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A distinctive locus among three *Passer* species inferred from allozyme data

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Abstract: This study was conducted on three of the four *Passer* species found in Turkey. The aim of this study was to determine the genetic variations and genetic differentiations of *Passer* subpopulations in Turkey. The population genetics of *Passer domesticus, P. montanus* and *P. hispaniolensis* were studied according to variations at allozymic loci. The allozyme variations at 23 loci were examined, among which *Ca*, *Ck*, *Est*, *Idh-s* and *Idh-m* were found to be polymorphic. The *Passer* subpopulations were separated into three main groups in a tree. Group I consisted mostly of subpopulations from Black Sea and Aegean regions, with *P. domesticus* and *P. hispaniolensis* subpopulations nested in the first part of the group. Group II was formed by Central Anatolian and Mediterranean *P. domesticus* subpopulations. Group III consisted only of subpopulations of *P. montanus*. Furthermore, *G3pdh-2* was identified as a distinctive locus that separated *P. montanus* from the other species.

Keywords: Genetic differentiations, *P. domesticus*, *P. hispaniolensis*, *P. montanus*, Turkey.

Introduction

The genus *Passer* includes four species in Turkey. Spanish sparrow *P. hispaniolensis* is migratory, whereas the two other widespread species, House sparrow *P. domesticus* and Tree sparrow *P. montanus*, are native, and Dead Sea sparrow *P. moabiticus* exhibits a narrow distribution that is restricted to southwest Turkey (Snow and Perrins, 1998; Mullarney et al., 2004). This study was conducted on *P. domesticus*, *P. montanus* and *P. hispaniolensis,* which are widespread in Turkey. Their subspecies have been described morphologically. Five subspecies of *P. domesticus* are found in Turkey: *P. d. domesticus* and *P. d. balearoibericus* have been observed in west Turkey, *P. d. colchicus* in northeast Turkey, *P. d. mayaudi* in eastern Turkey, and *P. d. biblicus* in south Turkey. Two subspecies of *P. montanus* are distributed in Turkey: *P. m. montanus* in the west and *P. m. transcausicus* in the east. *P. h. hispaniolensis* is one of the two subspecies of *P. hispaniolensis*, which has been observed in west Turkey; the other is *P. h. transcaspius*, from eastern Turkey (Roselaar, 1995).

Allozyme studies of *Passer* species were first conducted by Bush (1967) and Bush and Farrar (1969), in *P. domesticus*. St. Louis and Barlow (1987) compared six populations of *P. montanus* using 29 enzyme loci. St. Louis and Barlow (1988) performed an allozyme study of introduced, native and ancestral populations of *P. montanus* to clarify genetic differences. The introduced population exhibited less genetic variation than did the ancestral population, probably due to the founder effect. St. Louis and Barlow (1991) determined that the average heterozygosity and average number of alleles per locus in the introduced North American populations were higher than in the ancestral German populations. Bates and Zink (1992) compared *P. domesticus* individuals to detect variations in gene frequencies in seasonally collected specimens; these authors analyzed 29 allozyme loci. Fleischer and Murphy (1992) found a positive relationship between allozyme heterozygosity and the level of lipid deposition in winter. Thus, the previous allozyme studies of genetic variations in *Passer* sparrow populations have focused on *P. domesticus* and *P. montanus*.

Although a few studies have been conducted on the three widespread *Passer* species recorded in Turkey listed above, there are no comparative genetic analyses available. The aim of this study was to investigate the genetic characteristics of these species of *Passer* and to detect variations among subpopulations from Turkey. We

previously analyzed the allozyme variability of *P. hispaniolensis* (Saygılı and Yiğit, 2013), which we compare with those of the other two *Passer* species in the present work.

Materials and Methods

Passer domesticus and *P. montanus* subpopulations were sampled from 13 and 3 different localities, respectively. In our analyses, 109 *P. domesticus* and 34 *P. montanus* specimens were included. These native birds were compared with the migratory sparrow species *P. hispaniolensis*, of which 32 specimens were analyzed previously in Saygılı and Yiğit (2013). The sampling localities of all specimens are shown in Figure 1.

The sparrows were caught using standard mist netting methods and then killed with an overdose of ether to obtain muscle tissue samples, with permission from the Ankara University Local Ethics Committee for Animal Experiments. Homogenates obtained from breast muscle tissues were used for allozyme analysis. A total of 18 enzyme systems encoded by 23 loci were examined: ACON (4.2.1.3 Aconitase hydratase; *Acon-m*); ALD (4.1.2.13 Aldolase; *Ald*); CA (4.2.1.1 Carbonic anhydrase; *Ca*); CK (2.7.3.2 Creatine kinase; *Ck*); EST (3.1.1.1 Esterase; *Est*); FUM (4.2.1.2 Fumarase; *Fum*); G3PDH (1.1.1.8 Glycerol-3-phosphate dehydrogenase; *G3pdh-1*, *G3pdh-2*); GPI (5.3.1.9 Glucose-6-phosphate isomerase; *Gpi*); IDH (1.1.1.42 Isocitrate dehydrogenase; *Idh-s*, *Idh-m*); LDH (1.1.1.27 Lactate dehydrogenase; *Ldh*); MDH (1.1.1.37 Malate dehydrogenase; *Mdh-s*, *Mdh-m*); ME (1.1.1.40 Malic enzyme; *Me-s*, *Me-m*); PGD (1.1.1.44 Phosphogluconate dehydrogenase; *Pgd*); PGM (5.4.2.2 Phosphoglucomutase; *Pgm*); PK (2.7.1.40 Pyruvate kinase; *Pk*); PNP (2.4.2.1 Purine nucleoside phosphorylase; *Pnp*); SOD (1.15.1.1 Superoxide dismutase; *Sod-s*, *Sod-m*) and XDH (1.1.1.204 Xanthine dehydrogenase; *Xdh*). The applied starch gel electrophoresis and staining protocols were modified from Shaw and Prasad (1970), Harris and Hopkinson (1976), Aebersold et al. (1987), Hillis et al. (1996), May (1998), Verimli et al. (2000) and Manchenko (2003). The electrophoretic band patterns were analyzed according to Harris and Hopkinson (1976). The presumptive alleles were designated alphabetically according to the relative mobility of their corresponding product bands.

The electrophoretic data were analyzed using BIOSYS-II (Swofford and Selander 1989). We calculated

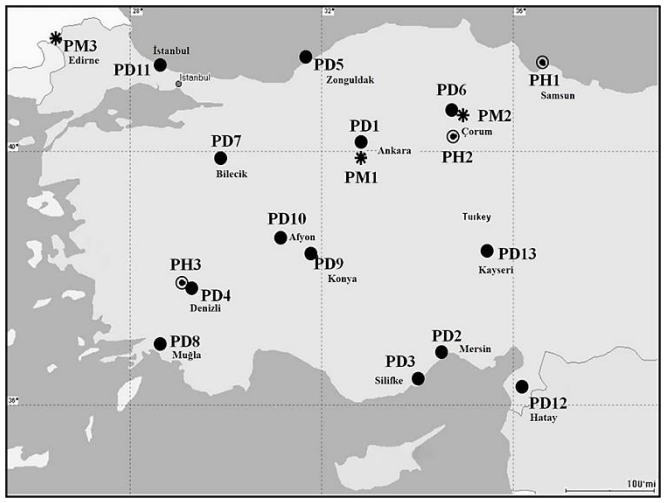

Figure 1. Sampling localities (PD; *P. domesticus*, PM; *P. montanus*, PH; *P. hispaniolensis*)

the following parameters: allele frequencies (f); the mean number of alleles per locus (A); the proportion of polymorphic loci (P, 95% criterion; a locus was considered polymorphic if the frequency of the most common allele was ≤0.95); and the mean heterozygosity (H; *Ho*=observed and *He*=expected frequencies of heterozygotes under Hardy-Weinberg equilibrium). The amount of genetic divergence between sub-populations was estimated with the indices of standard genetic identity (I) and distance (D). The genetic identity (I, the unbiased genetic identity) and distance (D, the unbiased genetic distance) values were calculated according to Nei (1978). F-statistics (F_{IS}, F_{IT} and F_{ST}) were used to summarize the distribution of genetic variation between and within the sub-populations. F_{IS} was used to represent the deficiency in heterozygosity due to inbreeding in subpopulations; F_{IT} was employed to represent the total deficiency in heterozygosity due to inbreeding; and F_{ST} was used to represent the total deficiency in heterozygosity due to subpopulations. The impact of migration on F_{ST} was determined from the *Nm* value, calculated with the formula [$Nm=(1-F_{ST})/4\ F_{ST}$] (N: population size, m: migration rate), according to Wright (1978). A UPGMA (unweighted pair-group method) diagram was produced using the NTSYS-pc 2.1 program (©2000 by Applied Biostatistics, Inc.) (Rohlf, 2000) using the Jaccard coefficient of the similarity matrix.

Results

Five of the 23 examined loci showed variability in all subpopulations; *Ca*, *Ck*, *Est*, *Idh-s* and *Idh-m*. *Ck* was the

Table 1. Allele frequencies of polymorphic loci in Passer domesticus and Passer montanus subpopulations

		Passer domesticus													*Passer montanus*			*Passer hispaniolensis**		
Locus	Allele	PD1	PD2	PD3	PD4	PD5	PD6	PD7	PD8	PD9	PD10	PD11	PD12	PD13	PM1	PM2	PM3	PH1	PH2	PH3
Ca	A	1.000	1.000	1.000	1.000	0.938	1.000	1.000	1.000	0.833	0.900	0.950	0.929	1.000	0.955	0.875	0.938	0.500	0.900	1.000
	B	0.000	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.167	0.100	0.050	0.071	0.000	0.045	0.125	0.063	0.500	0.100	0.000
Ck	A	0.167	0.150	0.143	0.429	0.313	0.429	0.556	0.500	0.500	0.600	0.650	0.500	0.500	0.045	0.625	0.125	0.667	0.233	0.250
	B	0.833	0.850	0.857	0.571	0.688	0.571	0.444	0.500	0.500	0.400	0.350	0.500	0.500	0.955	0.375	0.875	0.333	0.767	0.750
Est	A	0.350	0.000	0.375	0.071	0.250	0.286	0.278	0.222	0.250	0.333	0.750	0.357	0.200	0.786	0.500	0.750	0.125	0.208	0.250
	B	0.650	1.000	0.625	0.929	0.750	0.714	0.722	0.778	0.750	0.667	0.250	0.643	0.800	0.214	0.500	0.250	0.875	0.792	0.750
G3pdh-2	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**0.000**	**0.000**	**0.000**	1.000	1.000	1.000
	B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	**1.000**	**1.000**	0.000	0.000	0.000
Idh-s	A	1.000	1.000	1.000	0.714	1.000	1.000	0.944	0.889	0.833	1.000	1.000	0.857	1.000	0.864	1.000	1.000	0.944	0.800	0.500
	B	0.000	0.000	0.000	0.286	0.000	0.000	0.056	0.111	0.167	0.000	0.000	0.143	0.000	0.136	0.000	0.000	0.056	0.200	0.500
Idh-m	A	0.333	0.500	1.000	0.714	0.875	1.000	0.778	0.778	0.000	0.800	0.400	0.214	0.200	0.545	0.000	0.000	1.000	0.733	0.750
	B	0.667	0.500	0.000	0.286	0.125	0.000	0.222	0.222	1.000	0.200	0.600	0.786	0.800	0.455	1.000	1.000	0.000	0.267	0.250

*Saygılı and Yiğit (2013)

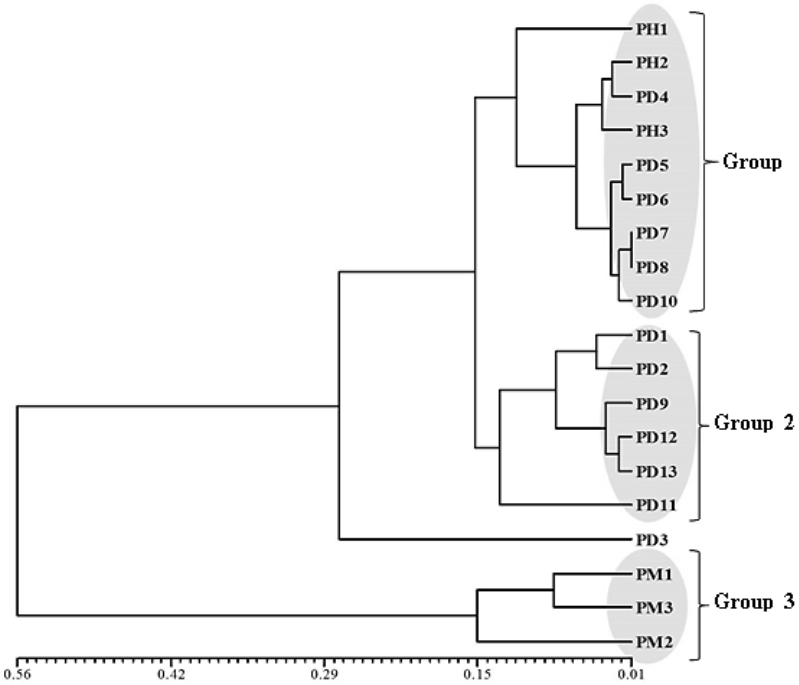

Figure 2. The UPGMA dendrogram of *Passer* subpopulations constructed based on Nei's unbiased genetic distances.

most polymorphic locus. The evaluated subpopulations exhibited variations in at least two but as many as all five loci. PD12, PM1 and PH2 subpopulations showed variations at all of the loci. Only PD2 subpopulation did not exhibit variation at *Est* locus; the B allele was fixed at this locus in this subpopulation. *G3pdh-2* did not display any variations, with the A allele fixed at this locus in *P. domesticus* and *P. hispaniolensis* and the B allele fixed in *P. montanus* subpopulations; therefore, this was the only distinctive locus among these three *Passer* species (Table 1).

Subpopulations of *P. domesticus* showed the highest percentage of polymorphic loci (*P*), at 21.7% for PD12, whereas the lowest *P* value was 8.7%, in PD2, PD3 and PD6. The average *P* value was 15.05% for all localities. All *P. montanus* subpopulations presented the same *P*-value at 13%. The highest observed heterozygosity (*Ho*) was 0.072, in PD10, and the lowest was 0.013, in PD2. The expected heterozygosity exhibited the highest value in PD12, at 0.075, followed by 0.071 in PD10, whereas the lowest value of 0.035 was found in PD2 and PD3. Although, *Ho>He* was confirmed for PD5 and PD10, the other *P. domesticus* subpopulations exhibited *Ho<He*, which may be interpreted to indicate heterozygote deficiency. The highest *Ho* value among the *P. montanus* subpopulations was 0.065, for PM2, and the lowest value was 0.018, for PM1. Although PM2 and PM3 exhibited high heterozygosity (*Ho>He*), heterozygote deficiency (*Ho < He*) was observed in PM1.

All *P. domesticus* subpopulations except PD3 (Mersin/Silifke) showed significant deviations from Hardy-Weinberg equilibrium at 1-3 loci, with 3 loci for PD12 (*Ck*, *Idh-s* and *Idh-m*) and PD13 (*Ck*, *Est and Idh-m*); 2 loci for PD1 (*Est and Idh-m*), PD4 (*Idh-s* and *Idh-*

Table 2. Genetic variability of all subpopulations at 23 loci.

Subpopulation and locality	Sample size	Mean number of alleles per locus (A)	Percentage of polymorphic loci* (P)	Mean heterozygosity (H)		Deviation from Hardy-Weinberg equilibrium			
				Direct-count (*Ho*)	Hardy-Weinberg expected** (*He*)	Locus	Chi-square	DF	P
PD1-Ankara	12	1.1	13.0	0.019	0.054	*Est*	7.121	1	0.008
						Idh-m	13.410	1	0.000
PD2-Mersin	10	1.1	8.7	0.013	0.035	*Idh-m*	11.111	1	0.001
PD3-Silifke	7	1.2	8.7	0.023	0.035	-	-	-	-
PD4-Denizli	7	1.2	17.4	0.043	0.067	*Idh-s*	8.889	1	0.003
						Idh-m	8.889	1	0.003
PD5-Zonguldak	8	1.2	17.4	0.054	0.053	*Idh-m*	15.077	1	0.000
PD6-Corum	7	1.1	8.7	0.037	0.042	*Est*	8.889	1	0.003
PD7-Bilecik	9	1.2	17.4	0.048	0.062	*Idh-m*	11.487	1	0.001
PD8-Mugla	9	1.2	17.4	0.063	0.064	*Idh-s*	17.067	1	0.000
						Idh-m	11.487	1	0.001
PD9-Konya	6	1.2	17.4	0.065	0.068	*Ck*	5.000	1	0.025
						Idh-s	11.111	1	0.001
PD10-Afyon	5	1.2	17.4	0.072	0.071	*Idh-m*	9.143	1	0.002
PD11-Istanbul	10	1.2	17.4	0.035	0.065	*Est*	10.182	1	0.001
						Idh-m	11.221	1	0.001
			21.7	0.062	0.075	*Ck*	13.000	1	0.000
						Idh-s	18.087	1	0.000
						Idh-m	16.343	1	0.000
PD13-Kayseri	5	1.1	13.0	0.043	0.055	*Est*	4.000	1	0.046
						Idh-m	9.143	1	0.002
							9.143	1	0.002
PM1-Ankara	22	1.2	13.0	0.018	0.055	Idh-m	23.066	1	0.000
PM2-Corum	4	1.1	13.0	0.065	0.059	-	-	-	-
PM3-Edirne	8	1.1	13.0	0.038	0.033	-	-	-	-
PH1-Samsun	9	1.2	17.4	0.069	0.059	*Ca*	8.000	1	.005
PH2-Çorum	15	1.2	21.7	0.027	0.071	*Est*	8.337	1	.004
						Idh-s	17.530	1	.000
						Idh-m	16.762	1	.000
PH3-Denizli	8	1.2	17.4	0.033	0.076	*Idh-s*	9.143	1	.002
						Idh-m	10.182	1	.001

* A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95
** Unbiased estimate (Nei, 1978)

m), PD8 (*Idh-s* and *Idh-m*), PD9 (*Ck* and *Idh-s*) and PD11 (*Est and Idh-m*); only the *Idh-m* locus for PD2, PD5, PD7, PD10; and only the *Est* locus for PD6. Among the *P. montanus* subpopulations, deviation from Hardy-Weinberg equilibrium was observed only in PM1 (Ankara) at the *Idh-m* locus (Table 2).

Wright's F_{ST} values were calculated to range from 0.0685 and 0.3694, with an average value of 0.2043 for the *P. domesticus* subpopulations and a consequent rate of genetic variation of 20.43%. High rates of genetic variation and F_{ST} values might indicate isolation between these subpopulations, and the Nm value was 0.9737, which is close to 1, indicating little gene flow among the *P. domesticus* subpopulations. At the *Ca* and *Ck* loci, F_{IS} showed a negative value, indicating higher heterozygosity relative to the other loci. In the *P. montanus* subpopulations, the F_{ST} values were between 0.0115 and 0.2975, and the mean value was 0.1710; thus, the rate of genetic variation was 17.10%. Additionally, a negative F_{IS} value was obtained for the *Ca* and *Ck* loci, indicating higher heterozygosity at these loci than at the others. The calculated Nm value of 1.2120 (>1) indicated that the contribution of genetic variation of the subpopulations to the total variation was relatively low. The differences between these subpopulations were smaller than for the *P. domesticus* subpopulations.

The relationships between the examined subpopulations of *Passer* species were presented in a UPGMA dendrogram (Fig. 2) based on Nei's unbiased genetic distances. The UPGMA dendrogram revealed that all subpopulations were separated into three main groups. Group I consisted mostly of subpopulations from Black Sea and Aegean regions, with *P. domesticus* and *P. hispaniolensis* subpopulations nested in the first part of

the group. Interestingly, PD4 and PH3 were from the same locality (Denizli). Group II was formed by the Central Anatolia and Mediterranean subpopulations, except for PD11. Group III consisted only of *P. montanus* subpopulations. PD3 appeared to form the only branch that did not belong to any group.

Discussion

Regarding previous allozyme studies of *P. domesticus* populations, Fleischer et al. (1984) found that the *Est*, *Idh-2* and *Idh-3* loci presented variations in introduced *P. domesticus* populations in Kansas. Bjordal et al. (1986) detected variations at the *Ada*, *Pep-D*, *Pep-T*, *Est-2*, *Idh-A, Idh-C*, *6-Pgd*, *Pgm-1*, *Pgm-2*, *Sordh* and *Acon* loci in Norway. According to Bates and Zink (1992), 23 of 29 loci examined in the USA did not show variations, in contrast to the other 6 loci: *Idh-s*, *Idh-m*, *Pgm*, *6pgd* and *La1* and *Lgg* peptidase. In the present study, no variation was found for *Acon-s, Acon-m, Ald, Fum, Ldh, Mdh, Me, Pgd* and *Sod*, similar to the results of Bates and Zink (1992), and *Gpi, Pk* and *Pnp* were also shown to lack variation. *Est* and *Idh* were observed to be the most polymorphic loci for *P. domesticus* in all of these studies. *Ca*, *Ck*, *Est*, *Idh-s* and *Idh-m* exhibited variations in both species. *G3pdh-2* did not show any variations within any of the subpopulations examined in this study, remaining fixed at either the A allele (*P. domesticus* and *P. hispaniolensis*) or the B allele (*P. montanus*). This locus separated to *P. montanus* from other *Passer* species. This phenomenon was not reported in the available literature on allozyme studies of *Passer* sparrows. In the present work, the ratios of 5 polymorphic loci observed in the subpopulations were as follows: (1) *P. domesticus*: *Ca* (5/13), *Ck* (13/13), *Est* (12/13), *Idh-s* (5/13) and *Idh-m* (10/13); (2) *P. montanus*: *Ca* (2/3), *Ck* (3/3), *Est* (3/3), *Idh-s* (1/3) and *Idh-m* (1/3).

Anderson (2006) determined that the average heterozygosity was 0.074–0.157 and the rate of polymorphic loci (*P*) was 27.8-50% in an allozyme study of natural *P. domesticus* populations. All of the populations of *Passer* species found in Turkey are known to be naturally occurring; the average heterozygosity was found to be 0.053 for *P. domesticus* and 0.078 for *P. montanus*. Heterozygote deficiency was identified in the *P. domesticus* subpopulations (*Ho<He*), whereas the *P. montanus* subpopulations showed high *Ho* values, except for PM1 (*Ho<He*). However, the average rates of polymorphism *(P)* were relatively high for both species, at 15.05% for *P. domesticus* and 13% for *P. montanus*. The average heterozygosity for bird species is 0.045-0.065 (Barrowclough, 1983; Evans, 1987; Bates, 2000), whereas the average rate of polymorphic loci is 0.222-0.240 (Corbin, 1983; Evans, 1987; Baker and Johnson, 1998), and the genetic distance (D) is 0.044 between bird species and 0.005 for subspecies (Barrowclough, 1980). According to Ohta et al. (2000), D is 0.148 for the Passeriformes order between species. In this study, the highest D values, calculated according to Nei (1978), were 0.051 for *P. domesticus* and 0.030 for *P. montanus*. The highest D was reported to be 0.028 between *P. hispaniolensis* subpopulations (Saygılı and Yiğit, 2013). The pairwise genetic distances of the subpopulations fell between 0-0.051 (*P. domesticus*) and 0.009-0.030 (*P. montanus*). The greatest genetic distance (D) values were found to be 0.051 (PD3-PD9) and 0.030 (PM1-PM2) within subpopulations and 0.956 (PD9-PM2) between these two species, indicating low levels of intrapopulation genetic differentiation. The low genetic variation of *P. domesticus* has been explained by its short-distance migrations and homogeneous distributions that allowed gene flow over large distances (Kekkonen et al., 2011). In this study, both of the species showed *Ho<He*, and their genetic structure therefore indicated heterozygote deficiency. However, the obtained P and F_{IT} values were high in *P. domesticus*.

In the UPGMA dendrogram, three groups appeared, among the examined *Passer* subpopulations. These groups partly corresponded to Roselaar's (1995) maps for *Passer* subspecies. It has been shown that *P. domesticus* and *P. hispaniolensis* are more closely related among the *Passer* species. One *P. domesticus* subpopulation, PD4, was found to be more similar to *P. hispaniolensis* (PH3) than to the others, interestingly, they were from the same locality (Denizli), and together, these subpopulations constituted part of the first branch. PD3 formed a separate group in this tree and did not show similarity to PD2 despite having come from the nearest location. PD11 was included in group II, although it was located far from the other subpopulations. Therefore, these three groups in the tree might indicate the existence of subspecies of *P. domesticus* in particular. These subpopulations of the first group were distributed within *P. d. domesticus* and *P. d. balearoibericus,* and those of the second group were distributed within *P. d. mayaudi* or *P. d. biblicus*, based on

comparison with the findings of Roselaar (1995). Furthermore, a distinctive locus was identified for *Passer* species by comparing the three examined species, as *P. montanus* formed a separate group in this tree (group III). It is presented also baseline information for the assessment of genetic variability on the species and population levels and which provides a new opportunity to evaluate their microevolution processes at the contemporary conditions of their existence on the territory of Turkey.

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References

Aebersold P.B., Winans G.A., Teel D.J., Milner G.B., Utter F.M. 1987. Manual for Starch Gel Electrophoresis: A Method for the Detection of Genetic Variation. U.S. Department of Commerce. National Oceanic and Atmospheric Administration (NOAA) Technical Report. National Marine Fisheries Service (NMFS) 61 p.

Anderson T.R. 2006. Biology of the Ubiquitous House Sparrow: From Genes to *Populations*. Oxford University Press, USA.

Baker M.C., Johnson M.S. 1998. Allozymic and Morphometric Comparisons among Indigo and Lazuli Buntings and Their Hybrids. The Auk, 115: 537-542.

Barrowclough G.F. 1980. Gene flow, effective population sizes and genetic variance components in birds. Evolution, 34: 789-798.

Barrowclough G.F. 1983. Biochemical studies of microevolutionary processes. In: A.H. Brush, G.A. Clark Jr (Eds.). Perspectives in ornithology. Cambridge University Press, England.

Bates J.M. 2000. Allozymic Genetic Structure and Natural Habitat Fragmentation: Data for Five Species of Amazonian Forest Birds. The Condor, 102: 770-783.

Bates J. M. and Zink R.M. 1992. Seasonal Variation in Gene Frequencies in the House Sparrow (*Passer domesticus*). The Auk, 109: 658-662.

Bjordal H., Cole S.R., Parkin D.T. 1986. Genetic differentiation among some populations of the house sparrow, *Passer domesticus*, from southwestern Norway. Hereditas, 105: 107-114.

Bush F.M. 1967. Developmental and populational variation in electrophoretic properties of dehydrogenases, hydrolases and other blood proteins of the house sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology, 22: 273-287.

Bush F.M., Farrar W.W. 1969. Dissociation-reassosiation of lactate dehydrogenase: reversed isozyme migration and kinetic properties. Proceedings of the Society for Experimental Biology and Medicine, 131: 13-15.

Corbin K.W. 1983. Genetic structure and avian systematics. In, R.F. Johnston (Ed.): Current ornithology, Plenum Press, New York. pp: 211-244.

Evans P.G.H. 1987. Electrophoretic variability of gene products. In, F. Cooke, P.A. Buckley (Eds.): Avian genetics, Academic Press, London. pp: 105-162.

Fleischer R.C., Lowther P.E., Johnston R.F. 1984. Natal dispersal in house sparrows: possible causes and consequences. Journal of Field Ornithology, 55: 444-456.

Fleischer R.C., Murphy M.T. 1992. Relationships among allozyme heterozygosity, morphology and lipid levels in house sparrows during winter. Journal of Zoology, 226: 409-419.

Harris H., Hopkinson D.A. 1976. Handbook of Enzyme Electrophoresis in Human Genetics. American Elsevier, New York.

Hillis D.M., Moritz C., Mable B.K. 1996. *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts.

Kekkonen J., Seppa P., Hanski I.K., Jensen H., Väisänen R.A., Brommer J.E. 2011. Low genetic differentiation in a sedentary bird: house sparrow population genetics in a contiguous landscape. Heredity, 106: 183-190.

Manchenko G.P. 2003. Handbook of Detection of Enzymes on Electrophoretic Gels. CRC Press, Florida.

May B. 1998. Starch Gel Electrophoresis of Allozymes. In, A.R. Hoelzel, (Ed.): Molecular Genetic Analysis of Populations, A practical Approach, Oxford University Press, USA, pp: 1-26.

Mullarney K., Svensson L., Zetterström D., Grant P.J. 2004. Birds of Europe. Princeton University Press. London.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics, 89: 583-590.

Ohta N., Kajita M., Kusuhara S., Kakizawa R. 2000. Genetic Differentiation and Phylogenetic Relationships among Species of *Gallus* (Jungle Fowl) and the Chicken. Japanese Poultry Sciences, 37: 33-39.

Rohlf F.J. 2000. NTSYS – pc, version 2.1. Numerical Taxonomy and Multivariate Analysis System. Exeter Publishing, Ltd.

Roselaar C.S. 1995.Taxonomy, morphology and distribution of the Songbirds of Turkey: an atlas of Turkey: an atlas of biodiversity of Turkish passerine birds. Pica Press, U.K.

Saygılı F., Yiğit N. 2013. *Passer hispaniolensis* subpopulations in Turkey: allozyme variations and brief ecobiological notes. Turkish Journal of Zoology, 37: 761-767.

Shaw R.C., Prasad R. 1970. Starch Gel Electrophoresis of Enzymes – A Compilation of Recipes. Biochemical Genetics, 4: 297-320.

Snow D., Perrins C.M. 1998. The Birds of the Western Palearctic. Volume 2- Passerines. Oxford University Press. USA.

St. Louis V.L., Barlow J.C. 1987. Comparisons between morphometric and genetic differentiation among populations of the Eurasian Tree Sparrow (*Passer montanus*). The Wilson Bulletin, 99: 628-641.

St. Louis V.L., Barlow J.C. 1988. Genetic Differentiation among Ancestral and Introduced Populations of the Eurasian Tree Sparrow Passer montanus. Evolution, 42: 266-276.

St. Louis V.L., Barlow J.C. 1991. Morphometric Analyses of Introduced and Ancestral Populations of the Eurasian Tree Sparrow. The Wilson Bulletin, 103: 1-12.

Swofford D.L., Selander R.B. 1989. Biosys-1: a computer program for analysis of allelic variation in population genetics and biochemical statistics. Illinois Natural History Survey, Champaign, IL.

Verimli R., Yiğit N., Çolak E., Sözen M. 2000. Nonspesific Esterase Patterns of *Rattus norvegicus*. Turkish Journal of Biology, 24: 825-831.

Wright S. 1978. Evolution and the Genetics of Population, Variability Within and Among Natural Populations. The University of Chicago Press, Chicago.