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RESEARCH

Towards more comprehensive population genetics of European Turtle Doves: microsatellite markers and cytochrome *b* from across the distribution range

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Abstract
The European Turtle Dove *Streptopelia turtur* has experienced a significant decline in population size since the 1980's, leading to its vulnerable status according to the IUCN Red List of Threatened Species. This species is an intercontinental migrant using different flyways from its breeding grounds towards its wintering grounds in sub-Saharan Africa. While habitat loss and hunting are known to pose significant threats, understanding the genetic structure of Turtle Dove populations is crucial to recommend effective conservation measures. So far, only two studies investigated population genetics in Turtle Doves with partly contradictory conclusions. We aimed to gain deeper insights by using microsatellites as an additional genetic marker as well as extending the dataset of mitochondrial DNA (cytochrome *b*) sequences to breeding regions that have not or very little been examined yet. In line with previous studies, we found no link between migratory flyways and genetic population structure, indicating a weak migratory connectivity. However, we found evidence for some genetic variability among certain breeding regions which explained 3% of the overall variability. Remarkably, birds from Egypt from the subspecies *S. t. rufescens* showed no significant differentiation to European Turtle Doves belonging to the nominate subspecies *S. t. turtur*. In contrast, Turtle Doves from Morocco (*S. t. arenicola*) as well as individuals from the more eastern distributions (Ukraine and Azerbaijan) were genetically the most differentiated compared to central European individuals. Genetic divergence within *S. t. turtur* tends to increase in further eastern distribution areas. Simultaneous research regarding tracking and population genetic studies are necessary for breeding birds in eastern European and Asian regions to better understand genetic diversity and behaviour and improve conservation efforts across the entire species range.

Keywords Population genetics · European Turtle Dove · Microsatellites · Cytochrome *b*

Introduction

Despite being widely distributed in the western Palearctic with 2.9–5.6 million breeding pairs in Europe (European Commission 2018), the European Turtle Dove *Streptopelia turtur* (hereafter Turtle Dove) is listed vulnerable by the IUCN since 2015 due to a long-term demographic decline (BirdLife International 2017). The European population size is estimated to have decreased by around 79% between 1980 and 2014 (European Commission 2018) with the most drastic changes in the northern edges of the breeding distribution area (Schumm et al. 2023). Habitat loss and hunting are considered the main threats for this species (European Commission 2018). Although hunting for Turtle Doves is predominantly practiced in the Mediterranean area, it can affect the whole European population due to the migration behaviour of the species (Marx et al. 2016). The Turtle Dove is a long-distance migrant wintering in sub-Saharan Africa using several flyways to minimize over-sea flying (Glutz von Blotzheim and Bauer 1994). Ring recovery and tracking

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studies revealed two main European migration routes: 1) the western flyway includes France, the Iberian Peninsula and Morocco; and 2) the Balkan countries, Italy, Malta, Libya, Greece and Egypt are part of the central/eastern flyway (Eraud et al. 2013; Marx et al. 2016; Schumm et al. 2021). A differentiation in migration routes can result in intraspecific genetic divergence between populations (Rolshausen et al. 2009; Delmore et al. 2016). Identifying the genetic structure within a species does not only give insights into its evolutionary background, it is a crucial step for successful conservation management (Younger et al. 2017; Funk et al. 2012). Knowledge of the Turtle Dove's population genetics is still very limited.

So far, two studies analysed the relationship between different flyways and population structure in Turtle Doves (Calderón et al. 2016; Prakas et al. 2021). Calderón et al. (2016) used mitochondrial DNA (cytochrome *b*) and genomic markers (SNPs) to examine the genetic structure of Turtle Doves from eight European countries. The cytochrome *b* (cyt *b*) sequences revealed two haplogroups separated by six mutational steps. However, genetic clusters that fit to the flyways of Turtle Doves could not be observed which led to the assumption of a panmictic population that might be caused by a weak migration connectivity (Webster et al. 2002) and a recent population expansion. Using cyt *b* and D-loop sequences, Prakas et al. (2021) found similar haplogroups showing no linkage to the migration routes. Genetic divergence between certain populations could, however, be detected. Especially birds from Morocco and the Ukraine were genetically the most distinguishable to all other groups (Prakas et al. 2021).

In our study, we aimed to gain a more complete insight by adding polymorphic microsatellite analyses as a method that has not yet been used in Turtle Dove research. Microsatellite loci – also called simple sequence repeats (SSR) – are shortly repeated, highly polymorphic and non-coding nucleotide sequences which make them a very useful and popular tool in population and conservation genetics (Abdul Muneer 2014, Gupta and Varshney 2000). We used this method to analyse the population genetics of birds sampled in Germany and Azerbaijan – both not or very little considered in previous studies. German breeding grounds are relevant to investigate because the segregation between the two main European flyways seems to occur in the central region of Germany. Turtle Doves breeding in the western part of the country use the western flyway and those breeding in the eastern part migrate east (Schumm et al. 2021). Azerbaijan, in turn, is located in the eastern European distribution area of Turtle Doves and was expected to show significantly differing results. Additionally, we used these and previously collected samples from Germany, Tenerife (Canary Islands), Egypt (subspecies *S.t. rufescens*) and Morocco (subspecies *S.t. arenicola*) for microsatellite and cyt *b* analyses. We integrated the cyt *b* samples into the data sets from aforementioned studies to get a broad picture of the Turtle Dove's genetic structure across the whole of Europe as well as parts of North Africa and the Caucasus region.

Materials and methods

Sample collection and data

For microsatellite analyses, we sampled 70 Turtle Doves (Table S1): 25 Turtle Doves from Germany with 11 specimens from eastern Germany representing the central-east flyway and 14 from western Germany representing the western flyway (Schumm et al. 2021). Because birds from these breeding regions use different migration routes, Germany is not regarded as one breeding region in this study but split into two. Additionally, individuals from Azerbaijan ($n=12$), Egypt ($n=8$), Morocco ($n=22$) and Tenerife ($n=3$) were included. Blood samples were taken from the brachial vein using a capillary and preserved on FTA Cards (Whatman International Ltd.).

For mitochondrial cyt *b* analyses, we used the samples mentioned above ($n=67$, respectively one sample from eastern Germany, Azerbaijan and Morocco did not work in the sequencing process) as well as cyt *b* sequence data from several previous publications: Calderón et al. (2016) including Turtle Doves from Spain, France, the UK, Germany, Italy, Malta, Bulgaria and Greece ($n=95$), Prakas et al. (2021) with individuals from Spain, Morocco and Ukraine ($n=258$), and Johnson et al. (2001) including one Turtle Dove caught in Kazakhstan. In total, 421 Turtle Dove individuals were used for genetic analyses. The Eurasian Collared Dove *Streptopelia decaocto* (Valente et al. 2017) was used as an outgroup in a phylogenetic tree reconstruction.

Genetic analyses of microsatellites

Genomic DNA was isolated from FTA card blood samples by using the ammonium acetate protocol (Merino et al. 2012). Ten microsatellite primers that were developed for Domestic Pigeons *Columba livia domestica* (Traxler et al. 2000, Lee et al. 2007, de Groot and van Haeringen 2017, Achmann et al. 2001a, Achmann et al. 2001b) worked successfully for *S. turtur* (Table 1). PCRs for amplifying microsatellite loci for 24 Turtle Dove samples were conducted in 15 µl reactions containing 7.5 µl Type-it Microsatellite PCR Master Mix (QIAGEN), 3 µM of each primer, 2–10 ng template DNA and nuclease-free water. Thermocycling steps included initial duration at 95 °C for 15 min, followed

Table 1 Locus characteristics of ten microsatellites designed for *Columba livia* that worked successfully for *Streptopelia turtur*. PG7 and CliμT13 were monomorphic and thus not further used for genetic analyses

Locus	Primer sequences (5'–3')	Allele range (bp)	T_a (°C)	Repeat motif	A	H_O	H_E	F_{IS}
PG4[1]	F: CCCATCTCCTTGCCTGATGC R: CACAGCAGGATGCTGCCTGC	130–169	58	TCCA	8	0.783	0.785	0.002^{ns}
PG2[1]	F: CCTTCCAACCCACATTATT R: CCAGCCTAAGTGAAACTGTC	265–308	58	ATTG	11	0.757	0.822	0.080^{ns}
PG6[1]	F: AAGCAATCAGAACAGTGCTTCG R: GTCCCTATGTTGCCTTCCCTC	126–150	58	AAAC	3	0.058	0.085	0.317^{**}
PG7[1]	F: CATTGGTCAGGAGGTGGTGGG R: TCTGCCACTCACTCGCCCTC	173–223	58	TTG	monomorphic			
CliμT47[2]	F: ATGTGTGTTTGTGCATGAAG R: ATGAAAGCCTGTTAGTGGAA	183–214	55	TATC	9	0.449	0.466	0.036^{*}
CliμT02[3]	F: AGTTTTAATGAAGGCACCTCT R: TGTAGCATGTCAGAAATTGG	93–113	55	CATC	6	0.269	0.681	0.607^{***}
PIGN57[4]	F: CTCTTGTATGTCCATCTGAAC R: ACCCATTTACCACTCTCTAA	153–189	55	TAGA	14	0.413	0.810	0.493^{***}
CliμT43[4]	F: GGGAAAGGAAATTTGACACTG R: ACTGTCGATGCCATTAAGAC	191–229	55	TGGA	14	0.743	0.765	0.023^{ns}
CliμT17[5]	F: ATGGGTTTGGAGATGTTTTG R: GTTTGATGGAGTTGCTATTTTGCT	208–244	55	CATC	6	0.523	0.580	0.089^{ns}
CliμT13[5]	F: CTGTCGAGCAGTAACAGTCC R: GTTTGCAAGCCCTGGTTATCTCA	198–240	55	GATA	monomorphic			

Markers originally developed by [1] Lee et al. 2007, [2] Achmann et al. 2001a, [3] Achmann et al. 2001b, [4] de Groot & van Haeringen 2017, [5] Traxler et al. 2000. T_a: Annealing temperature, A: number of alleles, H_O: observed heterozygosity, H_E: expected heterozygosity, F_{IS}: inbreeding coefficient. Significance tests indicate deviation from Hardy–Weinberg equilibrium (* $P<0.05$, ** $P<0.01$, *** $P<0.001$, ns: not significant).

by 32 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C/58 °C (depending on primer pair) for 90 s and elongation at 72 °C for 60 s, finishing with a final extension at 60 °C for 30 min. The fragment lengths were determined using QIAxcel systems as described in Dean et al. (2013). Two microsatellite loci were monomorphic and thus uninformative. Eight remaining microsatellites with a minimum repeat length of three base pairs (bp) were used for genetic structure analysis. We compared the results from eight markers with results from only four markers after removing four loci that deviated from HWE (Table 1), following the method of Quillfeldt et al. (2017). Because excluding those four loci did not seem to have an effect on the results, we present the final results from eight markers.

The screening for phylogenetically uninformative loci was performed with the 'poppr' package 2.9.5 (Kamvar et al. 2014) in R. The detection of null alleles was conducted as described in Quillfeldt et al. (2017). The number of alleles, observed and expected heterozygosity as well as the probability of deviation from Hardy–Weinberg equilibrium were determined using ARLEQUIN 3.5 (Excoffier et al. 2005). ARLEQUIN was also used for genetic structure investigations with a model-free analysis of molecular variance (AMOVA) with 1000 permutations for significance testing. The inbreeding coefficient was calculated with GENEPOP (Raymond and Rousset 1995).

We used STRUCTURE 2.3.4 (Pritchard et al. 2000) for model-based Bayesian clustering. STRUCTURE performed under the admixture ancestor model with correlated allele frequencies and without using sampling locations as prior. K values were predefined from 1–5 with 10 iterations consisting of 400,000 MCMC repetitions after a burn-in of 100,000 for each K value. For identifying the K value that most likely represents the actual number of populations, we used STRUCTURE HARVESTER (Earl and vonHoldt 2012) with the Evanno Method (Evanno et al. 2005). Results of the different iterations of each K value were aligned using CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and visualized with DISTRUCT 1.1 (Rosenberg 2004). For visualisation of genetic differences between individuals in space, we calculated a principal coordinates analysis (PCoA) with the *wcmdscale* function ('poppr' package) based on Bruvo's distance (Bruvo et al. 2004) in R.

Genetic analyses of cyt *b* sequences

Cyt *b* PCR was carried out with primers from Calderón et al. (2016): F_cyt_b_St (5' -TGATAACTCAAATCC TAACTGGTC-3') and R_cyt_b_St (5' -TTGTTTTCT AGGGCTCCGAT-3') for the amplification of an 880 bp fragment. PCR mixtures had a total volume of 30 µl containing 15 µl DreamTaq™ PCR Master Mix (Thermo Scientific™), 0.25 µM of each primer, 10 ng template DNA and nuclease-free water. Thermocycling steps included initial duration at 95 °C for 3 min, followed by 32 cycles of denaturation at 95 °C for 30 s, annealing at

58 °C for 60 s and elongation at 72 °C for 60 s, finishing with a final extension at 72 °C for 10 min. Bi-directional Sanger Sequencing of the PCR products was performed by Microsynth SeqLab GmbH. Sequences were aligned using BioEdit Sequence Alignment Editor and uploaded in GenBank (accession numbers PX849190 - PX849256). Haplotypes from 67 individuals were determined using the online tool FaBox 1.61 (Villesen 2007). Haplotype diversity and nucleotide diversity were calculated in DNASP v6 (Rozas and Rozas 1999). A Median-Joining Network was created using POPART (Leigh and Bryant 2015). A Bayesian phylogenetic tree (HKY + G model) to specify different haplogroups was created with an MCMC chain length of 10,000,000 in BEAST 2 (Bouckert et al. 2014). MCMC performance and parameter convergence was tested with Tracer v1.7.2. TreeAnnotator 2.7.6 calculated the best tree with 10% Burn in. The tree was visualized in FigTree v1.4.4.

Combined with the sequences of Calderón et al. (2016), Prakas et al. (2021) and Johnson et al. (2001), we calculated Kimura 80 distance using the 'ape' package (Paradis and Schliep 2019) and performed a PCoA using the *cmdscale* function with a total of 421 Turtle Dove individuals in R. PCoA results were visualised for every individual assigned with their rough migration route as well as for every breeding region using centroids. Examination of genetic structure was performed by AMOVA using ARLEQUIN 3.5 (Excoffier et al. 2005) for 420 individuals. Kazakhstan was excluded in this analysis due to its small sample size ($n = 1$). Pairwise F-statistics (F_{ST}) with 420 individuals were calculated with 1000 permutations and visualized with the R package 'corrplot' (Wei et al. 2017).

Results

Microsatellite analyses

Two of the ten used loci were monomorphic and thus excluded for further analyses (Table 1). 13 null alleles were identified among the loci and individuals with the highest number (7) were found in the marker PIGN57. Among the polymorphic loci, the number of alleles ranged from 3–14 per locus. Four loci showed a significant deviation from HWE (Table 1).

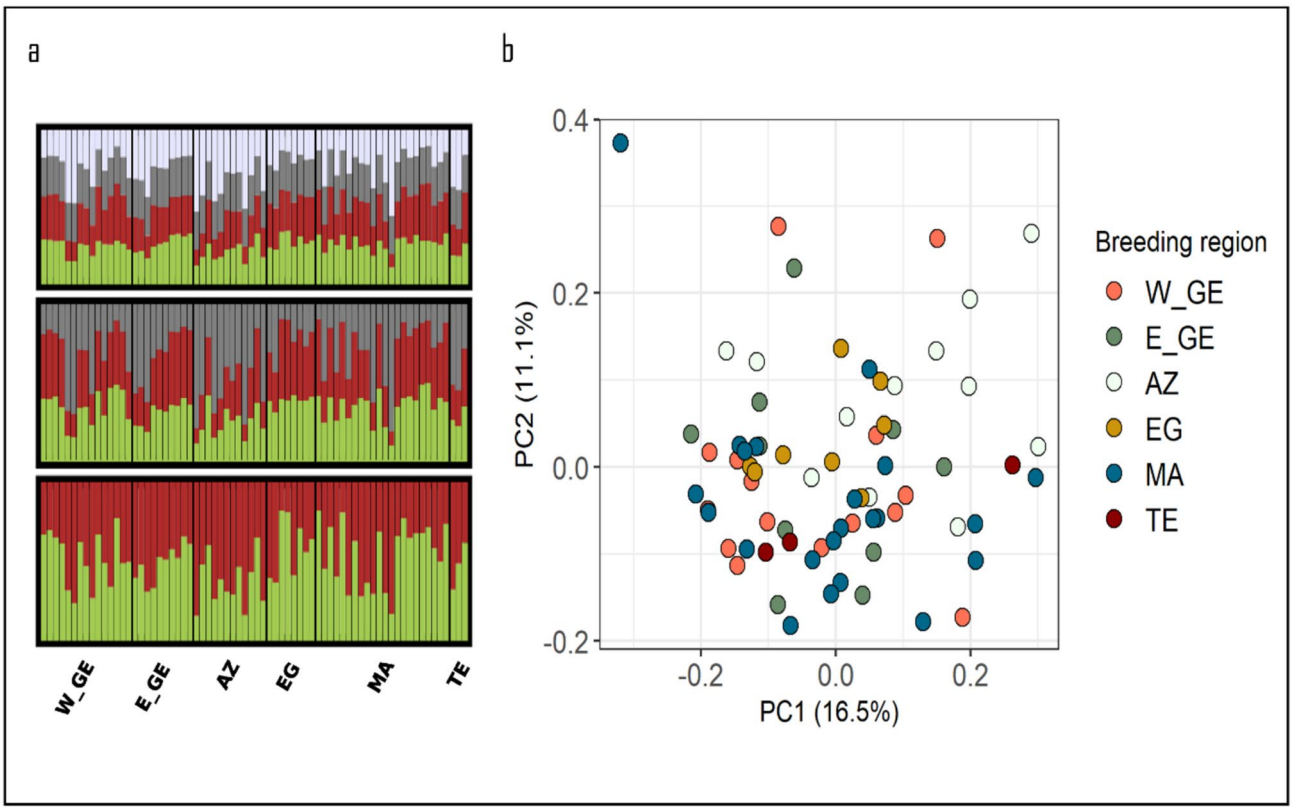

Fig. 1 Microsatellite analyses conducted with eight polymorphic markers in 70 Turtle Dove individuals from western Germany (W_GE), eastern Germany (E_GE) and Azerbaijan (AZ), Egypt (EG), Morocco (MA) and Tenerife (TE). **a** Results from Bayesian clustering with 2–4 possible genetic clusters. The coloured proportion of the bars depict the individuals' percentage of belonging to a certain cluster. **b** Genetic distances among the individuals calculated with a PCoA based on Bruvo's distance

We detected no genetic differentiation between the breeding regions based on Bayesian clustering (Fig. 1). The STRUCTURE results indicated randomly distributed genotypes among all breeding regions and individuals. No clusters corresponding to the individual's origin were visible. According to the Evanno method, the highest Delta K value (7.7) was observed for K = 2. All Delta K values ranged between 0.5 and 7.7 which is very low and implied a lack of actual genetic clusters. The PCoA revealed similar results with individuals being rather randomly distributed than assembled in groups. An influence of breeding regions on genotypes did not seem to be present. AMOVA calculated 1.6% as the proportion of explaining variance that results from differences among breeding regions. A total of 98.4% of genetic variation could be traced back to differences within breeding regions. Genetic differentiation was low among all breeding regions (F_{ST} = −0.04 – 0.04) and not significant for any combination.

Cyt *b* analyses

In 67 samples collected in western Germany (n = 13), eastern Germany (n = 11), Egypt (n = 8), Azerbaijan (n = 11), Morocco (n = 21) and Tenerife (n = 3), 26 haplotypes could be detected. The data showed a high genetic diversity (haplotype diversity (Hd) = 0.930, nucleotide diversity (π) = 0.0064) among all individuals. The median joining network revealed two haplogroups separated by six mutational steps which did not correspond to the birds' breeding origin or migration flyway (Fig. 2b). The phylogenetic tree (Fig. 2a) confirmed a genetic divergence and allowed us to specify the two haplogroups. Haplogroup "A" consisted of 42 samples with 17 haplotypes (Hd = 0.901, π = 0.0037), haplogroup "B" was smaller with only 26 samples yet still 11 different haplotypes (Hd = 0.837, π = 0.0034). Though both haplogroups contained samples from Germany, Egypt, Azerbaijan, Morocco and Tenerife, the genetic differentiation between them was

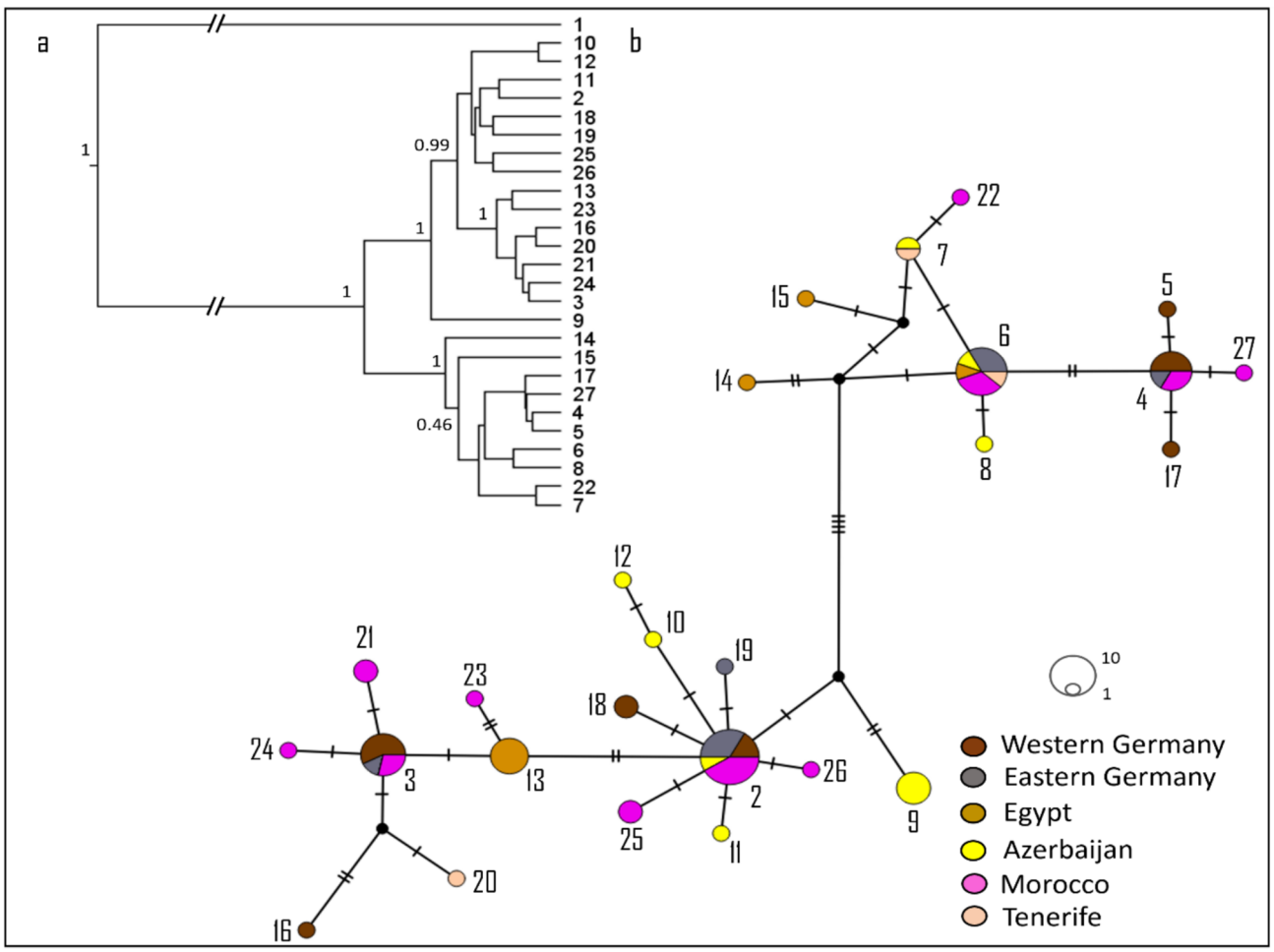

Fig. 2 Cytochrome *b* analyses of 67 Turtle Dove individuals collected in Germany, Azerbaijan, Morocco, Tenerife and Egypt. **a** Bayesian phylogenetic tree depicting unrooted relationships among 26 Turtle Dove haplotypes with posterior probability values showing the probability of a certain clade being correct. *Streptopelia decaocto* was used as an outgroup (Haplotype 1). **b** Median joining network depicting unrooted relationships among individuals. The size of the circles indicates the number of individuals sharing the sample haplotype (haplotypes are labelled with the same numbers as in the tree), the lines represent mutational steps

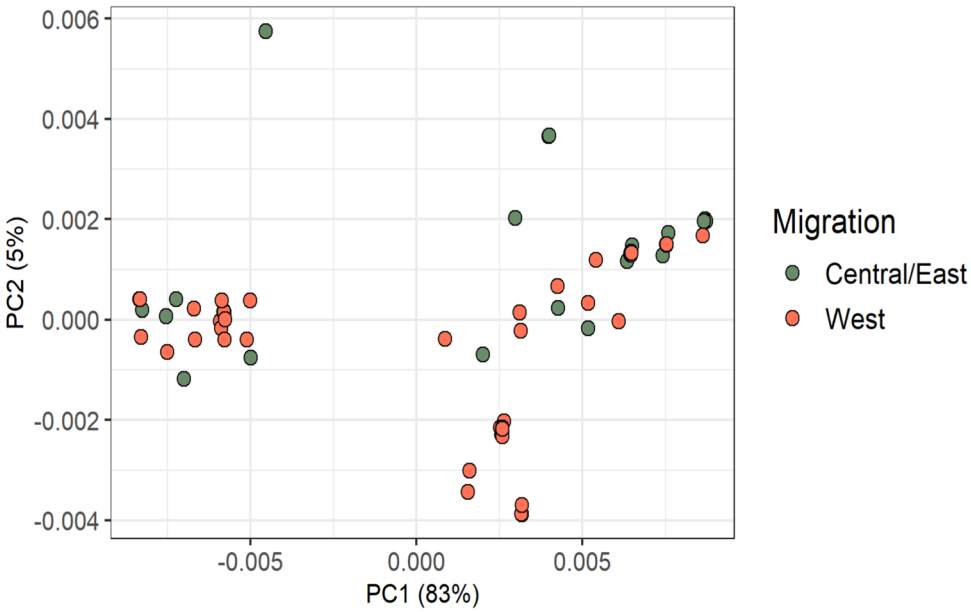

Fig. 3 Principal coordinates analysis (PCoA) showing genetic distances of 421 Turtle Dove individuals based on Kimura 80 distance in cytochrome *b* sequences. Migratory flyways used by the birds are visualized by colour. Though every dot represents one individual, far less than 421 are visible. Because many samples did not genetically differ in the cyt *b* locus, not all samples can be depicted in a distance-based visualisation

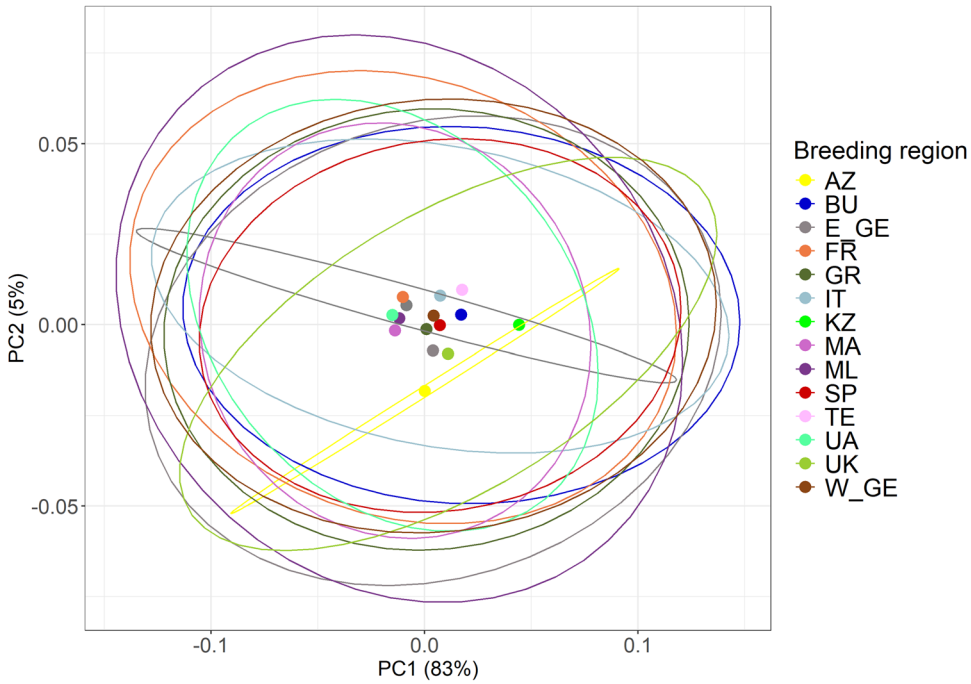

Fig. 4 Principal coordinates analysis (PCoA) depicting genetic differentiation calculated with Kimura 80 distance in cytochrome *b* sequences of 14 Turtle Dove breeding regions (421 individuals) based on PCoA centroids for every breeding region. Circles around the centroids indicate error ellipses. TE ($n=3$) and KZ (n = 1) were too small to calculate ellipses. Abbreviations: AZ: Azerbaijan, UA: Ukraine, MA: Morocco, BU: Bulgaria, EG: Egypt, UK: United Kingdom, TE: Tenerife, SP: Spain, FR: France, IT: Italy, W_GE: West Germany, ML: Malta, E_GE: East Germany, GR: Greece

strongly significant ($F_{ST}=0.621$, $p<0.001$). Similar results were visible when sequences from the literature were added Fig. S1.

The cyt *b* sequences of 421 Turtle Doves were used to create a PCoA based scatter plot (Fig. 3). Because many sequences were identical and thus not distinguishable in a plot that depicts distances, much less data points were visible. Still, two genetic groups were clearly apparent. These groups did, however, not correlate with the two main migratory pathways. The same PCoA results were used to show the spatial distribution of sampling groups by assembling the individuals to their breeding region (Fig. 4). Error ellipses are large for every breeding region and strongly overlap. The only breeding regions that have a slightly isolated position are Azerbaijan as well as Kazakhstan which only contains one individual and thus has no error ellipse.

Results from the AMOVA showed that most of the genetic variation is caused by variations within a breeding region (96.8%). The remaining 3.2% of the overall variation can be explained by differences among breeding regions ($F_{ST}=0.032$, $p=0.007$). This proportion is not high, but still significant. A genetic differentiation depending on breeding regions is therefore present. Though there seemed to be no connection between the birds' migratory pathway and their

genetic difference, certain breeding regions were genetically distinguishable from others (Fig. 5). Birds from Azerbaijan differed significantly from Turtle Doves caught in Ukraine, Morocco, Bulgaria, Egypt, Spain and France. Genetic differentiation was also detectable when comparing Ukraine with Bulgaria, UK and Spain. Morocco did furthermore differ from Bulgaria, UK, Spain and Italy. Every further sampling pair showed no significant differentiation. Greece, Malta, Tenerife, western and eastern Germany could not be distinguished from any other investigated breeding region (Fig 6).

Discussion

We examined genetic population structure in Turtle Doves using microsatellites and mitochondrial DNA (cyt *b*). Microsatellite analyses did not show genetic differentiation among the investigated breeding regions. A lack of genetic structure between these groups was supported by the mtDNA data in this study. However, based on the complete set of cyt *b* sequences, Turtle Doves from Azerbaijan could be distinguished from six other breeding regions. Individuals from Morocco and Ukraine as well showed a high number of breeding regions they significantly differed from (five and four). Remarkably, for some groups (namely Greece, western and eastern Germany, Malta and Tenerife) genetic differentiation could not be detected at all. A migration connectivity which is reflected by genetic groups could not be supported by our findings of two differentiated haplogroups that did not correspond to the geographical appearance of Turtle Doves in any way.

Previous studies detected intraspecific genetic differentiation correlating with migration flyways or geographical distribution of certain bird species (Delmore et al. 2016, Rolshausen et al. 2009; Ramos et al. 2016). However, nuclear DNA like microsatellite markers can show significantly different results compared to mitochondrial DNA (Jones et al. 2005; Ramos et al. 2016). Several phylogenetic investigations of Common Woodpigeons (*Columba palumbus*) obtained contrasting outcomes using different genetic markers (Butkauskas et al. 2019), partly revealing genetic divergence between sedentary and migratory populations (Butkauskas et al. 2013). For Turtle Doves, only two studies using mitochondrial DNA and SNPs were conducted (Calderón et al. 2016; Prakas et al. 2021). Our microsatellite

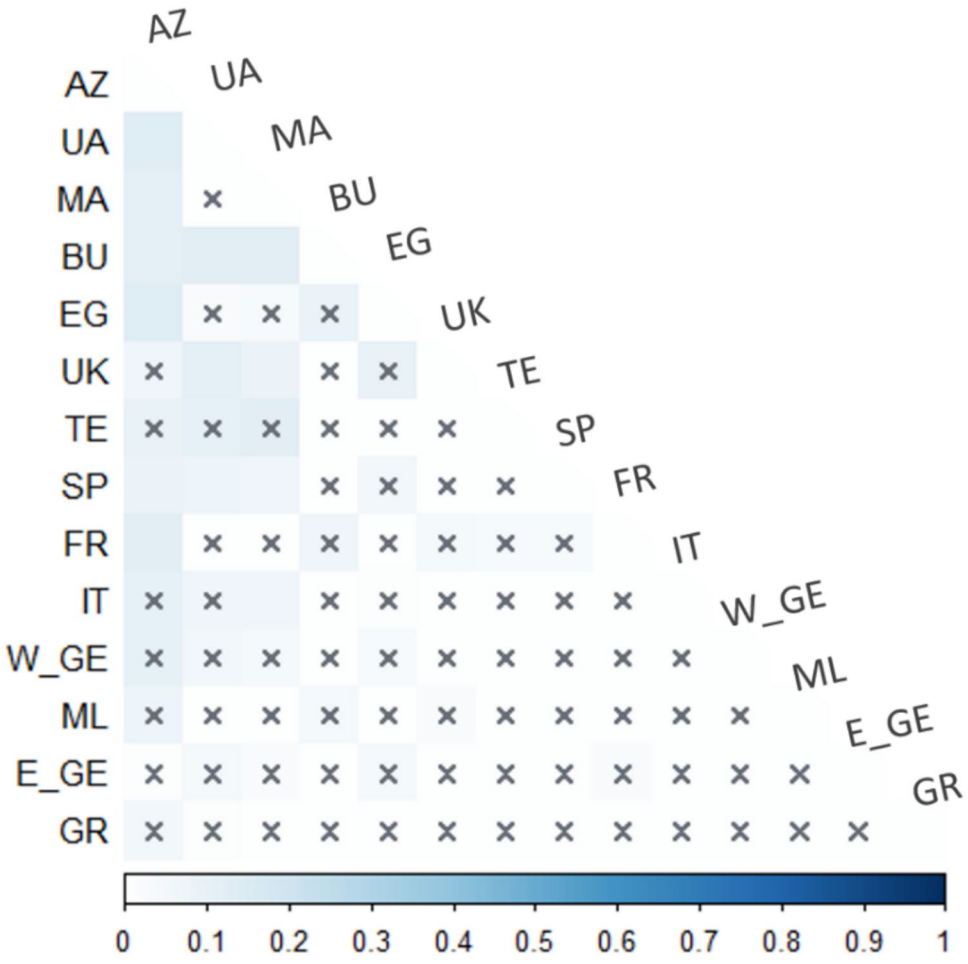

Fig. 5 Genetic differentiation (cytochrome *b*) among 14 Turtle Dove breeding regions based on F_{ST} values (0–1). Darker blue colours represent higher F_{ST} values and thus higher differentiation. Crosses within the boxes mean that the differences are not significant ($p > 0.05$). Abbreviations: AZ: Azerbaijan, MA: Morocco, BU: Bulgaria, UA: Ukraine, EG: Egypt, UK: United Kingdom, SP: Spain, IT: Italy, W_GE: West Germany, FR: France, ML: Malta, GR: Greece, E_GE: East Germany

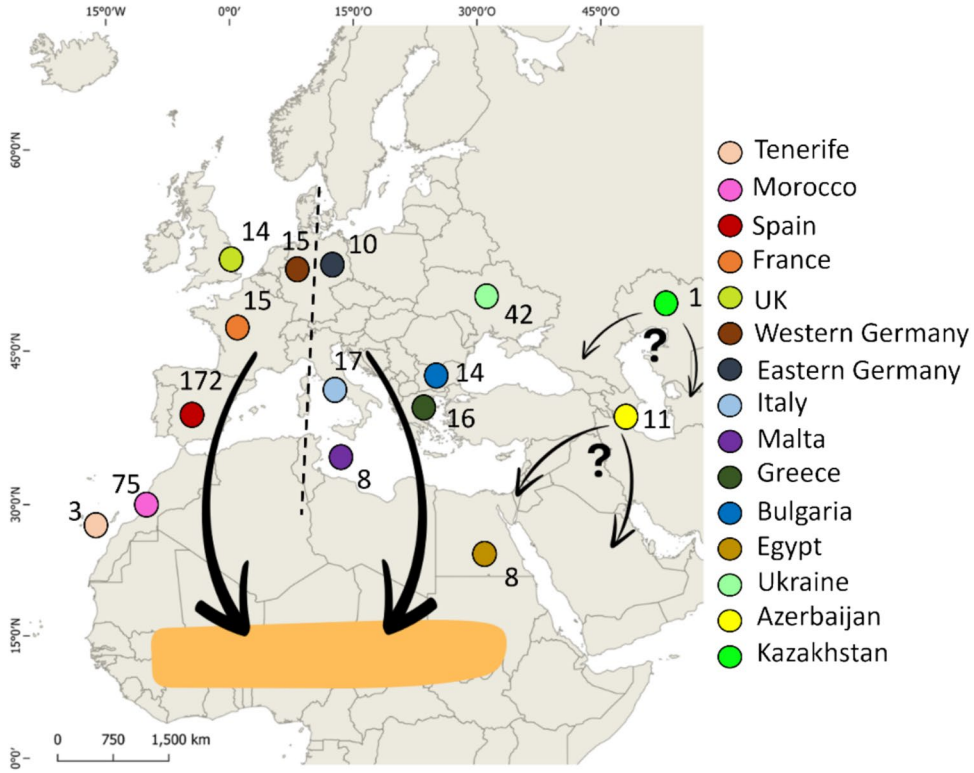

Fig. 6 Sampling locations of 421 Turtle Doves for cytochrome *b* analyses. Numbers represent how many individuals from a certain breeding region were collected. The arrows indicate the rough migration flyways, the orange areas represent the wintering grounds (unknown for Azerbaijan and Kazakhstan). The dashed line indicates the approximate segregation between the main European flyways. Data comes from own samples as well as previous papers (Calderón et al. 2016; Johnson et al. 2001; Prakas et al. 2021)

data showed no genetic structure that might reflect actual populations and did thus not differ from the mitochondrial cyt *b* data. Genetic differentiation (F_{ST}) among these groups was slightly higher in cyt *b* sequences than microsatellites but not significant in both methods. We expected a possible genetic divergence between the western and eastern German individuals due to the segregation of migration flyways between both breeding regions (Schumm et al. 2021). The lack of differentiation is not surprising when regarding the random distribution of microsatellite alleles between other groups that are far more distantly located than the German groups.

Similar to a previous study, cyt *b* sequences revealed two haplogroups divided by six mutational steps (Calderón et al. 2016). These haplogroups were strongly differentiated but can hardly be regarded as two populations because they did not correspond to migration routes or geographical areas. We assume that this split was caused by drastic changes in species distribution and abundance in glacial periods where large groups of birds were shifted into glacial refugia before recolonizing previously frozen areas in interglacial periods (Drovetski et al. 2018; Hewitt 1996). For the warm adapted Turtle Dove, a correlation between the effective population size and glacial expansion was revealed (Calderón et al. 2016). Multi-marker analyses are needed to determine exact divergence times for this species.

We did not find any relationship between the flyways and genetic haplogroups in Turtle Doves. Calderón et al. (2016) assumed that the lack of population structure does not reflect insufficient methods used to detect genetic differentiation between the flyways but is caused by a weak migratory connectivity. Our data support this assumption. The present migratory divide might have evolved fast after the last glacial maximum and is therefore not detectable in neutral markers yet. A missing linkage between migratory divides and genetic divergence in neutral markers was also observed in Willow Warblers (Bensch et al. 1999; Lundberg et al. 2017). For Turtle Doves, there is limited knowledge about the exact wintering grounds and flyways within Africa because ring recoveries are rare in these areas (Marx et al. 2016). Tracking studies revealed that there is a large overlap of migration routes in sub-Saharan Africa and relatively large distance movements within the wintering grounds (Schumm et al. 2021). Furthermore, one individual we tracked in the western German breeding region flew in the eastern direction (unpbl. data: Quillfeldt et al. 2024), indicating a lack of a clear segregation between the flyways and a mixing of populations in the non-breeding areas resulting in a weak migratory connectivity.

However, the often-stated idea of Turtle Doves being a panmictic population cannot be confirmed when comparing all available cyt *b* datasets of this species. Pairwise population comparisons revealed a small degree of genetic differentiation among certain breeding regions. Our results are in line with those from Prakas et al. (2021) showing that Turtle Doves from Morocco and Ukraine are genetically

differentiated to many other groups while being mutually very similar. Furthermore, birds from Azerbaijan differed significantly from six other breeding origins. So far there is no published data on the migration behaviour of Turtle Doves from Azerbaijan. There is, however, knowledge about the Black Sea/Eastern Mediterranean flyway that is used by Turtle Doves breeding in eastern European regions like Ukraine and Azerbaijan. The genetic divergence might be caused by the differentiation of this flyway. In this case, a genetic structure based on geographic distribution and migratory flyways is detectable which might indicate a genetic based conservation unit within this species. The lack of significant genetic divergence between certain central European breeding regions and the Azerbaijan breeding region might be caused by the relatively recent expansion of this species, as previously suggested (Calderón et al. 2016). However, the genetic differences do not seem to directly correlate with the groups' distances. There is, for instance, a significant difference between Azerbaijan and Bulgaria but not between Azerbaijan and the UK. One explanation might be the above mentioned glacial refugia hypothesis. Ice-free regions in the late Pleistocene were located in the Iberian Peninsula, Italy and the Balkans, but also the Caucasus region (including Azerbaijan) is expected to have served as a glacial refuge for European birds (Brito 2005; Drovetski et al. 2018). Interactions between central/northern European populations with Turtle Doves from Azerbaijan might have been a result of this natural event. Additionally, the quality of habitats and structure of landscapes can influence and shape population structure and genetics (Pavlacky et al. 2009; Razgour et al. 2014). Further analyses with landscape genomics (Forester et al. 2018) might be a next step to investigate the differences between breeding regions that cannot simply be explained by geographical distances. We however expect the genetic differences to increase in the further eastern distributions that were not investigated yet. This hypothesis is slightly supported by the isolated positions of Azerbaijan and Kazakhstan in the group based PCoA plot (Fig. 4) as well as a separation of at least four mutational steps between the one sample from Kazakhstan and every other haplotype in a median joining network (Fig. S1).

Beside *S. turtur turtur*, two subspecies were present in the cyt *b* dataset, namely *S. t. arenicola* (Morocco) and *S. t. rufescens* (Egypt) (Vaurie 1961). It has to be mentioned that birds from Egypt were genetically different from only one other group (Fig. 5) which strongly contradicted our expectations because individuals are morphologically distinguishable from the European subspecies (*S. t. turtur*). The plumage is more colourful with a smaller proportion of grey and a higher proportion of brown-orange (Fig. S2-S7) which can be seen as an adaptation to the desert habitat (Hering 2020). An explanation for the lack of genetic divergence in the cyt *b* region might be that cyt *b* has found to be evolving relatively slow in birds (Stanley and Harrison 1999). Additionally, differences in certain morphological traits like plumage colour can occur between populations while genome differentiation is extremely low. Whole genome comparisons in hybridizing warblers, for instance, revealed that traditional markers failed to distinguish populations because only very few genomic regions control feather pigmentation (Toews et al. 2016). Neutral markers like cyt *b* or microsatellites might not always be suitable to detect conservation units that emerged due to small morphological changes.

We found indications for an increased genetic differentiation in Turtle Doves that are distributed further east. Birds occurring in western Siberia and the Caucasus area are considered to belong to the nominate subspecies *S. t. turtur* which includes all Turtle Doves in Europe (Vaurie 1961). Mitochondrial DNA revealed stronger genetic divergence between birds from these areas and birds from central Europe than among central European breeding regions. This tendency needs to be further investigated particularly in regions towards Asia where research has not yet focused on. For a successful conservation management, it is crucial to investigate the whole distribution area of this species. In case of no clear population patterns, the species should be considered as a single conservation unit.

Conclusion

Similar to previous studies, we found no relationship between the genetic structure and migration flyways for the European Turtle Dove which we expect to be caused by a weak migration connectivity. Certain conservation units that are based on genetic patterns could not be defined in our study. Significant genetic differences were, however, apparent among certain breeding regions. Analyses with landscape genomics might be a next step for understanding the mechanisms behind these differences. Moreover, we found that birds with a further eastern distribution tend to be genetically more diverged. Additional genetic and tracking studies focusing on Turtle Doves occurring in Asia and the Middle East are necessary for a broad understanding of the whole species' population structure leading to an improvement of conservation efforts.

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Author contributions HR wrote the main manuscript and did the data analyses. Field work in Germany was carried out by PQ, BJM, UG, YRM, JFM, VM and HR. Samples from Azerbaijan were collected by PQ, YRS, ES and IMM. Samples from Tenerife were provided by JCI and samples from Morocco were collected by GR. JH and HJF provided samples from Egypt. Laboratory work was carried out by HR. All authors read and commented on the manuscript and approved the final version.

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Data availability Cyt *b* sequences are deposited in GenBank and Accession numbers provided in the manuscript.

Declarations

Competing interests The authors declare no competing interests.

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