla (Myanmar, males)		
Reg. no.	**Wing (mm)**	**Tail (mm)**
NHMUK 1948.80.3333 *	181	145
NHMUK 1948.80.3334	179	146
NHMUK 1948.80.3335	186	151 **
NHMUK 1948.80.3338	185	142
NHMUK 1948.80.3340	175	141
NHMUK 1948.80.3341	180	141
NHMUK 1908.5.30.33	181	142
Mean of seven adult males	**180**	**144**
Streptopelia decaocto (Assam/Bengal, males)		
NHMUK 1898.2.2.1508	175	130
NHMUK 1898.2.2.1509	171	137
NHMUK 1898.2.2.1510	169	137
NHMUK 1898.2.2.1511	177	135
NHMUK 1898.2.2.1513	168	130
NHMUK 1949.Whi.1.1877	168	134
NHMUK 1949.Whi.1.1878	177	134
Mean of seven adult males	**172**	**134**
Streptopelia decaocto (China, males)		
NHMUK 1908.1.2.46	179	142
NHMUK 1908.1.2.47	177	144
NHMUK 1908.1.2.51	180	135
NHMUK 1908.1.2.52	179	145
NHMUK 1889.3.2.105	185	151
NHMUK 1902.8.5.89	180	138
NHMUK 1907.12.17.414	181	144
Mean of seven adult males	**180**	**143**
Streptopelia decaocto (Europe, males)		
Bodenstein (1950) (Germany)	176–185	140–149
Korneisl-Ruckner (1957) (Serbia)	169–185	136.0–157.5
Niethammer (1962) (Germany)	172–184	130–153

* Neotype (Fig. 12).

** Probably a bird more than four years old and therefore with a significantly longer tail (see also Fig. 12).

Figure 6. The black-and-white tail pattern of Burmese Collared Dove *Streptopelia xanthocycla* (pictured) is identical to Eurasian Collared Dove *S. decaocto* (compare Figs. 4–5) and the increase in length and the amount of white with age appears to be also present in Burmese Collared Dove; from left to right, juvenile male (NHMUK 1948.80.3330), adult male presumably younger than four years (NHMUK 1948.80.3333, neotype, see Fig. 12), and adult male presumably at least four years old (NHMUK 1948.30.3335) (Jonathan Jackson, © Trustees of the Natural History Museum, London)

dove gets older. There is no reason to believe that the same is not true of *xanthocycla* (Fig. 6). So, if compared with nominate *decaocto* throughout its range, there is no significant difference in size or in the amount of white in the tail.

Song can differ among individual male *xanthocycla*, some of which have a two-note strophe of which the first is emphatic and clipped, and the second note falling and drawn-out, whilst others 'coo' a three-note strophe (https://birdfinding.info/burmese-collared-dove/, accessed 7 March 2024). The latter differs only slightly from the three-note strophe of *decaocto*, with the same rhythm and structure but higher pitched at the start, with the two following notes successively lower pitched, creating a greater cadence (del Hoyo & Collar 2014). Differences between individual *decaocto* males in the height of the notes and the speed of delivery are also not uncommon, and males with a two-note song are known (Slabbekoorn 1998; HvG pers. obs.). The typical call, more like a human cry, in flight is unique to Eurasian Collared Dove. None of the related *Streptopelia* species, or as far as we are aware any other pigeon species, calls in flight. Burmese doves, however, also call in flight (Smith 1943: 251) and their call

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Figure 7. The only significant visible difference between Eurasian Collared Dove *Streptopelia decaocto* and Burmese Collared Dove *S. xanthocycla* is the latter's bright yellow orbital ring, which is clearly visible even at a distance; Bagan, Mandalay, Myanmar, 3 January 2017 (© Nick Athanas)

does not differ from *decaocto*. Overall, other than the bright yellow orbital ring (Fig. 7), morphological differences between them appear insignificant, and therefore a molecular study to clarify the taxonomy was necessary. The results are presented herein.

Methods

DNA extraction and quantification.—Three *Streptopelia decaocto xanthocycla* dry toepad samples from the Natural History Museum, Tring, were analysed. The samples date from between 1905 and 1936 and were collected in central Myanmar; NHMUK 1908.5.30.32, female, 30 December 1905, Monywa, Lower Chindwin (= Monywa District); NHMUK 1948.80.3335, male, 26 July 1936, Kondau (= Meiktila District); NHMUK 1948.80.3340, male, 6 February 1932, Shwebo (= Swebo District). For DNA extraction and preparation for sequencing, toepads were digested whole in a PCR-free laboratory dedicated to ancient DNA processing at the Globe Institute, Univ. of Copenhagen. We followed the extraction method described by Campos & Gilbert (2012). More specifically, we washed the samples with a 1 ml 7% diluted commercial-strength bleach solution, followed by washing with 1 ml 70% ethanol, and finally rinsing with two rounds of molecular-grade water. The samples were then submerged in 1 ml extraction buffer for overnight digestion at 56°C. Afterwards, DNA was recovered using a modified binding buffer and MinElute silica columns (Qiagen) and eluted in a final volume of 42 µl of EBT. Extract concentration was measured using a Qubit (ng/µl). An extraction blank was included to control for any possible contamination.

Genomic library building and sequencing.—Illumina libraries were constructed following the Santa-Cruz Single Stranded Reaction (SCR) protocol (Kapp *et al*. 2021) with a final volume of 42µl of EBT. Libraries were amplified using Q5U Hot Start High-Fidelity DNA Polymerase (New England Biolabs Inc). Amplified libraries were purified using MinElute silica columns (Qiagen), were eluted in 40µL of EBT, and quantified using the Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Inc) and 2100 BioAnalyzer (Agilent). Finally, samples were sequenced on an

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Illumina NovaSeq using 150bp PE sequencing at Novogene UK's commercial facility. The generated raw sequence reads have been deposited at the European Nucleotide Achieve (ENA) and can be accessed at Project ID PRJEB71607.

Dataset.—In addition to the three newly re-sequenced *xanthocycla* genomes, the final dataset included public available reference whole genomes of seven African Collared Doves *S. risoria*, seven Eurasian Collared Doves *S. decaocto* (for details see van Grouw *et al*. 2023), one Band-tailed Pigeon *Patagioenas fasciata* used as an outgroup (Murray *et al*. 2017) and (for mtDNA analyses) the whole mitochondrial genome of Oriental Turtle Dove *S. orientalis* (KY827037.1) (Table S1).

Data processing.—Whole-genome sequence reads were mapped to the *S. turtur* reference genome (bStrTur1.1; Dunn *et al*. 2021) using the BAM pipeline as implemented in PALEOMIX v.1.2.13.4 (Schubert *et al*. 2014). The different BAM pipeline steps include (1) trimming sequencing adapters using AdapterRemoval v.2.2.0 (Schubert *et al*. 2016) with default parameters; (2) alignment of the sequence reads to the reference genome using the backtrack algorithm in BWA v.0.7.17 (Li & Durbin 2009), disabling the use of a seed parameter, discarding unmapped reads, and applying a map quality filter of 30; (3) removing PCR duplicates using Picard MarkDuplicates (https://github.com/broadinstitute/picard), and (4) local realignment around indels using IndelRealigner module in GATK v.3.8.3 (McKenna *et al*. 2010).

To assess the substitution patterns and the level of DNA damage in the historical *xanthocycla* sequence reads mapDamage v.2.0.9 (Jónsson *et al*. 2013) was used with the default parameters. The sequences showed low levels of the cytosine deamination that is typical to ancient or historical DNA as a result of post-mortem damage, thus overall indicating good DNA preservation in the samples (Table S2).

Sex identification.—The biological sex of the *xanthocycla* specimens was confirmed by comparing the Z sex chromosome depth of coverage and the mean coverage of the autosomal chromosomes. If the Z sex chromosome depth of coverage was similar or higher than the mean coverage of the autosomal chromosomes the specimen was identified as male, but if the Z sex chromosome depth of coverage was approximately half the mean coverage of the autosomal chromosomes it was identified as female (Table S2).

Maximum likelihood phylogenetic analyses.—To explore the evolutionary relationships between *xanthocycla* and the other samples, two phylogenetic analyses were performed using the whole mitochondrial genome and nuclear genome sequences, respectively. To estimate the whole mitochondrial genome phylogeny, sequence reads were first mapped to the *S. decaocto* mitogenome (NC_037513.1) using PALEOMIX v.1.2.13.4 as described above. Then, the alignment files were used to generate consensus sequences per sample using the '-dofasta2' function in ANGSD v.0.937 (Korneliussen *et al*. 2014). All mitochondrial genome consensus sequences were aligned using the global pair iterative method as implemented in MAFFT v.7.515 (Katoh & Standley 2013). Finally, a maximum likelihood (ML) phylogeny was estimated under the GTR (generalised time reversible) + G model using RAxML-ng v.1.2.0 (Kozlov *et al*. 2019). The Oriental Turtle Dove mitochondrial genome was included as an outgroup in the analysis.

To infer a nuclear genome phylogeny, genomic consensus sequences were generated using ANGSD v.0.937 ('-dofasta2' function) and the *S. turtur* as reference genome. Subsequently, 1,000 non-overlapping random regions of 2,000 bp were selected from the reference genome using the '*random*' function in BEDTools v.2.30 (Quinlan & Hall 2010) to estimate 1,000 independent ML phylogenetic trees in RAxML-ng v.1.2.0 under the GTR+G evolutionary model. A species tree was inferred by summarising all the independent gene trees using ASTRAL-III (Zhang *et al*. 2018). The mitochondrial and nuclear genome phylogenetic trees were visualised using the Tree Of Life (iTOL) v4 online tool (Letunic & Bork 2019).

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Dimensionality reduction analyses.—To explore population structure among the samples in the dataset and visualise their genetic distances, a principal components analysis (PCA) and a multidimensional scaling (MDS) analysis were performed on different genomic variant datasets. First, a single nucleotide polymorphism (SNP) dataset was created using ANGSD v.0.937 '-dohaplocall 1' function by randomly sampling one read per site and retaining the base that satisfies the implemented filter parameters (-minMinor 2, -maxMis 3, -minMapQ 30, -minQ 20, -uniqueOnly 1, -remove_bads 1, -only_proper_pairs 1, -skipTriallelic 1, -doMajorMinor 1). SNP sampling was restricted to scaffolds with more than 1 Mb length, and transitions were discarded to avoid incorporating noise derived from miscoding lesions caused by deamination of the DNA as typically found in historical samples. After applying a MAF filter to discard sites with a minor allele frequency below 0.01 using Plink v.1.9.0 (Chang *et al*. 2015), the final SNPs database contained 1,568,831 transversion sites. As next steps, the SNP dataset was used to estimate pairwise identity-by-state (IBS) genetic distances between all the samples excluding the outgroup. Subsequently the genetic distance matrix was used to estimate a MDS analysis with Plink v.1.9.0.

Genotype likelihoods were estimated to perform a PCA using ANGSD v.0.937 with the parameters -GL 2, -doGlf 2, -doMajorMinor 1, -doMaf 2, -doCounts 1, -SNP_pval 1e-6, -rmTrans 1, -minQ 20, -minmapq 30, -setMinDepth 3. Then, a covariance matrix was calculated using PCAngsd v.1.10 (Meisner & Albrechtsen 2018). Finally, the eigenvalues estimation and plotting were generated in R.

Estimated effective migration surface (EEMS).—The software EEMS (Petkova *et al*. 2016) was implemented to explore the population structure and gene flow patterns of *decaocto* and *xanthocycla* in the context of their geographic distribution, allowing us to detect potential barriers or corridors between populations. Sites with missing data were removed from the SNPs dataset. EEMS was implemented using the parameters: nIn-div = 10, nSites = 1,111,540, nDemes = 200, diploid = false, numMC-MCIter = 2,000,000, numBurnIter = 1,000,000, numThinIter = 9999. Finally, the results were visualised using the R package reemsplots2 (https://github.com/dipetkov/reemsplots2).

Weighted pairwise fixation index (F_{st}).—The genetic differentiation between *xanthocycla* and other *decaocto* populations was measured by estimating the weighted pairwise F_{st} in Plink v.1.9 using the previously generated SNPs dataset. Populations per geographic region were defined, each one including three samples: *xanthocycla* (BCD-01, BCD-02, BCD-03), Indian *decaocto* (ECD-01, ECD-02, ECD-03), Arabian *decaocto* (ECD-04, ECD-05, ECD-06) and Arabian *risoria* (ACD-10, ACD-11, ACD-12). The *risoria* samples (classified as the former subspecies *arabica* from the Arabian Peninsula) were included to measure their genetic differentiation from *decaocto* populations, due to the results obtained from the PCA and MDS (Figs. 5, S1) that suggest affinity between these two species.

Admixture analyses.—To test possible admixture between *decaocto* and *risoria* suggested by the observed population structure patterns in the PCA and MDS results (Fig. 8), as well as by the obtained weighted pairwise F_{st} values (Table 2), we implemented *D*-statistics tests and estimated admixture graphs using TreeMix v.1.13 (Pickrell & Pritchard 2012). *D*-statistics was implemented in ADMIXTOOLS v.7.0.2 (Patterson *et al*. 2012) using the SNPs dataset. The tests were conducted in the form *D* (*Patagioenas fasciata*, *risoria*; *decaocto*, *xanthocycla*) where *Patagioenas fasciata* was used as an outgroup and the *risoria* and *xanthocycla* samples were grouped into single populations. Each *decaocto* sample was tested independently. If the *D*-value is higher than 0, it indicates possible gene flow between *risoria* and *xanthocycla*, whilst *D*-values less than 0 indicate gene flow between *risoria* and *decaocto*. Deviations from 0 were considered statistically significant if Z-score was ≤-3 or ≥3. Z-score was estimated using weighted block jackknife procedure over 1 Mb blocks.

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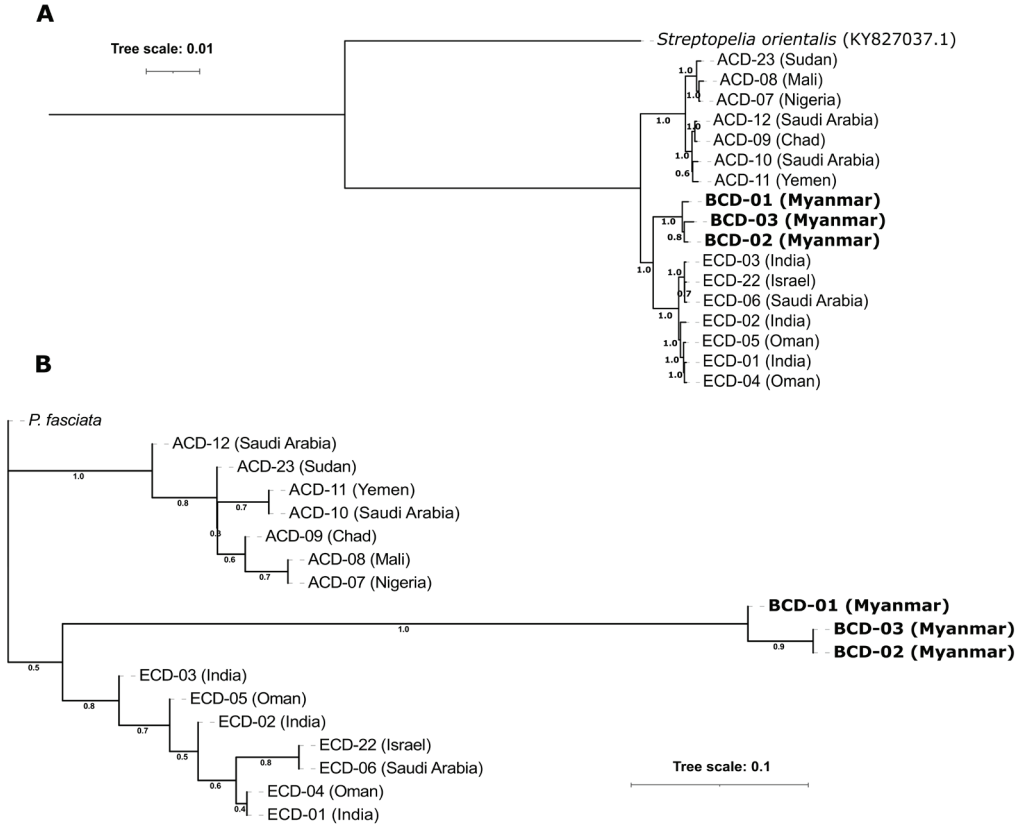

Figure 8. Estimated phylogenetic trees. (A) Maximum likelihood (ML) whole mitochondrial genome phylogeny. Oriental Turtle Dove *Streptopelia orientalis* was used as an outgroup. (B) Species tree based on 1,000 independent ML trees generated from random nuclear genome regions. Bootstrap values shown next to internal nodes. Burmese Collared Dove (BCD) *S. xanthocycla* samples in bold.

TABLE 2

Weighted pairwise F_{st} values. For an even comparison, three samples were used to define each population: (1) *Streptopelia xanthocycla*; (2) *S. decaocto* from India (ECD-01, ECD-02, ECD-03); (3) *S. decaocto* from the Arabian Peninsula (ECD-04, ECD-05, ECD-06); and (4) S. *risoria* from the Arabian Peninsula formerly classified as the *arabica* subspecies (ACD-10, ACD-11, ACD-12).

	xanthocycla	***decaocto* (India)**	***decaocto* (Arabia)**	***risoria* (Arabia)**
xanthocycla	/			
decaocto (India)	0.298259	/		
decaocto (Arabia)	0.298194	0.00691106	/	
risoria (Arabia)	0.378685	0.203463	0.204862	/

TreeMix admixture graphs were estimated using sites without missing data in our SNPs dataset. The *risoria* and *xanthocycla* samples were grouped into single populations whilst *decaocto* was grouped into populations based on their geographic origin (India, Arabia and Israel). The analyses were estimated for 0–2 migration events and grouping SNPs in windows of 500. Ten replicas were performed and those graphs with the best likelihoods were selected.

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Results

We generated genome sequencing data from three historical *xanthocycla* samples to a mean depth of nuclear genome coverage spanning *c*.3.8–6.4X, yielding mitochondrial genome coverage between 363X and 498X (see Table S2). The phylogenetic analyses show that *xanthocycla* forms a monophyletic group sister to *decaocto*, whilst the *risoria* clade is sister to the other two, as expected (Fig. 8). Interestingly, the *xanthocycla* clade presents a long branch in the species tree, indicating clear divergence (Fig. 7B). On the other hand, the population structure observed in the PCA plot (Fig. 9) shows that *xanthocycla* is differentiated from *decaocto* along principal component (PC) 2, and *risoria* from *decaocto* and *xanthocycla* along PC1 which represents 22.1% of the total variation. The distance along the

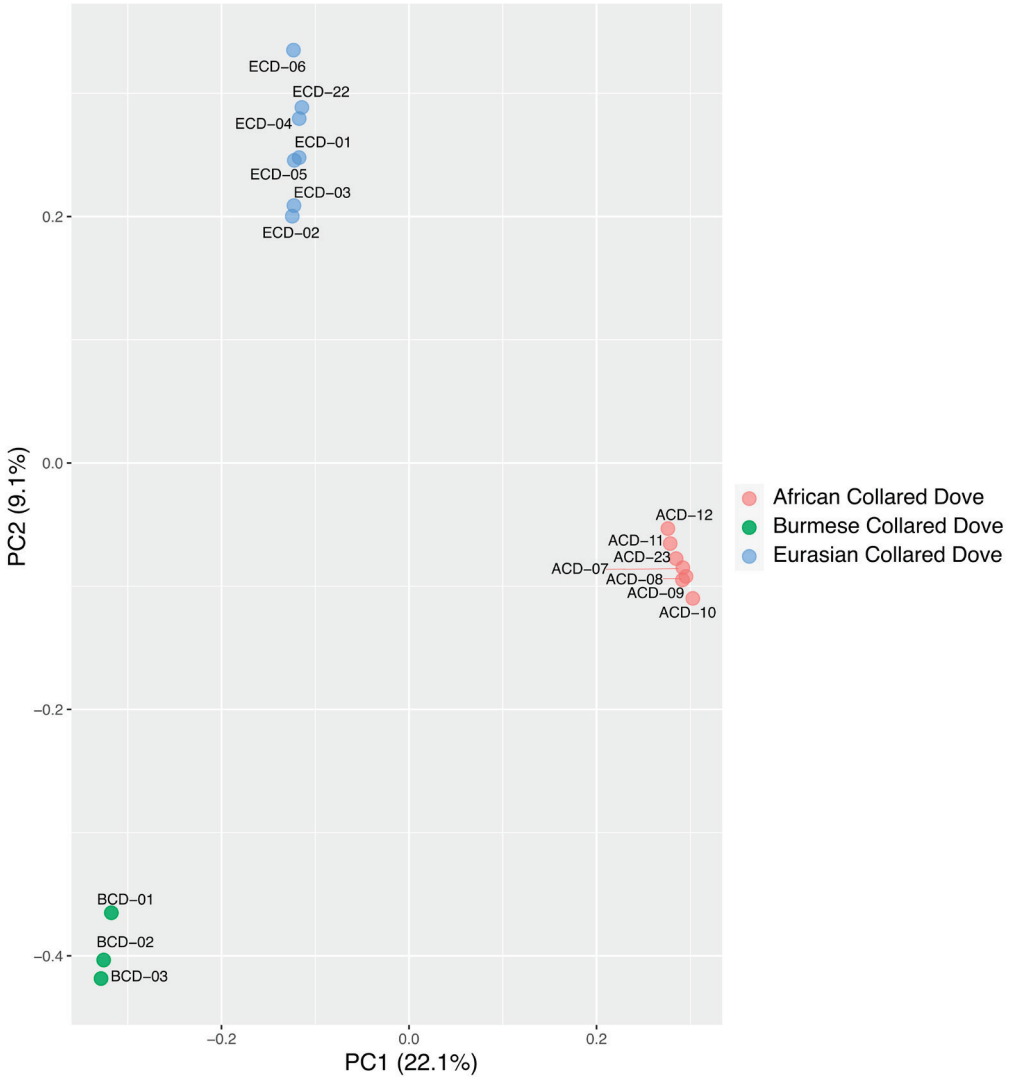

Figure 9. Principal component analysis (PCA) based on estimated genotype-likelihoods: the plot shows the population structure among African Collared Dove *Streptopelia risoria* (ACD), Eurasian Collared Dove *S. decaocto* (ECD) and Burmese Collared Dove *S. xanthocycla* (BCD). Principal component (PC) 1 explains 22.1% of the total variance in the dataset, whilst PC2 explains 9.1%.

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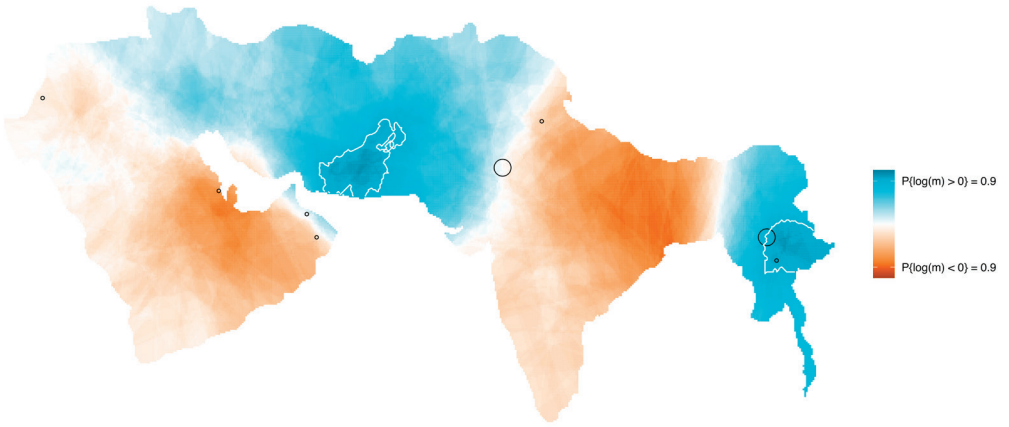

Figure 10. Effective migration rates estimated for Eurasian Collared Dove *Streptopelia decaocto* (ECD) and Burmese Collared Dove *S. xanthocycla* (BCD) populations. The plot represents the posterior log mean migration rate with the 95% confidence interval indicated by the polygons outlined white. Colours indicate higher migration rates than the average (blue), lower rates than the mean (orange), and in white the mean migration rate under a model of isolation by distance. Circles show the sample's geographic locations; small circles represent a single sample and big circles two samples per site.

PC1 between *decaocto* and *risoria* suggests that these two clusters are more closely related, possibly due to admixture. Similar patterns are observed in the MDS results (Fig. S1).

Effective migration rates estimated with EEMS suggest that *xanthocycla* is isolated from *decaocto* by a probable gene flow barrier in north-east India and Bangladesh (Fig. 10). The main biome in this region is tropical moist broadleaf forest, which potentially acts as a barrier between their populations. The same analysis suggests a gene flow corridor in southern Iran and Pakistan indicating probable connectivity between *decaocto* populations in Arabia and South Asia via the Gulf of Oman and Strait of Hormuz. The isolation of *xanthocycla* and genetic differentiation was later confirmed via the obtained weighted F_{st} values (Table 2). When *xanthocycla* was compared to *decaocto*, F_{st} was 0.29, indicating a high level of differentiation. When *decaocto* populations were compared to each other, F_{st} values obtained were low (F_{st} = 0.006) indicating a high level of gene flow. Unexpectedly, the F_{st} values obtained by comparing *decaocto* populations and *risoria* from Arabia were lower (F_{st} = 0.2) than when comparing *xanthocycla* and *decaocto*. This result agrees with the population structure observed in the PCA and MDS plots (Figs. 9 and S1), wherein *decaocto* seems closer to *risoria*.

Finally, we explored whether admixture between *decaocto* and *risoria* could explain these results. The *D*-statistics tests revealed clear signals of admixture between *risoria* and *decaocto* (Fig. 11A). When the *decaocto* samples from Arabia are tested, the admixture signals are stronger than the admixture signals obtained from *decaocto* in India. Similarly, the TreeMix graphs estimated for 1 and 2 migration edges (Fig. 11B–C) show stronger gene flow signals between *risoria* and *decaocto* from the Levant and Arabia, but also reveal a weaker signal between *risoria* and *decaocto* from India (Fig. 11C). We believe it is probable that admixture between *decaocto* and *risoria* occurred in Arabia, which both species inhabit, whilst the observed admixture signals in Indian *decaocto* can be explained by contact with Arabian Peninsula *decaocto*.

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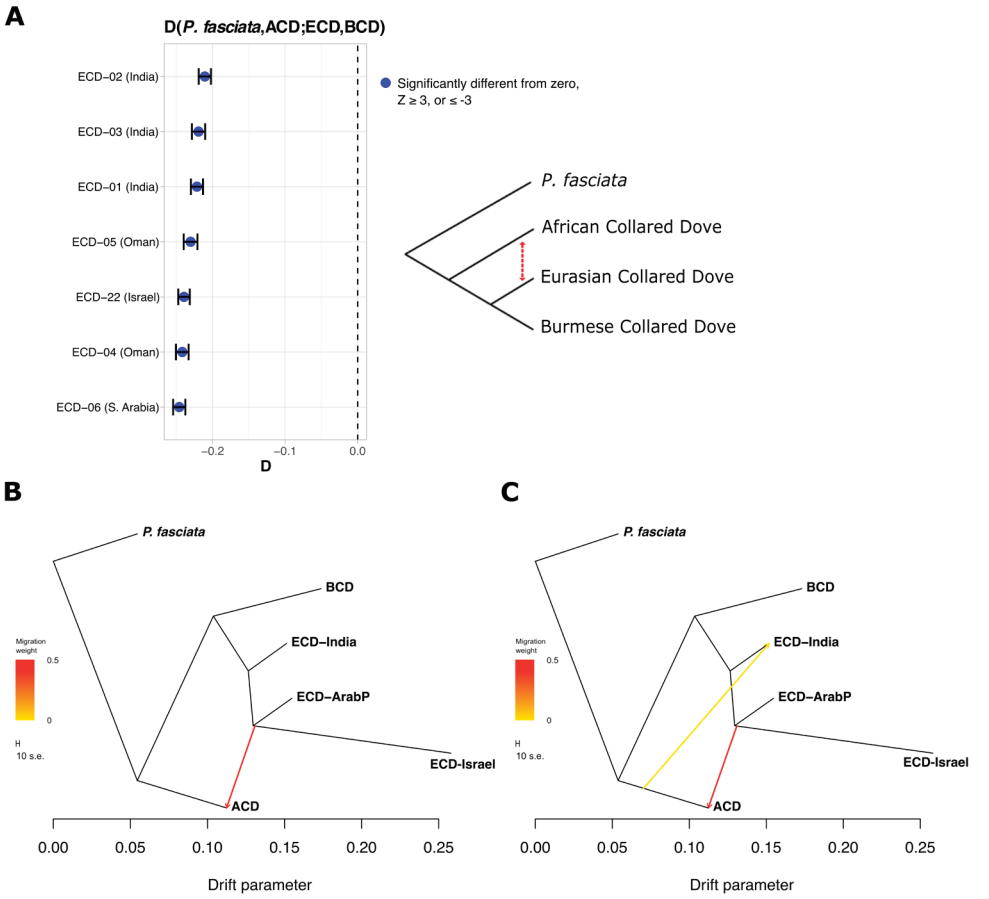

Figure 11. Admixture assessment between African Collared Dove *Streptopelia risoria* (ACD) and Eurasian Collared Dove *S. decaocto* (ECD). (A) *D*-statistics testing the tree topologies shown in Fig. 8. African Collared Dove and Burmese Collared Dove *S. xanthocycla* (BCD) samples were grouped in single populations. Band-tailed Pigeon *Patagioenas fasciata* was used as an outgroup. Horizontal bars represent the estimated three standard errors. Tests with Z-score >3 were considered statistically significant. (B–C) Admixture graphs estimated by TreeMix for one and two migration edges respectively. The arrows represent admixture events and the colours indicate the intensity of the estimated admixture. Eurasian Collared Dove samples were grouped into populations according to their geographic origin (India, Arabian Peninsula and Israel).

Conclusions and Discussion

Our molecular analysis indicates that, as a result of long isolation from Eurasian Collared Dove, Burmese Collared Dove is sufficiently differentiated to warrant consideration as a separate species. Both are sister to African Collared Dove. No admixture was identified between Eurasian and Burmese Collared Dove, probably because neither species occurs naturally in the other's range. Admixture between populations of African Collared Dove and Eurasian Collared Dove from the Arabian Peninsula has occurred (see van Grouw *et al*. 2023).

Like Eurasian Collared Dove, within its isolated range Burmese Collared Dove prefers open dry areas and human settlements. Currently, the only natural barrier separating them is the tropical moist broadleaf forests of north-east India and Bangladesh. If this forest is reduced then it is possible that Eurasian Collared Dove will expand into the range

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Figure 12. Neotype of *Streptopelia xanthocycla*, NHMUK 1948.80.3333, male, 22 December 1936, Mandalay District, Burma, collected by H. C. Smith (Jonathan Jackson, © Trustees of the Natural History Museum, London)

of Burmese Collared Dove, given the former's propensity for opportunistic expansion. Furthermore, a possible future introduction of Eurasian Collared Dove into Myanmar by humans is quite likely. Examples of how invading Eurasian Collared Doves on the Canaries and in Florida have genetically diluted or even wiped out local populations of feral African Collared Dove (van Grouw 2022) offer little hope for Burmese Collared Dove under either scenario. Currently, Burmese Collared Dove is listed as Least Concern on the IUCN Red List (2024). Hybridisation with Eurasian Collared Dove, however, should be considered a serious threat in the future.

Given the threat of admixture with *decaocto* and the lack of any extant type material for *xanthocycla* (Newman 1906), a neotype for the latter is assigned herein (Fig. 12). Designation of a neotype is regulated under Art. 75.3 of the *International code of zoological nomenclature* (1999) which states that only if there is an exceptional need should a neotype be designated. The need for a neotype is the threat of admixture with *decaocto* in the future. By designating a neotype, we help to clarify the taxonomic status of Burmese Collared Dove (Art. 75.3.1). We have already mentioned the phenotypical (orbital ring colour) and genotypical characters differentiating *xanthocycla* from its closest relative *decaocto* (Art. 75.3.2 and 75.3.3). Because *xanthocycla* was described from a live bird that was not preserved as a specimen (Newman 1906), Art. 75.3.4 is satisfied. The neotype is of the same life stage and sex (Art. 75.3.5) as the lost holotype, is roughly from the same type locality (Art. 75.3.6) and is housed in NHMUK (Art. 75.3.7).

Based on the above, and to our knowledge, the conditions in Art. 75.3 of the *International code of zoological nomenclature* (1999) apply, and we assign neotype status to the following specimen: NHMUK 1948.30.3333, an adult male collected on 22 December 1936 in Mandalay District, Burma (= Myanmar), by H. C. Smith.

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This results in the following sequence: *Streptopelia xanthocycla* (Newman, 1906). Type specimen NHMUK 1948.30.3333 (neotype designation herein). Synonym: *Turtur decaocto xanthocyclus* Newman, 1906.

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Figure S1. Multidimensional scaling (MDS) plot to explore population structure among Burmese Collared Dove *Streptopelia xanthocycla* (BCD), Eurasian Collared Dove *S. decaocto* (ECD) and African Collared Dove *S. risoria* (ACD). MDS analysis was based on the SNPs dataset.

Figure S2. Extended TreeMix admixture graph and residual plots related to Fig. 7B–C. (A) TreeMix graph for 0 migration edges and its residual plot representing the residual fit from the estimated pairwise likelihoods. The scale bar indicates ten times the mean standard error. Higher values indicate close related pairs of populations that could have admixed but are not present in the best-fit modelled tree. (B–C) Residual plots of the TreeMix graph estimated for one and two migration edges.

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