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Mitotyping of random bred cats and pure breed cats (Turkish Angora and Turkish Van) using non-repetitive mitochondrial DNA control region

Nüket Bilgen [a], Mervenur Güvendi [b], Efe Sezgin [c], Hüseyin Can [b], Ahmet Efe Köseoğlu [d], Sedef Erkunt Alak [b], Mert Döşkaya [e], Cemal Ün [b,*]

[a] Ankara University, Faculty of Veterinary Medicine, Department of Animal Genetics, Ankara, Türkiye
[b] Ege University, Faculty of Science, Department of Biology Molecular Biology Section, İzmir, Türkiye
[c] İzmir Institute of Technology, Department of Food Engineering, İzmir, Türkiye
[d] Biruni University, Faculty of Engineering and Natural Sciences, Department of Molecular Biology and Genetics, İstanbul, Türkiye
[e] Ege University, Faculty of Medicine, Department of Parasitology, İzmir, Türkiye

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ABSTRACT

The Fertile Crescent appears to be the most plausible region where the domestication of cats commenced through a mutually beneficial relationship between wild cats and early agrarian societies. These domesticated cats then journeyed across the globe mirroring the paths of human migration. An examination of mitochondrial DNA (mtDNA) control region-based mitotyping suggested that a significant majority, exceeding 80%, of globally sampled random-bred and pure-bred cats could be categorized into 12 predominant mitotypes. However, the extent of mitotype diversity within random-bred cats from regions proximate to the Fertile Crescent remains inadequately explored. In light of this we aimed to investigate the mitotype diversity in random bred cats sampled from various regions across Turkey. Additionally, we sought to establish a comparison with the mitotype profiles of locally recognized pure breeds, namely the Turkish Angora and Turkish Van. To unravel their evolutionary narratives, we engaged in comprehensive population genetics analyses at both the individual and mitotype-based levels. Our study encompassed a sample size of 240 specimens, forming the basis for both mitotyping and population genetics scrutiny. Our analysis yielded the identification of nine 'universal' mitotypes (A—J), alongside an 'outlier' mitotype group I. Notably mitotypes A and D emerged as particularly prevalent in contrast to the lesser occurrence mitotypes C, G, and H. With the realm of random bred cats the structure of haplotypes exhibited remarkable diversity presenting distinctions from Turkish Angora and Van breeds. Nucleotide diversity was higher compared to previous reports from Turkey and was one of the highest among reported world cat population estimates. Intriguingly, our investigations did not unveil any pronounced instances of strong selection, population expansions or contractions within any specific population or mitotype. To conclude, our study represents a pioneering effort in uncovering the mitotype profiles and haplotype structures inherent to both random-bred and pure breed cats in Turkey. This endeavor not only broadens our understanding of the feline genetic landscape within the region but also lays the foundation for future inquiries into the evolutionary trajectories and genetic legacies of these feline populations.

1. Introduction

Domestic cats (*Felis catus*) are one of the most popular pets throughout the world and more than 600 million cats live with humans (Driscoll et al., 2009). Although the skeletal remains of domestic cats date back to about 4000 BC due to mummification and artistic activities in Egypt, archaeological evidence shows that the remains of the first domestication of wild cats were found in the Near East, together with important finds in Cyprus about 9000–10000 years ago (Vigne et al., 2004; Lipinski et al., 2008; Kurushima et al., 2012). The human/cat relationship is thought to have started about 10,000–11,000 years ago, especially in the Fertile Crescent, with the domestication of some wild grains and grasses, when humans began to switch to sedentary agriculture, and cats were used to control crop-destroying rodents (Lipinski

Abbreviations: mtDNA, mitochondrial DNA; Cyt b, cytochrome *b*; COI, cytochrome oxidase I; CR, control region; mtDNA CR, mitochondrial DNA control region.

* Corresponding author.
E-mail address: cemaluen@gmail.com (C. Ün).

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et al., 2008). Along trade routes between ancient civilizations, cats probably spread to nearly all parts of the Old World and gene flow occurred between wild and domestic modern cats (Lipinski et al., 2008; Nilson et al., 2022). Among the domestic cats, 16 natural breeds including Turkish Van and Korat are accepted as regional variants among the 41 breeds recognized by the Cat Fanciers' Association (CFA) (Lipinski et al., 2008; Kurushima et al., 2013). The remaining purebred fancy cats that have been bred purely to preserve or change their aesthetic characteristics evolved over the 50 years by intensive artificial selection are generally accepted as natural breed derivative single-gene variants (Lipinski et al., 2008).

The mitochondrial DNA (mtDNA) is extensively used as a genetic marker in evolutionary and ecological studies with its properties such as rapid evolutionary rate, near-neutrality, maternal inheritance, and lack of recombination (Dong et al., 2021). Although there are protein-coding mtDNA regions involving the cytochrome *b* (Cyt b) and cytochrome oxidase I (COI) with these properties, the evolution rate of the mtDNA control region (CR) is 2–5 times faster, and that makes mtDNA CR much more suitable in intraspecific evolutionary studies (Jamandre et al., 2014). Together with its exceptional fast-evolving segments, the mtDNA CR has been used as a marker for evolutionary, phylogeographical, and population genetics analyses in different lineages of animals including mammals, birds, turtles, fish, and insects (Jamandre et al., 2014; Maté et al., 2004; Huang et al., 2009; Encalada et al., 1996; Vila and Björklund,2004). The mitotyping based on mtDNA CR was first used in cats for forensics because the cat hair transferring to cloths or personal objects provides resource material for DNA profiling (Grahn et al., 2011; Tarditi et al., 2011). To provide a database of cats for forensic studies, Grahn et al. (2011) performed a mitotype analysis (mitotyping) based on a 402 bp cat mitochondrial DNA control region (mtDNA CR) among 1394 cats representing 25 distinct worldwide populations and 26 breeds and found that 83% of the cats were represented by 12 major mitotypes called universal mitotypes.

Based on this mitotype analysis performed by Grahn et al., (2011), in this study, we aimed to study the cat mitotype diversity in Turkey using 402 bp cat mtDNA CR, and conduct population genetics analyses with the identified mitotypes to compare their evolutionary histories. We focused on random bred cats sampled from the Aegean, Central Anatolia, and Southeastern Anatolia regions of Turkey. The analyses are extended to Angora and Van regional breeds.

2. Material and method

2.1. Cat samples

A total of 240 cat DNA samples which were belonging to random bred cats and pure breed cats (Turkish Angora and Turkish Van) were used for mitotyping analysis. Of the 240 cat DNA samples, 163 belonged to random bred cats whereas the remaining 77 belonged to pure breeds including Turkish Angora (n = 28) and Turkish Van (n = 49) cats. Of the 163 cat DNA samples, 108 were obtained from random bred cats living in İzmir province located in Aegean region of Turkey whereas 48 were obtained from random bred cats living in Ankara province located in Central Anatolia and 7 were obtained from random bred cats living in Siirt province located in the Southeastern Anatolia Region (Fig. 1). Also, for Angora cats, specimens were sourced from participants of breed-specific cat beauty competitions and from established Angora cat breeding facilities. In the case of Van cats, samples were procured from dedicated Van cat breeding establishments. This approach ensured the acquisition of representative samples from both Angora and Van cat breeds for further analysis. The samples were collected from both street or feral cats and veterinary clinics.

2.2. Mitotype determination

For mitotype determination, 402 bp long mitochondrial control region including nucleotide variations that identify the universal mitotypes was amplified using the JHmtF3-5′-GATAGTGCTTAATCGTGC-3′ and JHmtR3-5′-GTCCTGTGGAACAATAGG-3′ primers as described previously (Grahn et al., 2011). PCR products belonging to mitochondrial DNA were sequenced by ABI3730XL and generated sequences were aligned by MEGA7.0 software to compare with reference cat mitotypes including mitotype A (EU864495.1), mitotype A6 (KU314498.1), mitotype B (EU864496.1), mitotype C (EU864497.1), mitotype D (EU864498.1), mitotype D5 (GQ497299.1), mitotype E (EU864499.1), mitotype J (EU864504.1), mitotype F (EU964500.1), mitotype H (EU864502.1) and mitotype I (KT344778.1).

Fig. 1. The map shows the regions where samples were collected. The green shaded region shows the extension of ancient Mesopotamia, the northern part of the fertile crescent, into the South Eastern Anatolia region of Turkey.

2.3. Genetic diversity and haplotype analyses

DNASP6 program was used for genetic diversity analysis based on the number of mutation (Eta), number of haplotype (h), haplotype diversity (Hd), and nucleotide diversity (Pi) (Librado and Rozas, 2009). Allele frequency spectrum-based neutrality tests including Tajima's D (Tajima, 1989), Fu and Li's D* (Fu and Li 1993), Fu and Li's F* (Fu and Li 1993), Fu's Fs (Fu, 1997) and Ramos-Onsins and Rozas R2 (Ramos-Onsins and Rozas, 2006) were also performed by DNASP6 program. All haplotype networks were generated in PopArt using the TCS network (Leigh and Bryant, 2015; Clement et al., 2000). The degree of variation within populations and differentiation between populations were calculated in Arlequin v3.5 (Excoffier and Lischer, 2010) using Analysis of Molecular Variance (AMOVA) (Excoffier and Smouse, 1992) and F_{st} values (Weir and Cockerham, 1984). Phylogenetic tree was constructed by the Maximum Likelihood method using the Kimura-2 parameter with 1000 bootstraps in order to compare mitotypes detected in this study to the reference mitotypes.

3. Results

3.1. Mitotype and haplotype analyses

Analysis of 240 mtDNA control region sequences from five cat populations (two pure breeds and three random bred populations) from Turkey identified nine 'universal' mitotypes (A—J), and one 'outlier' mitotype group 1 (Table 1). Among these mitotypes, A, A1, A6, B, C, D, E1, F, J, and I mitotypes were detected in random bred cats living in İzmir province located in the Aegean region of Turkey, while A, D, E1, F, H, J, and I mitotypes were detected in random bred cats living in Ankara province located in Central Anatolia. In random bred cats living in Siirt province located in the Southeastern Anatolia Region, only A6, D, E1, and J mitotypes were detected. Among pure breed cats including Angora and Van breeds, A, A7, B, D, D1, D3, D5, E1, F, G, H, J, and I were detected. As these two pure breeds were compared each other, A, A7, B, D, D3, D5, and J mitotypes were detected in Angora breeds while A, D, D1, E1, F, G, H, and J mitotypes were detected in Van breeds (Table 1).

The prevalence of these mitotypes varied from 0.42% to 43,33% among all cats analyzed. A (43.33%) and D (22.5%) mitotypes were

Table 1
Mitotype distribution among random bred and pure breed cat populations.

Region/Province	Random bred cats /Pure Breed	Mitotypes detected															
		A	A1	A6	A7	B	C	D	D1	D3	D5	E1	F	G	H	J	1
Aegean region/İzmir (n = 108)	Random bred cats	52	2	10		2	2	18				5	6			4	7
Central Anatolia/Ankara (n = 48)		17						15				5	5		1	2	3
Southeastern Anatolia/Siirt (n = 7)				3				1				1				2	
Central Anatolia/Ankara	Angora breeds (n = 28)	16						5	1			1	1	1	2	1	
	Van breeds (n = 49)	19			1	4		15		1	1					8	

among the most prevalent mitotypes in both random bred cats and pure breed cats. Contrary to these prevalent mitotypes, mitotypes C, G, and H were the least common mitotypes (Table 1).

A median-joining network tree depicted that the haplotype structure in random bred cats was rather diverse and different compared to Angora and Van breeds (Fig. 2). Considering a single population, random bred samples had a higher number of mitotypes compared to the pure breed (Angora and Van) populations (Chi-square = 45,89; df = 21; P < 0.01), where all ten mitotypes were observed in the random bred population (Table 1). Angora breed population had higher mitotype diversity compared to the Van breed (Table 1, Fig. 2B and 2C). Several major mitotypes, such as C and I, were not observed in Ankara or Van breeds. Also, mitotypes E, F, G, and H were not observed in the Van breed.

Both the phylogenetic and median-joining network trees indicate that most mitotypes differ by only a few mutations without forming well-supported distinct clades. Mitotypes A, D, E, H, and I can be considered as the most diverged mitotypes clustering in separate groups (Fig. 3; Supplemental Fig. 1).

3.2. Population genetic analyses

The degree of variation within populations, and differentiation between populations were estimated by AMOVA. The five populations compared were the individual random breeds from three different cities, and the Angora and Van breeds. Ninety-five percent of the genetic diversity was within populations, and only five percent was between populations. Overall F_{st} between populations was 0.046. The largest population differentiation was observed between the Angora and Van breeds (F_{st} = 0.10, p = 0.02), Siirt and Angora (F_{st} = 0.09, p = 0.001), and Izmir and Van breeds (F_{st} = 0.08, P = 0.001).

Following mitotype structure, population level variation and differentiation analyses, molecular population genetic analyses were conducted within each population and major mitotypes. Both the haplotype and nucleotide diversity estimates were higher in random bred populations compared to Angora and Van breed populations (Table 2). With 15 different haplotypes, the highest haplotype diversity and the highest nucleotide diversity based on segregating sites (θ) were observed in random bred cats from Ankara. Together with Izmir random bred cats, Ankara random bred population also had one of the highest nucleotide diversity based on average pairwise nucleotide differences (π). Comparing pure bred populations, the Angora breed cats had higher

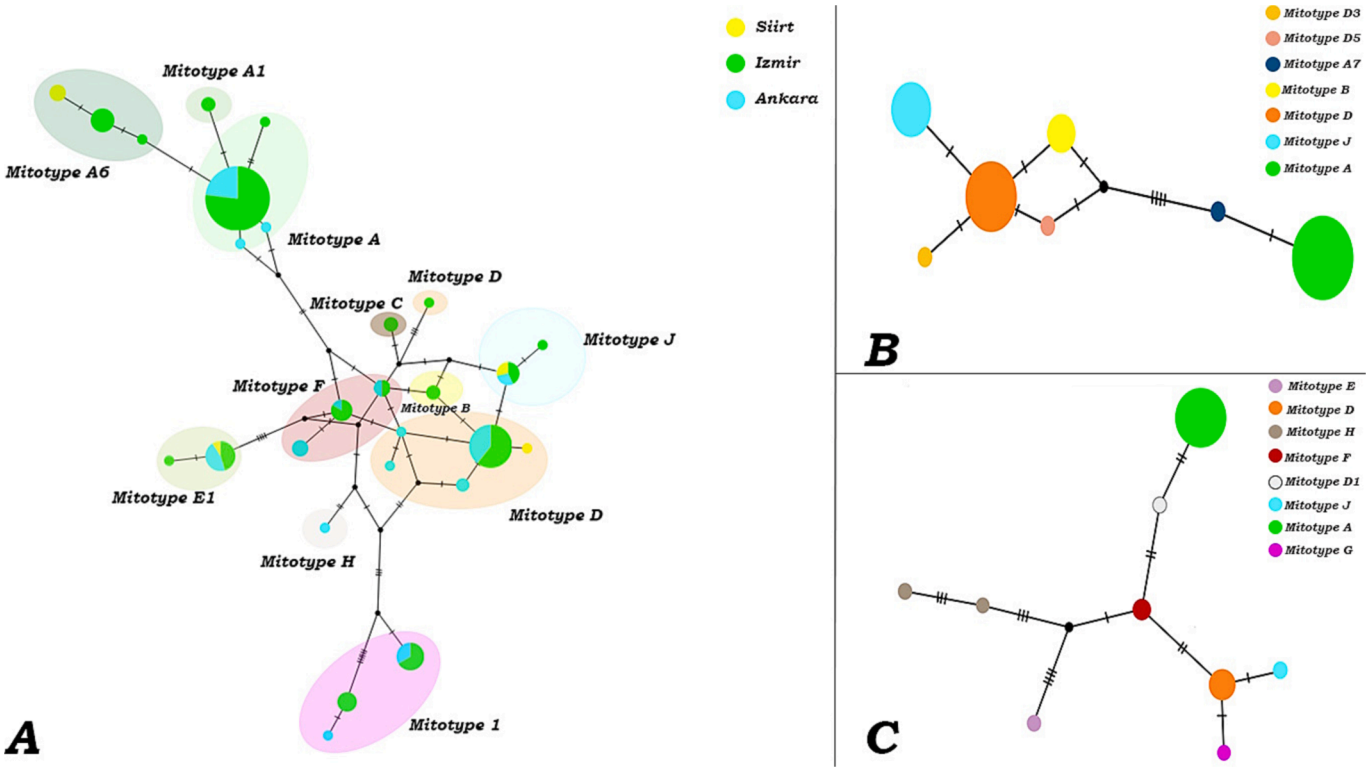

Fig. 2. The haplotype analyses showing mitotype diversity within **A)** random bred cats **B)** Van breeds and **C)** Angora breeds.

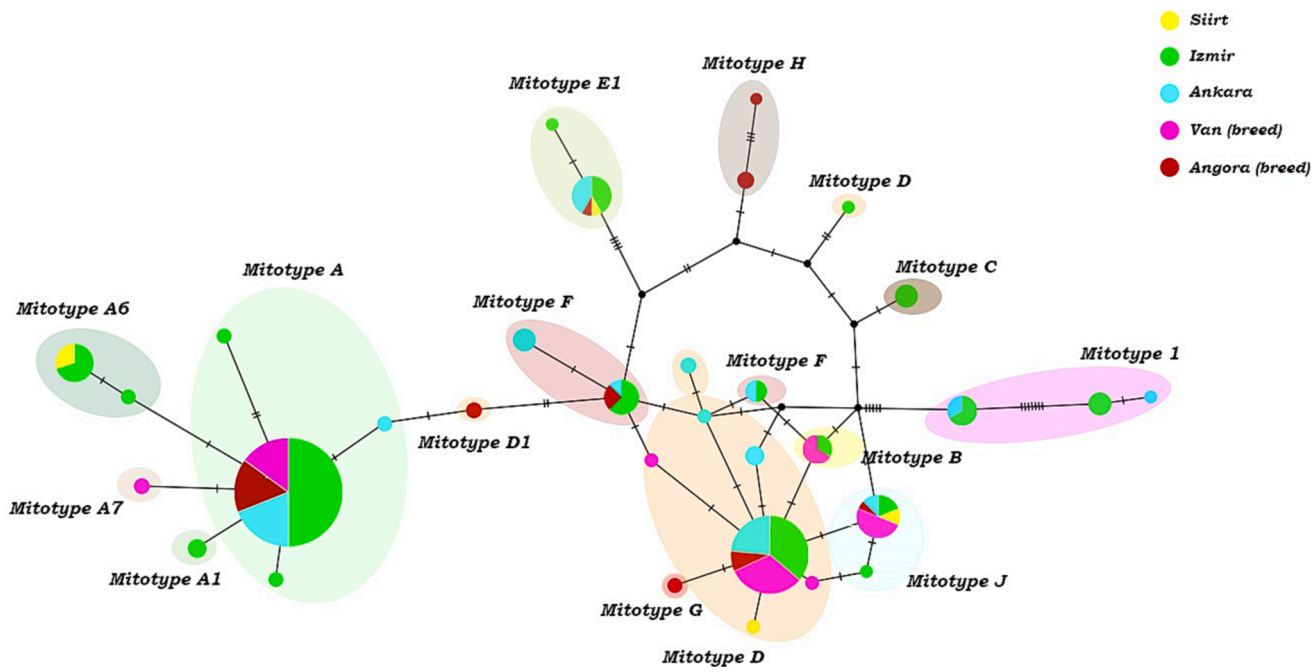

Fig. 3. The haplotype analyses showing mitotype diversity within all cats analyzed.

Table 2
Population genetic summary statistics for mtDNA control region sequences stratified by mitotype and population.

Mitotype/Population	N	S	H	Hd	θ (JC)	π (JC)	TD	Fu-Li's D	Fu-Li's F	Fu's Fs	R2
Mitotype A	120	8	8	0.28	37.5	11.9	−1.62	−2.88*	−2.90*	−5.19	0.04
Mitotype B	6	0	1	0							
Mitotype C	2	0	1	0							
Mitotype D	54	16	11	0.39	88.7	19.2	−2.38**	−3.24**	−3.86**	−8.28	0.05
Mitotype E	12	1	2	0.17	8.3	4.2	−1.14	−1.33	−1.44	−0.48	0.28
Mitotype F	12	3	3	0.57	25.7	20.2	−0.75	−0.87	−0.95	0.16	0.21
Mitotype G	1	0	1	0							
Mitotype H	3	3	2	0.67		50.5					0.47
Mitotype J	17	2	3	0.39	14.6	10.2	−0.74	−0.88	−0.82	−6.65	0.14
Mitotype 1	10	8	3	0.62	68.5	101.7	1.92#	0.93	1.33	4.35	0.24
Ankara	48	26	15	0.85	146.8	131.1	−0.12	−0.30	−0.28	−0.80	0.11
Izmir	108	30	17	0.75	143.1	131.3	−0.05	−0.08	−0.08	0.36	0.09
Siirt	7	14	4	0.81	142.1	157.7	1.00	0.64	0.79	2.43	0.21
Angora (breed)	28	15	9	0.66	96.8	93.7	−0.15	−0.39	−0.37	−0.13	0.12
Van (breed)	49	9	7	0.74	50.6	83.6	2.46*	0.70	1.50#	2.91	0.21
All Samples	240	34	32	0.78	141.1	122.0	−0.41	−0.88	−0.82	−6.65	0.07

Notes: N shows the number of sequences analyzed. S: Number of segregating sites, JC: Jukes-Cantor correction applied estimates, H: Number of haplotypes, Hd: Haplotype diversity. θ and π values represent percent sequence diversity, and for exact estimates table values should be multiplied by 10^{-4}. TD: Tajima's D test. # $0.05 < P < 0.1$, * $P < 0.05$, ** $P < 0.01$.

nucleotide diversity compared to the Van breed, however, haplotype diversity was slightly higher in the Van population (Table 2). When mitotypes were compared, mitotypes I and H had the highest haplotype diversity. Mitotype I also showed the highest nucleotide diversity based on segregating sites (θ), whereas mitotype D had the highest nucleotide diversity based on average pairwise nucleotide difference (π) (Table 2). Although mitotype A was the most common mitotype observed among all populations, it showed one the of lowest haplotype and nucleotide diversity estimates (Table 2).

Comparison of allele frequency spectrum summary statistics for neutrality tests showed mostly similar parameter estimates among mitotypes suggesting similar demographic and evolutionary histories, such as lack of positive or negative selection, drastic expansion or contraction, affecting the evolutionary histories of the mitotypes. However, Tajima's D and Fu-Li tests were more negative in mitotypes A and D indicating an abundance of rare, low frequency polymorphisms driven by recent mutations (P values <0.05). The star-like topology network structure in mitotypes D and A was rather different compared to other mitotypes, where many low frequency derived haplotypes are distributed among all cat populations (Supplemental Fig. 2). In contrary, the Tajima's D and Fu-Li tests were more positive in the mitotype I indicating abundance of intermediate frequency polymorphisms. Frequency spectrum neutrality tests among populations also showed similar parameter estimates among different populations suggesting similar demographic and evolutionary histories with no indication of selection or drastic population expansion or contraction. However, the Van breed showed rather positive Tajima's D and Fu-Li tests indicating an excess of intermediate frequency polymorphisms compared to rare variants segregating within the population.

4. Discussion

The captivating world of the domestic cat, a beloved and cherished companion, continues to intrigue researchers seeking to uncover the

origins of this remarkable species. While domestic cats hold a place as popular pets akin to dogs, their history remains less explored. In contrast to their canine counterparts, the evolutionary journey of domestic cats offers unique insights into the dynamic interaction between humans and animals. Turkey stands as the sole country encompassing nearly all three of the world's 34 biodiversity hotspots: Mediterranean, Irano-Anatolian, and the Caucasus. Additionally, it operates as a pivotal crossroads, linking Europe, the Middle East, Africa and Central Asia (Şekercioğlu et al., 2011). Beyond its geographical significance near the Fertile Crescent, a vital region for the evolution of neolithic agriculture and animal husbandry, Turkey accommodates almost half of the world's domesticated animals and breeds. These include goats, sheep, cattle, pigs, donkeys, mules, camels, horses, domestic birds, ducks, rabbits, bees, silkworms, dogs, and cats (Arbuckle et al., 2014; Yilmaz et al., 2016). Hence, the animal studies conducted here hold significant value in terms of enhancing our understanding of global animal biodiversity and safeguarding crucial disease-resistant animal genetic resources. Based on the distinctive characteristics of Turkey, we present a comprehensive report of mitotype and genetic diversity of both random bred and regional breed cats sampled from Aegean, Central Anatolia, and Southeastern Anatolia regions of Turkey. In this context, our study delves into the mitotype and genetic diversity of domestic cat populations, including the renowned Angora and Van breeds. These two pure breeds, originating in Turkey, bear significant historical and genetic importance. The Angora breed, characterized by its long, silky coat, and the Van breed, known for its distinct color patterns and affinity for water, provide valuable insights into the country's feline genetic heritage. A previous study involving 1394 cats from 25 diverse global populations indicated that 84% of all cats could be categorized into 12 universal mitotypes (Grahn et al, 2011). Our own analysis, based on mitotype classification, revealed the presence of nine universal mitotypes and one outlier mitotype in Turkey. Notably, we did not observe any unique mitotypes (sequences that cannot be assigned to any previously defined mitotypes).

Mitotypes A and D, making up over 70% of the observed mitotypes, emerged as the most prevalent in both random bred and pure-bred populations, aligning with previous findings (Grahn et al., 2011). In contrast, mitotypes B, C, G, and H were the rarest mitotypes observed in our samples. While these mitotypes are common in cat populations along the United States and Indian Ocean trade routes they appeared infrequently or were absent in the Southeastern Anatolia cat populations (Grahn et al., 2011). Interestingly, mitotype J displayed a distinct pattern being almost absent in the majority of random bred cat populations examined, with an exception for the Southeastern Anatolia random bred cat populations (Grahn et al., 2011). In our samples, however, mitotype J emerged as the third most frequent mitotype. It was predominantly observed in the Central Anatolia, Southeastern Anatolia random bred, and Van breed populations.

The historical bond between humans and cats is deeply rooted, with evidence suggesting that cats have shared symbiotic relationships with humans for thousands of years. Their role in controlling vermin and scavenging refuse heaps marks their enduring partnership with humans, shaping their evolutionary trajectory over time (Clutton-Brock, 1988). Unlike species that underwent radical transformation due to selective breeding, the form and function of cats remained relatively stable, undergoing more pronounced changes only in recent history with the advent of selective breeding for specific aesthetic traits (The Cat-Show, 1871). Drawing from genetic analyses of cat populations across the globe, our study aims to illuminate the intricate interplay between genetics, migration, and domestication. Through the lens of genetic polymorphisms, we unveil the dispersal patterns and migration histories of these feline companions. Notably, the genetic data accentuate the Fertile Crescent region as a significant hub of domestication, echoing findings from other domesticated species and suggesting a pivotal role of this region in shaping human-animal relationships (Vigne et al., 2004; Driscoll et al., 2007; Lipinski et al., 2008). While the most substantial population differentiation was evident between the Angora and Van breeds, none of the mitotypes displayed exclusivity to a particular population or breed. This absence of breed-defining mitotypes and the lack of sub structuring based on mitotypes underscored our observations. However, scrutiny of haplotype network analyses highlighted intriguing aspects. Breed cats, particularly the Van breed, exhibited closely related mitotypes, implying a lineage stemming from fewer common ancestors and featuring less admixture history than the Angora breed. The positive results of Tajima's D and Fu-Li tests in the Van breed might signify an older breed with selective pressure for or against certain mitotypes to maintain desired breed attributes. Comparative analysis revealed that nucleotide diversity in the Angora and Van breeds lagged behind that of random bred populations. When encompassing all samples, estimated nucleotide diversity surpassed prior reports from Turkey and ranked among the highest in global cat population estimates (Grahn et al., 2011).

However, several limitations are inherent in our study. Notably, population and breed sample sizes were uneven, with the Southeastern Anatolia Siirt population exhibiting a notably smaller sample size compared to other populations. Additionally, our study focused on populations from only three cities, thus warranting exploration of regions within the Fertile Crescent and along the Mediterranean coast. Moreover, our conclusions solely relied on mitochondrial control region sequence data. A more comprehensive understanding of genetic relatedness and evolutionary histories demands genome-wide sequence or nucleotide polymorphism data.

5. Conclusion

Mitotype profile was analyzed for the first time in random bred cats as well as pure breed (Turkish Angora and Turkish Van) by a comprehensive study. Accordingly, nine 'universal' mitotypes (A—J), and one 'outlier' mitotype group I were detected. Among these mitotypes, A and D were among the most prevalent mitotypes while C, G, and H were the least common mitotypes. Moreover, the haplotype structure in random bred cats was rather diverse and different compared to Angora and Van breeds. Future studies analyzing more samples from other regions that are part of the Fertile Crescent in Turkey may be helpful to reveal a more accurate mitotype profile and genetic diversity among random bred cats.

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Authors' contributions

Conceived and designed the experiments: CÜ, HC, ES. Performed the experiments: NB, MG, ES, HC, AEK, SEA. Analysed the data: HC, ES. Wrote the paper: ES, AEK, HC. Reviewed and edited the paper: CÜ, HC, ES, MD, NB. All authors have read and approved the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gene.2023.147849.

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