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Allozyme Variation in *Spalax leucodon* Nordmann, 1840 (Rodentia: Spalacidae) in the Area between Ankara and Beyşehir

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Abstract: Eighty-one specimens belonging to 3 populations of *Spalax leucodon* collected in the area between Ankara and Beyşehir were electrophoretically analyzed. Three enzyme systems, isocitrate dehydrogenase (*Idh*), esterase (*Est*) and α-glycerophosphate dehydrogenase (*α-Gpdh*), were screened using horizontal starch gel electrophoresis, and 5 loci were determined. Three loci (*Idh-1*, *Est-1*, *Est-3*) were polymorphic, and 2 (*Idh-2*, *α-Gpdh*) were monomorphic. Heterozygosity ranged from 0.1804 (in population A) to 0.2254 (in population K). Genetic divergency in 3 the populations resulted from the locus *Idh-1* (F_{st} = 0.0372). The mean value of the fixation index in 3 the populations (F_{st} = 0.0266) reflected little genetic differentiation. Genetic diversity estimated by Shannon's information index was moderate (I = 0.3202).

Key Words: *Spalax leucodon*, Allozyme, Genetic diversity, Turkey

Ankara ve Beyşehir Arasında Yayılış Gösteren *Spalax leucodon* (Rodentia: Spalacidae)'da Allozim Varyasyonu

Özet: Ankara-Beyşehir hattında yayılış gösteren 3 *Spalax leucodon* populasyonuna ait 81 örnek elektroforetik olarak incelendi. Izositrat dehidrojenaz (*Idh*), esteraz (*Est*) ve α-gliserofosfat dehidrojenaz (*α-Gpdh*) olmak üzere üç enzim sistemi horizontal nişasta jel elektroforezi kullanılarak analiz edildi ve beş enzimatik gen lokusu belirlendi. Üç lokus (*Idh-1*, *Est-1*, *Est-3*) polimorfik ve iki lokus (*Idh-2*, *α-Gpdh*) monomorfik bulundu. Populasyonlar arası heterozigotluk 0.1804 (populasyon A'da) ile 0.2254 (populasyon K'de) arasında değişti. İncelenen 3 populasyonda genetik farklılaşma *Idh-1* lokusundan kaynaklandığı tespit edildi (F_{st} = 0,0372). 3 populasyonda fixation indeksi'nin ortalama değeri (F_{st} = 0,0266) düşük düzeyde genetik farklılaşmayı yansıttı. Shannon'nun information indeksi ile tahmin edilen genetik çeşitlilik orta seviyedeydi (I = 0,3202).

Anahtar Sözcükler: *Spalax leucodon*, Allozim, Genetik farklılaşma, Türkiye

Introduction

Mursaloğlu (1979) recorded *Spalax leucodon* from Anatolia and *Spalax ehrenbergi* from the southern Taurus Mountains and SE Turkey. Kıvanç (1988) reviewed Turkish *Spalax* based on morphological and biometrical aspects, and recorded *Spalax leucodon* and *Spalax ehrenbergi* along with 7 subspecies from Turkey. Recent studies on Turkish *Spalax leucodon* focused on the karyology of the species, and 19 karyotypic forms (2n = 36-62, NF = 68-84) were recorded (Soldatovic and Savic, 1978; Savic and Soldatovic, 1979; Yüksel, 1984; Gülkaç and Yüksel, 1989; Butler et al., 1993; Nevo et al., 1994, 1995; Coşkun, 1996a, 1996b; Ivanitskaya et al., 1997; Sözen and Kıvanç, 1998a, 1998b; Sözen et al., 1999, 2000a, 2000b; Coşkun, 1999; Yüksel and Gülkaç, 2001; Tez et al., 2002; Coşkun, 2003). It has been discussed whether these karyotypic forms determined in Turkey are separate species. Although karyotypic forms are considered by Nevo et al. (1994, 1995) as biological species, genetic studies on karyotypic forms are poor in Turkey.

Nevo et al. (1994) determined an increasing trend in heterozygosity in *S. leucodon* in Turkey toward the ecologically harsh, arid, and climatically unpredictable and geologically young central Anatolian Plateau from the west, north, south, and east, repeating from all directions. According to Nevo et al. (1995), heterozygosity in 4 specimens from the Ankara population of 2n = 62 is high, and it is lower in five specimens from the Beyşehir population of 2n = 40. The

studies mentioned above were performed on small series collected from 2 localities, Ankara and Beyşehir. This may be insufficient to determine genetic changes in mole rat populations along an area extending from the south to the north. In this study, it was aimed to determine the level of genetic differentiation in the area between Ankara and Beyşehir, and to contribute to the population genetics and evolution of *S. leucodon*.

Materials and Methods

Eighty-one subterranean mole rat specimens collected between Ankara and Beyşehir in 2000-2003 were studied electrophoretically. All specimens were karyotyped as described by Ford and Hamerton (1956). Genetic variation was assessed at 5 presumptive loci encoding 3 enzyme systems (Table 1). The samples were electrophoresed on horizontal starch gels. Tissues were preserved in the laboratory at -70 °C until electrophoresis. Electrophoresis was performed on gels composed of 11% hydrolyzed starch. α-Naphthyl acetate was used as the substrate for esterase. Genotype and allele frequencies were calculated directly from observed banding patterns. The genetic interpretation of electrophoretic patterns was based on the genotype of an individual as a homozygote or heterozygote. The information given by Harris and Hopkinson (1976) was also used for analysis of the structures of the proteins studied. Alleles were designated alphabetically in order of their relative mobility, with most anodally migrating electromorph designated "A''. The resulting data matrix of alphabetically designated allele phenotypes was analyzed using POPGENE version 1.31 (Yeh et al., 1997) to estimate genetic diversity parameters: observed number of alleles per locus (*A*), expected heterozygosity (*He*), and Wright's F_{st} value for polymorphic loci (Wright, 1978). Nei's unbiased genetic distance (*D*) between populations was computed using the program (Nei, 1978). Genetic diversity was also estimated using Shannon's information index (I) (Lewontin, 1972). A locus is considered polymorphic if the frequency of the common allele is not greater than 0.99 or 0.95, respectively. To examine the genetic relationship among populations, a dendrogram was constructed by unweighted paired group cluster analysis (UPGMA) using POPGENE version 1.31 (dendrogram based Nei, 1978).

Results

Eighty-one specimens and 6 populations of *S. leucodon* collected from 20 localities (Figure 1) were studied. Five loci (*Idh-1*, *Idh-2*, *Est-1*, *Est-3*, and *α-Gpdh*) were analyzed. Because of the difficulties in the *Est-2* locus, 2 loci (*Est-1*, *Est-3*) were evaluated. Three loci (*Idh-1*, *Est-1*, *Est-3*) were polymorphic, and 2 (*Idh-2*, *α-Gpdh*) were monomorphic.

Isocitrate dehydrogenase (*Idh-1* and *Idh-2*): Two isozymes were determined. One (*Idh-1*) of them moved anodally, and the other (*Idh-2*) remained in its origin. *Idh-1* was called the cytosolic form, and *Idh-2* was called the mitochondrial form (Figure 2). *Idh-1* was polymorphic, and had 2 alleles. The fast and slow alleles were considered as A and B, respectively. Because this enzyme system has a dimeric structure, in heterozygotes specimens have 3 bands in the zymograms.

Table 1. Reaction systems using for each enzyme system.

Enzymes	Electrode buffers mM	Gel buffers mM	References	Electrophoresis conditions	References for histochemical stains
Est (E.C. 3.1.1.1)	300 nM boric acid, 60 nM NaOH, pH: 8.2	76 nM tris, 5 nM citric acid pH: 8.65	Ayala et al. 1972	8 v/cm 5 h	Hillis and Moritz 1990
Idh (E.C. 1.1.1.42)	0.687 M tris 0.157 M citric acid, pH: 8.0	Electrode buffer diluted at ratio 1/29	Selander et al. 1971	7 v/cm 5 h	Ayala et al. 1972
α-Gpdh (E.C. 1.1.1.8)	0.687 M tris 0.157 M citric acid, pH: 8.0	Electrode buffer diluted at ratio 1/29	Selander et al. 1971	7 v/cm 6 h	Harris and Hopkinson 1976

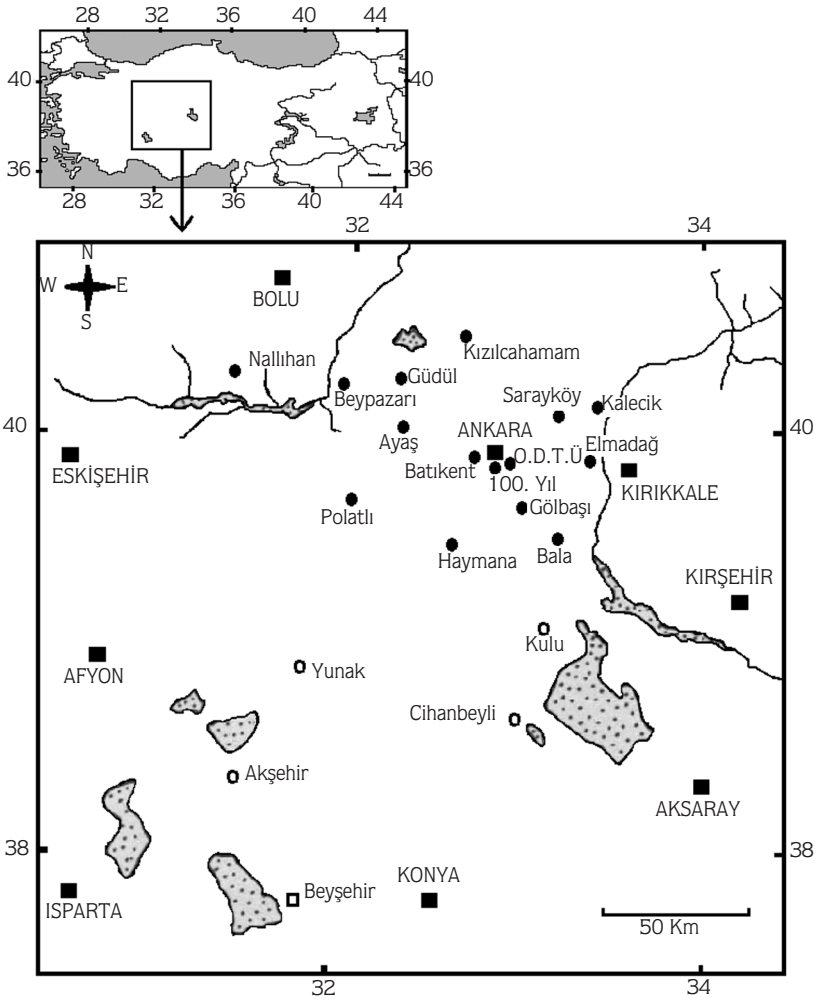

Figure 1. Map showing 20 localities of *S. leucodon* between Ankara and Beyşehir. ● = population A, ❍ = population K, ❑ = population B, and ■ = city center.

Esterase (*Est-1* and *Est-3*): Three isozymes (*Est-1*, *Est-2*, *Est-3*), which moved anodally, were recorded. All isozymes were also polymorphic. Only *Est-1* and *Est-3* were evaluated. *Est-2* locus was not recorded due to its poor banding pattern. There were 3 alleles in the *Est-1* locus. They were named A, B, C according to their relative mobility. The monomeric structure of this locus gave a phenotype with 2 bands (AB) in heterozygotes. The *Est-3* locus had 4 alleles, named A, B, C, and D. Five heterozygote phenotypes (AB, BC, CD, AC, and CD) were observed in the *Est-3* locus (Figures 3, 4).

α-Glycerophosphate dehydrogenase (α-*Gpdh*): This locus was monomorphic, and fixed for a single allele (Figure 5).

The *F* values of Wright (1978) are useful for estimating the amount of genetic differentiation between species (Table 2). High values of F_{st} are considered to reflect substantial differences at any given locus, and are expected when studying separate species or populations that have diverged to a certain degree. The mean value observed for the individual inbreeding coefficient was F_{is} = 0.2828. The mean value of the overall individual coefficient was F_{it} = 0.3019. The mean value of the fixation index was F_{st} = 0.0266, indicating that 2.66% of genetic variation in the 3 mole rat populations reflected little genetic differentiation. On the basis of 3 polymorphic loci, genetic divergency in the 3 populations resulted from the locus *Idh-1* (F_{st} = 0.0372) rather than form *Est-1* or *Est-3*.

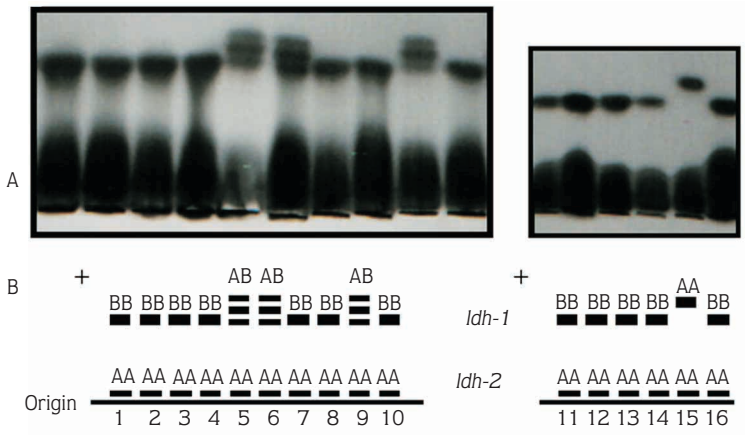

Figure 2. Zymogram (A) and diagrammatic presentation (B) of 2 isozymes (*Idh-1* and *Idh-2*) of isocitrate dehydrogenase in *S. leucodon*. 1- 4. Beyşehir, 5-6. Yunak, 7. Akşehir, 8-10. Kalecik, 11-13. Gölbaşı, 14. Beyşehir, 15. Akşehir, 16. Gölbaşı.

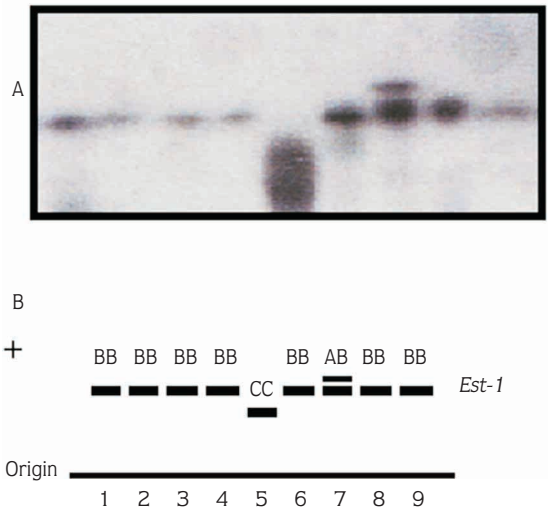

Figure 3. Zymogram (A) and diagrammatic presentation (B) of esterase (*Est-1*) in *S. leucodon*. 1-4. Gölbaşı, 5-7. Beypazarı, 8-9. Bala.

Table 2. Variable loci and Wright's non-hierarchical *F*-coefficients for all the population samples.

Locus	Sample Size	F_{is}	F_{it}	F_{st}
Idh-1	81	0.102	0.1354	0.0372
Est-1	81	0.1444	0.1483	0.0046
Est-3	81	0.4008	0.4145	0.0228
Mean	81	0.2828	0.3019	0.0266

The overall mean heterozygosity with respect to 5 loci for the 3 populations was $He = 0.2491$ and ranged from 0.1804 (population A) to 0.2254 (population K). The overall mean number of alleles per locus was $A = 2.2$. The highest values of A appeared in population K. The

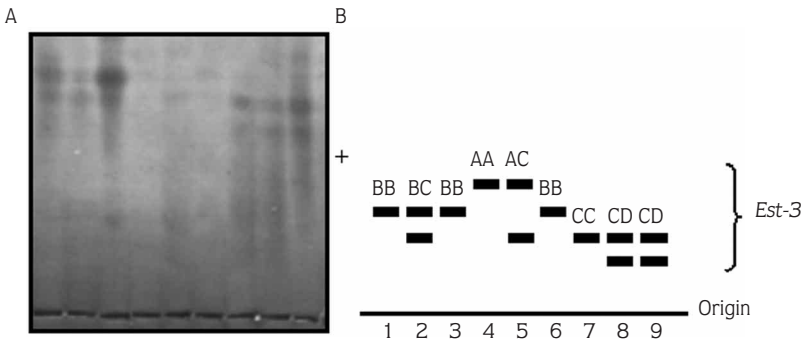

Figure 4. Zymogram (A) and diagrammatic presentation (B) of esterase (*Est-3*) in *S. leucodon*. 1-3 Beyşehir, 4-5. Yunak, 6. Akşehir, 7-9. Kalecik.

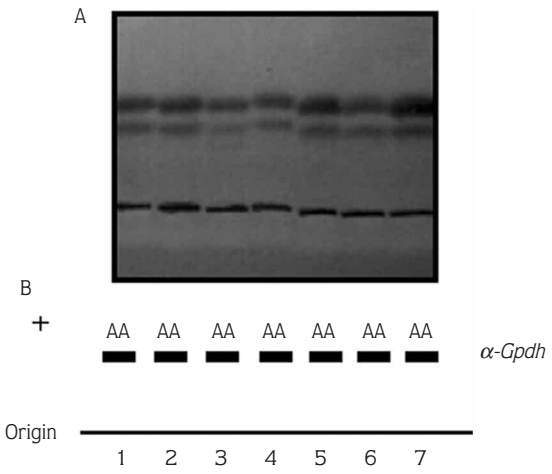

Figure 5. Zymogram (A) and diagrammatic presentation (B) of α-glycerophosphate dehydrogenase (*α-Gpdh*) in *S. leucodon*. 1-2. Elmadağ, 3. Ayaş, 4. Güdül, 5. Nallıhan, 6-7. Haymana.

Shannon information index (I) ranged from 0.2693 to 0.3459, with an average of 0.3202 for the 3 populations (Table 3).

The highest genetic differentiation was in *Idh-1*, and the lowest in *Est-1* and *α-Gpdh* based on genetic indices. The DD genotype was only observed at *Est-3* in Nallıhan (n = 1) and Beypazarı (n = 3). Similarly, the genotypes BC and CC of *Est-1* were only determined in Ayaş and Beypazarı (Table 4). According to Nei's genetic identity matrix (Nei, 1978), the smallest genetic distance was observed between populations K and B ($D = 0.0026$), and the greatest was between populations A and K ($D = 0.0123$) (Table 5). The UPGMA dendrogram separated population A from populations B and K (Figure 6).

Table 3. Mean values of genetic variation based on 5 allozymic loci in 3 populations of *S. leucodon* between Ankara and Beyşehir. SE: standard error, n: the number of specimens, Obs-Het (Ho): observed heterozygosity, Exp-Het (He): expected heterozygosity (expected heterozygosity was computed using Levene, 1949 and Nei, 1978), A: observed number of alleles, I: Shannon's information index.

Population	Collecting Site	n		Obs-Het (SE)	Exp-Het (SE)	*A* (SE)	I (SE)
	Kızılcahamam	4		0.2000	0.2286	1.6000	0.3204
	Güdül	1		0.2000	0.2000	1.2000	0.1386
	Ayaş	1		0.2000	0.2000	1.2000	0.1386
	Nallıhan	1		0.2000	0.2000	1.2000	0.1386
	Beypazarı	3		0.2000	0.3067	1.8000	0.4220
	Kalecik	4		0.1000	0.0857	1.2000	0.1125
	Sarayköy	3		0.1333	0.2133	1.4000	0.2546
Population A	Elmadağ	10		0.1000	0.0958	1.2000	0.1295
	Batıkent	3		0.2000	0.1733	1.4000	0.2174
	100. Yıl	3		0.0667	0.0667	1.2000	0.0901
	O.D.T.Ü.	1		0.0000	-	1.0000	0.0000
	Polatlı	6		0.1000	0.1061	1.2000	0.1358
	Gölbaşı	7		0.1143	0.1055	1.2000	0.1366
	Haymana	6		0.0667	0.1091	1.2000	0.1386
	Bala	2		0.2000	0.1667	1.4000	0.2079
	Total:	55	Mean:	0.1236 (0.2102)	0.1804 (0.2468)	1.3483 (0.5590)	0.3082 (0.4038)
Population B	Beyşehir						
	Total:	12	Mean:	0.1500 (0.1807)	0.1833 (0.2217)	1.6000 (0.5477)	0.2693 (0.3029)
	Cihanbeyli	6		0.1667	0.1909	1.6000	0.2748
Population K	Kulu	2		0.0000	0.0000	1.0000	0.0000
	Yunak	2		0.3000	0.2333	1.4000	0.2511
	Akşehir	4		0.1000	0.0857	1.2000	0.1125
	Total:	14	Mean:	0.1429 (0.1821)	0.2254 (0.2800)	1.8000 (0.8367)	0.3459 (0.4194)
All Population	Total:	81	Grand Mean:	0.1309 (0.1773)	0.1904 (0.2491)	2.2000 (1.3038)	0.3202 (0.4019)

Table 4. Allelic frequency of 3 polymorphic loci analyzed for 3 populations of *S. leucodon* between Ankara and Beyşehir. Pop: (population).

Pop	Collecting Site	Alleles								
		Idh-1		*Est-1*			*Est-3*			
		A	B	A	B	C	A	B	C	D
	Kızılcahamam	0.250	0.750	-	1.000	-	0.250	0.500	0.250	-
	Güdül	-	1.000	-	1.000	-	0.500	0.500	-	-
	Ayaş -	1.000	-	1.000	-	0.500	0.500	-	-	
	Nallıhan	1.000	-	-	1.000	-	-	-	0.500	0.500
	Beypazarı	-	1.000	-	0.667	0.333	-	0.333	0.333	0.333
	Kalecik	0.250	0.750	-	1.000	-	-	-	1.000	-
	Sarayköy	0.667	0.333	-	1.000	-	-	0.667	0.333	-
Pop. A	Elmadağ	-	1.000	-	1.000	-	-	0.650	0.350	-
	Batıkent	0.333	0.667	-	1.000	-	-	0.167	0.833	-
	100. Yıl	1.000	-	-	1.000	-	-	0.833	0.167	-
	O.D.T.Ü.	-	1.000	-	1.000	-	-	-	1.000	-
	Polatlı	0.167	0.833	0.083	0.917	-	-	0.333	0.667	-
	Gölbaşı	-	1.000	-	1.000	-	-	0.429	0.571	-
	Haymana	-	1.000	-	1.000	-	-	0.500	0.500	-
	Bala -	1.000	-	1.000	-	-	0.250	0.500	0.250	
	Mean:	0.164	0.836	0.009	0.973	0.018	0.036	0.445	0.482	0.036
Pop. B	Beyşehir									
	Mean:	0.208	0.792	0.042	0.958	-	-	0.625	0.375	-
	Cihanbeyli	0.167	0.833	0.083	0.917	-	-	0.333	0.667	-
Pop. K	Kulu -	1.000	-	1.000	-	-	1.000	-	-	
	Yunak	0.500	0.500	-	1.000	-	0.750	-	0.250	-
	Akşehir	0.750	0.250	-	1.000	-	-	1.000	-	-
	Mean:	0.357	0.643	0.036	0.964	-	0.107	0.571	0.321	-
All Pop	Grand Mean:	0.204	0.796	0.018	0.969	0.012	0.043	0.494	0.438	0.025

Table 5. Values of Nei's genetic identity (above diagonal) and genetic distance (below diagonal) between the 3 populations of *S. leucodon* between Ankara and Beyşehir (Nei, 1978).

Populations	Population A	Population B	Population K
Population A	******	0.9965	0.9878
Population B	0.0036	******	0.9974
Population K	0.0123	0.0026	******

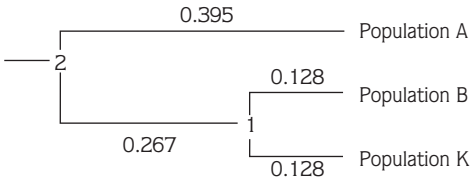

Figure 6. UPGMA dendrogram summarizing the genetic relationships among the studied populations of *S. leucodon*. D = Nei's (1972) unbiased genetic distance, based on 5 enzyme loci. The cophenetic correlation coefficient is 1.00.

Discussion

Nevo et al. (1994) studied 37 gene loci of 55 specimens of *S. leucodon* from 20 localities in Turkey. According to Nevo et al. (1994), in *S. leucodon*, mean number of alleles per locus (*A*) is 1.081, observed heterozygoty (*Ho*) is 0.038, and expected heterozygoty (*He*) is 0.038. The values *A, Ho*, and *He* in populations of *S. leucodon* between Ankara and Beyşehir were higher than those given by Nevo et al. (1994) for *S. leucodon* (Tables 3, 4).

Nevo et al. (1995) analyzed 37 gene loci, and determined a genetic distance (*D*) of 0.154 between the Beyşehir population, which has 2n = 40, and the Ankara population, which has 2n = 62. According to Nevo et al. (1995), (*A*) is 1.027, and (*He*) is 0.014 in the Beyşehir population, (*A*) is 1.243 and (*He*) is 0.088 in Ankara population, and (*A*) is 1.135 and (*He*) is 0.045 in the Konya population (2n = 62). The genetic distance between the Konya and Ankara populations is 0.010, and that between Beyşehir and Konya populations is 0.152. We compared the values (*A*) and (*He*) of 5 loci analyzed in the 3 populations between Ankara and Beyşehir with those given by Nevo et al. (1995) for Beyşehir, Konya and Ankara populations of *S. leucodon*, and found that our genetic values were higher than those given by Nevo et al. (1995) (Tables 3, 4).

On the basis of 5 genetic loci, this study shows that there is no increase in heterozygosity in *S. leucodon* populations in the area from Beyşehir (southern part of this area) to Ankara (northern part). These findings are not consistent with the published data (Nevo et al., 1994, 1995). The value of *Ho* ranges from 0.00 to 0.300 in population A (Ankara populations), being changeable even in localities very close to each other. That is, this value is 0.0667 in 100. Yıl, but it is 0.200 in Batıkent, 6 km away. In contrast to Nevo et al. (1994, 1995), who analyzed 2 karyotypic forms (2n = 40 and 2n = 62), in our study, heterozygosity values do not increase in the karyotypic form 2n = 60 distributed between Ankara and Beyşehir. Notwithstanding, according to Nevo et al. (1994, 1995), Beyşehir and Ankara populations presumably represent 2 distinct species; the value of the genetic distance between Beyşehir and Ankara populations ($D = 0.036$) in this study is lower than those found in other subterranean rodent species (Nevo, 1999) and other rodents (Filippucci et al., 1991). However, genetic diversity based on *He, Ho, A*, Shannon's information index (I), and Wright's fixation index (F_{st}) of the 3 populations investigated showed a moderate genetic differentiation in populations A, B and K. The value of F_{st} (0.0266) indicates that the amount of gene flow between subpopulations is high. Nevo et al. (1994) described an increasing trend in heterozygosity in *S. leucodon* in Turkey toward the ecologically harsh, arid, and climatically unpredictable and geologically young central Anatolian Plateau. Ankara, Beyşehir and Konya have the same climate. Therefore, genetic analysis reflected a moderate genetic differentiation between 3 populations. However, the climate of Kızılcahamam, located in the most northerly part of the Beyşehir-Ankara area, is more rainy than that of the other localities studied. Heterozygosity (*Ho*) in this locality is 0.200. There is no geographical barrier between the populations examined in this study. This supports a parapatric speciation model in the population of *S. leucodon* between Ankara and Beyşehir.

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