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TEMPORAL EFFECTS AND GENETIC DIVERSITY: AN EXAMPLE FROM THE SOUTHERN PLAINS WOODRAT (*Neotoma micropus*)

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Abstract

Temporal effects on genetic diversity were investigated within a large, panmictic population of Southern Plains Woodrats (*Neotoma micropus*). Microsatellite genotypes obtained from 549 individuals, collected during a 4-year period, were assigned to groups according to capture site and year of capture. Most (99.84%) of the genetic variation was attributable to among-individual comparisons. No significant differences were observed among years relative to allelic richness, observed heterozygosity, gene diversity, F_{IS} , F_{ST} , and relatedness values. However, pairwise tests of genetic differentiation indicated significant differences in allele frequencies among collecting sites during the 4-year period, suggesting that even though levels of genetic diversity between collecting sites were fairly homogeneous for a given year, allele frequencies within each site evolved independently with respect to time. Low heterozygosity values associated with the number of alleles in each group were indicative of a pattern consistent with a recent (within the last 3,000 years) population expansion.

Key words: genetic diversity, microsatellites, *Neotoma micropus*, population genetics, Southern Plains Woodrat, temporal effects

INTRODUCTION

Estimates of parameters of genetic diversity and structure in vertebrate populations can be expected to change over time due to a number of biological events including natural fluctuations in population size, demographic stochasticity, genetic drift (Tessier and Bernatchez 1999; Planes and Lenfant 2002), selection (Planes and Lenfant 2002), and non-random sampling of populations (Allendorf and Phelps 1981; Tessier and Bernatchez 1999). These events can remain undetected unless examined under a temporal sampling scheme (Wang et al. 2002). Moreover, temporal factors can influence estimates of population diversity, underestimating the actual long-term genetic structure present in populations (Wang et al. 2002). For example, a population may appear to be genetically homogeneous when samples from multiple cohorts (different sampling periods of the same population) are pooled. However, if samples are divided according to cohort, significant amounts of structure may be detected in the data. Therefore, it is necessary to examine the potential impact of temporal effects to obtain accurate assessments of genetic diversity in natural populations.

Although there have been several studies pertaining to temporal variation and genetic diversity of vertebrates, especially fish (Lacson and Morizot 1991; Jordan et al. 1992; Jorde and Ryman 1996; Laikre et al. 1998; Tessier and Bernatchez 1999; Garant et al. 2000; Planes and Lenfant 2002), with temporal patterns ranging from no significant change to considerable change over time, few have been reported for mammalian populations. This is due to the difficulty in obtaining sufficiently large sample sizes from several consecutive generations (and consequent problems with low statistical power) and caveats associated with overlapping generations. Similar to the studies on fish (above), the few examples pertaining to mammals (Rossiter et al. 2000; Queney et al. 2000; Wisely et al. 2002; Wang et al. 2002; Hoffman et al. 2009; Phillips et al. 2011; Forcada and Hoffman 2014) reported varying levels of temporal variation. For example, Rossiter et al. (2000) found no evidence of temporal variation among populations of bats from Europe during a 5-year study period. Queney et al. (2000) and Wisely et al. (2002) reported low levels of genetic variation within rabbits and Black-footed Ferrets, respectively, even though the populations they studied were known to have undergone severe bottlenecks. Although these

studies included samples collected from a period that exceeded 10 years, they did not find high levels of temporal variation. Conversely, Wang et al. (2002) detected considerable genetic variation among years in a large unrestricted population of Roe Deer in Europe. However, their study included samples spanning three decades that could have resulted in more accurate estimates of temporal variation.

Recently, Méndez-Harclerode et al. (2007) examined genetic diversity in a large, well-established population of relatively long-lived rodents (maximum recorded life-span in the wild is about three years), the Southern Plains Woodrat (*Neotoma micropus*). This study provided an opportunity to investigate temporal effects in a single population of mammals, which possessed high levels of genetic variation and lacked significant amounts of genetic structure (Méndez-Harclerode et al. 2007). Additionally, results of genetic diversity analyses (low nucleotide and high haplotype diversity) were consistent with a recent population expansion (Méndez-Harclerode et al. 2005, 2007).

The purpose of this study was to reexamine the population described by Méndez-Harclerode et al. (2005, 2007) under a temporal framework and further test for patterns of population expansion or contraction. This was achieved by partitioning genotypes temporally and spatially, by season, year, and capture site, respectively.

MATERIALS AND METHODS

All specimens were collected as part of studies on the ecology of the Catarina virus (Arenaviridae) in southern Texas (Cajimat et al. 2007; Milazzo et al. 2013). Ruthven and Synatzske (2002), Fulhorst et al. (2002), and Suchecki et al. (2004) provided detailed descriptions of the 36-km² study area (Chaparral Wildlife Management Area - CWMA), located 85 km north of Laredo, Texas. Three mark-recapture webs (Anderson et al. 1983) were used to collect samples following methods outlined by Méndez-Harclerode et al. (2005, 2007) and Milazzo et al. (2013). Toe and ear punches obtained from individuals were deposited in the Genetic Resources Collection of the Natural Science Research Laboratory, Museum of Texas Tech University (Méndez-Harclerode et al. 2005, 2007 and Appendix) and served as the DNA source as described in Méndez-Harclerode et al. (2007). Five microsatellite loci (Nma01, Nma04, Nma06, Nma10, and Nma11) were amplified using the methods described by Castleberry et al. (2000) as reported in Méndez-Harclerode et al. (2007). Microsatellite genotypes were obtained from 549 individuals collected during 16 trapping periods (once per season over four years) and are listed by Méndez-Harclerode (2005). Individuals were genotyped upon initial capture; however, if an individual was captured during more than one trapping period, its corresponding genotype was included in the appropriate time-frame to represent their presence over the span of the study (Table 1, Fig. 1). Specimen catalog numbers are available in Méndez-Harclerode et al. (2007).

		Capture Site		
Trapping Period	Web I	Web II	Web III	Total
January 2001	3	0	5	8
March 2001	11	10	11	32
June 2001	29	15	32	76
October 2001	20	19	27	66
January 2002	4	21	8	33
March 2002	11	11	4	26
June 2002	4	4	12	20
October 2002	11	22	18	51
January 2003	11	16	7	34
March 2003	8	8	11	27
June 2003	22	39	14	75
October 2003	27	36	18	81
January 2004	21	17	8	46
March 2004	16	9	13	38
June 2004	18	21	20	59
October 2004	10	16	10	36
Total	226	264	218	708

Table 1. Sample size (number of individuals) from each capture site (web) according to trapping period. Sample size is adjusted to include recaptures as well as novel individuals; therefore, the total number of individuals included is greater than 549, as many individuals were recaptured across several trapping periods.



Figure 1. Histogram depicting cumulative woodrat captures (new and recaptured) by date. Dark portions of each bar reflect new captures and light portions depict recaptures.

Although the major reproductive activity of N. micropus in south Texas occurs primarily in the spring and early summer, a lesser amount occurs throughout the year (Conditt and Ribble 1997; Merkelz and Kerr 2002; Suchecki et al. 2004). In order to delineate a set of biologically meaningful periods to utilize in the temporal analysis (given the problem presented by the continuous reproductive activity), F-statistics (F_{TT} , F_{1S}, and F_{ST}; Weir and Cockerham 1984) and relatedness parameters (Queller and Goodnight 1989) were estimated for each of the 16 trapping sessions using the software program FSTAT (Goudet 2001). These estimates were then graphed with their corresponding confidence intervals (Fig. 2). No obvious temporal trend that would aid in the separation of cohorts was detected in the variation of the parameters across trapping periods; therefore, genotypes were examined by web and year in order to investigate temporal effects. Years were used, not seasons, because small sample sizes per trapping web per season could result in a lack of statistical power.

Genetic variability through time (years) and space (trapping webs) was examined by means of an Analysis of Molecular Variance (AMOVA; Excoffier et al. 1992) using the software program Arlequin 2.0 (Schneider et al. 2000). To investigate the possibility of temporal effects, null hypotheses of no significant differences among years were tested with respect to allelic richness, observed heterozygosity, gene diversity (Nei 1987), relatedness (Queller and Goodnight 1989), and F_{IS} and F_{ST} (Weir and Cockerham 1984) using the software program FSTAT (Goudet 2001), and 2-sided p-values were estimated after 10,000 random permutations generated from the original dataset. In an effort to separate age cohorts (juvenile, sub-adult, and adult), this test was repeated as described above with only adult individuals-identified as such by pelage color (evidence of completion of molting) and size (nose-torump length greater than 250 mm).

An additional test of heterogeneity in allele frequencies based on the G-statistic (Goudet et al. 1996) was performed by utilizing the pairwise test of differentiation in the software program FSTAT (Goudet 2001) to examine differences among webs and among years. Unlike the previous tests, this analysis was performed under two schemes. First, each web was compared to all other webs per year. This resulted in a 12x12 matrix, with each sample representing a web-year combination, and *p*-values were estimated after 1,320 randomized permutations of the original dataset. Second, all webs were grouped according to year (disregarding web of provenance), resulting in a 4x4 matrix, with *p*-values estimated after 120 permutations. Significance of the results of each of these tests was adjusted to compensate for multiple comparisons following sequential Bonferroni corrections (Holm 1979; Rice 1989). Tests for Hardy-Weinberg equilibrium were performed using the software program FSTAT (Goudet 2001) as follows: individual samples were partitioned according to web and year, and two estimates of Hardy-Weinberg equilibrium were produced (per locus and among loci). Estimates of *p*-values for this test were obtained after 1,200 random permutations and significance levels were adjusted after sequential Bonferroni corrections.

The possibility of a recent reduction or expansion in the effective population size was investigated under the 2-phased (TPM - Valdés et al. 1993; Di Rienzo et al. 1994), step-wise mutation (SMM - Kimura and Ohta 1978), and infinite-alleles (IAM - Kimura and Crow 1964) mutation models using the software program Bottleneck (Cornuet and Luikart 1996; Piry et al. 1999). This analysis is based on the observation that during initial phases of a bottleneck the number of alleles is reduced faster than corresponding heterozygosity values (Cornuet and Luikart 1996; Piry et al. 1999). Because heterozygosity is largely dependent on the frequency of common alleles, and rare alleles are probabilistically the first to disappear at the onset of a bottleneck, heterozygosity is expected to decrease at a slower rate than the number of alleles. A Wilcoxon signed-rank test performed with the software program Bottleneck (Cornuet and Luikart 1996) was used to determine whether a significant number of loci per web exhibited an excess of observed gene diversity (heterozygosity) per year. Results of the bottleneck analysis also were used to determine which of the three models of evolution (IAM, TPM, or SMM) best fit the data. Because of the null hypothesis (no relationship between the data and the model), a low *p*-value indicates the fit of the model. Therefore, a count of the significant p-values for each of the mutation models produced by this test was used as a non-linear indicator of the lack of fit of the models (Stevens et al. 2006).



Figure 2. Estimates of relatedness (A), F_{IT} (B), F_{IS} (C), and F_{ST} (D), along with their respective 95% confidence intervals, and number of sampled individuals (E) for each of the trapping periods during the 4-year study.

A contiguous clustering method (Chesser and Van Den Bussche 1988) was employed to test for the presence of statistically significant clusters of genotypes relevant to geographic proximity. Because this method assumes trapping homogeneity and can analyze only one locus at a time, each locus from each trapping web was analyzed separately with genotypes grouped by year.

RESULTS

Genetic variation was partitioned as follows: among years (0.00%), among webs within years (0.03%), among individuals within webs (0.13%), and among individuals (99.84%). Ranges for population genetic parameters estimated from the whole sample from each year were: allelic richness (12.647–13.631), observed heterozygosity (0.787-0.806), gene diversity $(0.821-0.845), F_{IS} (0.019-0.056), F_{ST} (0.016-0.018),$ and relatedness (0.031-0.033). None of the variation observed in any of these parameters was significant (Table 2). Ranges for these same parameters estimated from only the adults were similar to those obtained from the entire sample (Table 2); however, the variation in observed heterozygosity and F_{IS} was significant (p =0.049 and p = 0.009, respectively). Additionally, tests of genetic heterogeneity (G-statistic) produced significant values under two schemes. The first examined differences in allele frequencies among webs and years and revealed significant differences (p = 0.001) among all sample pairs with three exceptions: webs I and III were not significantly different in three of the four years (Table 3). The second test, which combined data from the three webs and compared allelic frequencies among years, revealed significant differences among all sample pairs with two exceptions: 2002 was not significantly different from 2003, and 2003 was not significantly different from 2004 (Table 4). Only one deviation from Hardy-Weinberg equilibrium was observed after corrections, suggesting the possible presence of heterozygote deficiency at locus Nma10 in web III-2001 (p = 0.001).

The Bottleneck analysis produced 18, 17, and 24 statistically significant results under the three mutation models (IAM, TPM, and SMM, respectively). Therefore, following the rationale employed by Stevens et al. (2006), the SMM was considered to be the most appropriate model for this data. This was assumed because analyses under this model yielded the highest number of instances (24) in which the null hypothesis of no relationship between the data and the model was rejected. Under the SMM, the Wilcoxon test identified

Table 2. Allelic richness (AR), observed heterozygo	sosity (H_0), gene diversity (H_s), F_{IS} , F_{ST} , relatedness (R) and their
respective p-values by year and by year including on	nly adults. Sample sizes (SS) for each period are provided.

Year	SS	AR	H _o	H _s	F _{IS}	F _{st}	R
2001	182	13.631	0.800	0.845	0.053	0.017	0.032
2002	130	12.998	0.789	0.835	0.056	0.018	0.033
2003	217	12.647	0.787	0.827	0.048	0.018	0.033
2004	179	12.753	0.806	0.821	0.019	0.016	0.031
<i>p</i> -value		0.596	0.794	0.506	0.121	0.994	0.998
2001 adults	83	10.798	0.757	0.842	0.101	0.018	0.033
2002 adults	66	10.924	0.833	0.839	0.007	0.007	0.014
2003 adults	87	10.146	0.802	0.824	0.026	0.010	0.020
2004 adults	78	10.727	0.821	0.819	-0.002	0.025	0.049
<i>p</i> -value adults		0.701	0.049	0.731	0.009	0.468	0.461

Table 3. Matrix of pairwise G-statistics from the test of pairwise differentiation among webs and years. Roman numerals refer to web designation. Above the diagonal is pairwise significance after standard Bonferroni corrections at the 5% nominal level (p = 0.001) obtained after 1,320 permutations. Below the diagonal are non-adjusted *p*-values for each pairwise comparison. NS = non-significant; * = significant.

			2001		2002		2003			2004			
Year	Web	Ι	II	III	Ι	II	III	Ι	II	III	Ι	II	III
2001	Ι		*	*	NS	*	*	*	*	*	*	*	*
	Π	0.001		*	*	NS	*	*	*	*	*	NS	*
	III	0.001	0.001		*	*	NS	*	*	*	*	*	*
2002	Ι	0.158	0.001	0.001		*	*	NS	*	*	NS	*	*
	II	0.001	0.005	0.001	0.001		*	*	NS	*	*	NS	*
	III	0.001	0.001	0.036	0.001	0.001		*	*	NS	*	*	NS
2003	Ι	0.001	0.001	0.001	0.217	0.001	0.001		*	*	NS	*	*
	II	0.001	0.001	0.001	0.001	0.442	0.001	0.001		*	*	NS	*
	III	0.001	0.001	0.001	0.001	0.001	0.533	0.001	0.001		*	*	NS
2004	Ι	0.001	0.001	0.001	0.036	0.001	0.001	0.497	0.001	0.001		*	*
	II	0.001	0.002	0.001	0.001	0.006	0.001	0.001	0.506	0.001	0.001		*
	III	0.001	0.001	0.001	0.001	0.001	0.316	0.001	0.001	0.881	0.001	0.001	

Table 4. Matrix of pairwise G-statistics from the test of pairwise differentiation among years. Above the diagonal is pairwise significance after standard Bonferroni corrections at the 5% nominal level (p = 0.001) obtained after 120 permutations. Below the diagonal are non-adjusted *p*-values for each pairwise comparison. NS = non-significant; * = significant.

	2001	2002	2003	2004
2001		*	*	*
2002	0.001		NS	*
2003	0.001	0.267		NS
2004	0.001	0.001	0.517	

five web/year samples exhibiting a significant number of loci with a deficiency of observed gene diversity (heterozygosity), suggesting population expansion (Cornuet and Luikart 1996). These samples were: web I-2001 (p = 0.031), web I-2002 (p = 0.016), web I-2003 (p = 0.016), web III-2003 (p = 0.031), and web I-2004 (p = 0.031). The contiguous clustering analysis (Chesser and Van Den Bussche 1988) failed to detect statistically significant clusters of genotypes during any year. That is, clusters of closely related genotypes were not found in geographically close proximity relative to year of collection.

DISCUSSION

Analyses of five microsatellite loci indicated that the probability of unique identity was one individual in 65,005,424; further, the high levels of allelic variation, polymorphic information content, and low overall relatedness values between individuals suggest that a sufficient number of loci appear to have been examined (Méndez-Harclerode et al. 2007). Based on the results from the AMOVA, most of the genetic variation (99.84%) was among individuals. The lack of significant differences among years relative to allelic richness, gene diversity, relatedness, and F_{sT} reported in the present study supported the hypothesis that the majority of genetic variation was among individuals. However, it is of interest that when only adult individuals were included in analyses, the observed heterozygosity and F_{1S} each differed significantly across time (p = 0.049and p = 0.009, respectively). This indicates that the temporal variation in this population may be obscured by the overlapping generations (relatively high survivorship and longevity) inherent to N. micropus.

Significant differences in allele frequencies were detected among most web/year pairs; however, when webs were compared among years none of the comparisons among webs within a year were significant. This result suggests that although webs were homogeneous during the same year, each web evolved independently with respect to time. Within-web and among-year comparisons revealed interesting trends. None of the webs was significantly different from itself during immediately subsequent years (e.g. web I-2001 was not significantly different from web I-2002, but was significantly different from web I-2003). When webs were grouped according to year, 2001 was significantly different from all other years and 2002 was significantly different from 2004. This may be a product of several factors. First, it may be a result of a heterogeneous distribution of allele frequencies by year; for example, the highest number of alleles (111) was observed during 2001 and the lowest (93) during 2004. Second, web I was the only web that exhibited a pattern consistent with population expansion (see below) during all four years and may have produced significant differences in allele frequencies. Third, this may have been due to environmental conditions as the study site experienced a drought during 2001 and 2002 (Bradley et al. 2006), which may have produced a shift in allele frequencies.

Only web I possessed a significant heterozygosity deficiency over all loci across all years even though many loci in the web/year samples produced significant results in the bottleneck analysis. Motro and Thomson (1982) theorized that bottlenecks combined with cyclic populations would result in a reduction in heterozygosity levels. Conversely, Cornuet and Luikart (1996) reported that heterozygosity deficiency for microsatellite data under the SMM was indicative of population expansion. Based on these findings (no evidence of a bottleneck), we interpreted these data as evidence that this population of woodrats has undergone a recent expansion. We define "recent" as approximately 3,284 years ago following the formula provided by Piry et al. (1999). Further support for population expansion was provided by Méndez-Harclerode et al. (2005), where patterns indicative of population expansion were detected with a nested-clade analysis (Templeton et al. 1987; Templeton et al. 1995) and Fu's F_s statistic (Fu 1996). Additionally, Méndez-Harclerode et al. (2005, 2007) reported high haplotype diversity and low nucleotide diversity based on mitochondrial D-loop sequence data, also indicative of a population expansion as proposed by Grant and Bowen (1998). Alternatively, null alleles or the Wahlund effect (Wahlund 1928) may be responsible for the significant heterozygosity deficiency observed in this study. However, the fact that multiple analyses based on different markers indicate this population is expanding suggests that the Wahlund effect is not likely to account for this pattern.

Although no obvious temporal trend was observed when population-genetic parameters were compared across the 16 trapping periods (Fig. 2), a few interesting patterns were observed. For example, F_{IT} and F_{IS} produced nearly identical patterns with F_{IT} values being slightly higher than F_{IS} values. This suggests that genetic variabilities between the individual and the subpopulation and between the individual and the total population were comparable and, therefore, that most of the variability can be attributed to be among individuals. This supports the presence of a single population as reported by Méndez-Harclerode et al. (2007). A similar conclusion can be drawn from the pattern observed during June 2002. During this trapping period, the highest values were recorded for relatedness F_{II} , F_{IS} , and F_{SI} . This suggests that the increase in genetic structure concomitant with increased relatedness was proportionally distributed across all hierarchical levels, thereby indicating a nearly panmictic population. The increase in population genetic parameters observed during June 2002 coincided with the lowest sample size during the 4-year study. This decrease in the number of trapped individuals probably was caused by the 13-month drought that ended in July 2002 (Bradley et al. 2006). The nature of the apparent correlation between the increase in population parameters and the decrease in sample size, however, is unclear. It could be that the reduction in sample size produced a bottleneck effect resulting in higher levels of genetic structure. Although no bottleneck was detected, the microsatellite markers may be indirectly reflecting some selective pressure that could have acted on the low population size (pre-July 2002) enabling a droughthardy lineage to thrive during the drought conditions. Therefore, a simulation was conducted to estimate the effective population size required to generate a statistically detectable bottleneck that would be capable of impacting genetic diversity in subsequent generations. Approximate Bayesian Computation (ABC, Cornuet et al. 2014) was used to simulate 10 scenarios (Table 5) involving possible population sizes ranging from one to 10,000 individuals. In these scenarios, four sets of hypothetical population conditions (N1-N4) were selected to represent the current population (N1),

bottleneck population (N2), pre-bottleneck population (N3), and ancestral population (N4). The selection of an upper limit for the population size under a bottleneck (N2) was based on the results from the LDNE program (Waples et al. 2008), which estimated an effective population size of 407 individuals at which time a bottleneck effect could be detected. Scenario 1 allowed for a possible constant population size, whereas scenarios 2-10 involved a step-wise population reduction from 500 individuals (scenario 2) and concluded with two individuals (scenario 10). Three million simulated datasets were generated and posterior probabilities were estimated for each of the scenarios using the software package DIYABC (Cornuet et al. 2014). The posterior probabilities were then used to rank the accuracy of the 10 scenarios and infer the affect of possible bottleneck events.

Results of these simulations indicated that scenario 1 produced the highest posterior probability value (prob = 0.972; Table 5) of matching the observed data. The remaining nine scenarios based on population sizes ≤ 500 produced much lower posterior probabilities (prob ≤ 0.060 ; Table 5). This finding indicates that a bottleneck reducing the total population size to an effective population size of ≤ 500 would produce a significant difference in genetic diversity. Further, the simulations support the contention that the drought

Table 5. Information used to conduct the simulation analyses as outlined in the text. Abbreviations are as follows: N1-N4 = population size, ranging from lowest to upper set limit; T1-T3 = generation size, ranging from lowest to upper set limit; PV = posterior probability values; and CI = confidence interval values.

Scenario	N1	T1	N2	T2	N3	Т3	N4	PV	CI
1	(1, 10,000)	(1, 20)	(1, 10,000)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.972	(0.961, 0.983)
2	(1, 10,000)	(1, 20)	(1, 500)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.060	(0.000, 0.268)
3	(1, 10,000)	(1, 20)	(1, 250)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.060	(0.000, 0.737)
4	(1, 10,000)	(1, 20)	(1, 125)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.000	(0.000, 0.000)
5	(1, 10,000)	(1, 20)	(1, 62.5)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.000	(0.000, 0.000)
6	(1, 10,000)	(1, 20)	(1, 31.3)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.000	(0.000, 0.000)
7	(1, 10,000)	(1, 20)	(1, 15.6)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.000	(0.000, 0.000)
8	(1, 10,000)	(1, 20)	(1, 7.8)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.006	(0.000, 0.074)
9	(1, 10,000)	(1, 20)	(1, 4)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.002	(0.000, 0.041)
10	(1, 10,000)	(1, 20)	(1, 2)	(1, 20)	(1, 1000)	(1, 300)	(1, 10,000)	0.000	(0.000, 0.000)

(Bradley et al. 2006) did not adversely affect this population.

Overall, little evidence of temporal variation was identified in this study. This could have been due to at least four factors. First, the length of the study may have been insufficient to detect any significant temporal variation. A 5-year study on bats failed to detect evidence of temporal variation among populations (Rossiter et al. 2000); other mammalian studies encompassing samples collected from a period of time exceeding 10 years have found little evidence of temporal variation (Queney et al. 2000; Wisely et al. 2002). The fact that allele frequencies in web I and web III were significantly different at the end points of the study (2001 and 2004) suggested that a longerterm study may have been more successful in detecting temporal variation. Second, failure to detect significant temporal variation could be due to the inherent overlap of generations in our species of study. Woodrats in

southern Texas are known to breed year round (Conditt and Ribble 1997; Merkelz and Kerr 2002; Suchecki et al. 2004) and have a life-span in the wild of at least three years (Raymond et al. 2003; Mendez-Harclerode et al. 2007). Consequently, it is likely we were unable to obtain congruent results across all the analyses due to a mixing of cohorts. Third, this population may be, in fact, sufficiently large and stable over time, that temporal variation could not be detected during the study time. Analyses detected no evidence of a bottleneck despite the occurrence of a substantial drought causing a reduction in population size during the study. Fourth, examination of only five microsatellite loci may not have been sufficient to detect changes in genetic diversity over such a short time-span. However, given the probability of unique identification (1 in 65,005,424) this seems unlikely. Additional samples collected during a greater period of time in conjunction with a greater number of microsatellite loci may be needed to clarify possible patterns of temporal variation in N. micropus.

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Méndez-Harclerode et al.—Genetic Diversity in the Southern Plains Woodrat

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13

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APPENDIX

Individual genotypes are listed by TK number (unique reference number assigned to each specimen examined). Also provided are allelic scores for each microsatellite locus (Nma01, Nma04, Nma06, Nma10, and Nma11), collecting site (Web Sites I–III), sex, and age associated with each individual.

TK	Nm	a01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
100021	333	333	129	129	213	226	185	200	144	146	III	М	A
100048	321	327	149	161	213	213	158	158	142	144	Ι	М	SA
100066	327	331	168	168	185	229	185	230	142	144	III	F	А
100071	321	343	168	178	206	234	206	234	142	163	Ι	F	А
100072	335	337	132	149	217	221	235	242	144	144	Ι	М	А
100082	321	327	130	168	215	229	217	230	144	146	III	М	А
100083	321	341	129	168	204	219	217	250	144	144	III	М	SA
100084	321	337	168	168	215	217	217	249	142	144	III	F	SA
100102	325	335	130	157	208	234	215	225	142	150	Ι	F	SA
100126	333	339	130	130	240	247	213	223	142	154	III	М	А
100127	335	341	130	168	247	247	246	268	142	144	III	F	А
100128	335	341	149	164	237	247	240	246	142	142	III	М	SA
100129	329	339	130	168	234	234	217	219	144	144	Ι	F	А
100130	331	337	149	168	185	240	185	240	142	144	III	F	А
100131	317	321	130	172	186	204	187	204	142	144	III	F	J
100132	321	333	130	168	185	186	187	246	144	152	III	F	SA
100133	333	337	130	149	235	247	213	230	142	142	III	F	J
100149	329	335	159	168	217	221	234	234	144	163	Ι	F	А
100150	325	335	130	168	213	219	215	236	142	146	Ι	F	SA
100151	321	339	130	168	219	221	245	246	142	144	Ι	F	А
100152	329	335	159	166	213	223	213	223	142	146	Ι	М	SA
100153	313	335	130	157	213	219	204	204	142	144	Ι	М	А
100154	329	339	130	159	219	221	234	234	142	144	Ι	М	А
100155	325	339	130	174	221	221	194	246	142	146	Ι	М	J
100156	329	329	159	166	210	245	211	245	142	142	Ι	М	J
100157	335	337	132	172	235	247	213	221	144	163	Ι	М	А
100158	329	337	130	172	213	221	237	254	144	144	II	М	J
100159	325	331	130	149	213	217	235	240	142	142	II	F	А
100160	317	337	130	168	213	219	213	219	144	163	III	М	J
100161	325	325	130	193	217	217	236	249	142	142	III	F	А
100162	327	339	130	164	179	247	219	221	142	142	III	М	J
100163	317	337	130	168	213	226	204	204	142	144	III	F	J
100189	325	325	130	130	217	219	194	249	142	144	II	F	А

TK	Nm	ia01	Nm	a04	Nm	a06	Nm	ia10	Nm	a11	Web	Sex	Age
100190	329	337	130	161	221	227	204	204	142	144	II	F	А
100191	321	339	149	161	215	226	242	242	142	144	II	М	J
100192	321	339	149	168	217	226	235	242	142	142	II	F	J
100205	325	325	149	168	217	226	240	242	144	148	II	F	J
100206	333	341	151	168	217	219	179	254	142	159	II	F	SA
100207	321	335	130	149	213	215	204	234	142	142	II	F	J
100208	335	337	130	172	219	221	237	254	161	163	II	М	J
100224	329	333	130	170	213	221	213	221	142	146	Ι	F	J
100225	325	339	130	161	219	221	194	240	142	146	Ι	М	J
100226	329	333	159	168	215	217	234	235	142	163	Ι	F	J
100227	335	335	130	159	206	221	204	231	144	159	Ι	М	SA
100228	321	327	159	172	213	217	185	237	142	144	Ι	М	J
100229	329	329	161	168	237	241	189	217	144	144	Ι	F	А
100230	329	333	130	168	215	217	234	235	142	163	Ι	F	J
100231	321	329	161	168	204	206	179	181	144	144	Ι	F	J
100232	321	329	151	159	213	223	242	242	144	146	Ι	М	J
100233	329	329	130	132	206	219	230	240	144	144	Ι	М	J
100280	321	337	130	164	217	226	237	237	144	146	III	М	А
100281	321	339	161	168	219	219	185	187	142	144	III	М	J
100282	329	339	130	149	215	229	204	204	142	144	III	F	А
100283	313	339	130	153	219	221	204	204	142	144	III	М	А
100284	327	333	130	168	221	223	189	230	142	144	III	F	SA
100285	317	331	155	168	204	219	204	217	142	144	III	М	А
100286	329	339	130	168	204	213	235	235	142	154	III	F	J
100287	335	337	168	168	215	226	185	239	144	146	III	М	J
100288	321	337	168	168	204	213	204	245	144	146	III	F	SA
100309	325	335	157	168	210	226	234	242	142	148	Ι	F	J
100310	313	335	168	168	217	219	206	246	142	144	Ι	F	SA
100311	315	321	149	157	213	217	237	250	142	146	Ι	F	SA
100312	335	337	157	168	213	213	206	244	142	142	Ι	М	А
100313	321	329	130	168	239	245	239	246	142	142	Ι	М	J
100314	335	337	159	172	210	221	234	242	144	144	Ι	М	SA
100315	329	333	130	159	213	215	189	242	142	142	Ι	М	А
100316	333	333	130	166	204	245	185	239	142	142	Ι	М	А
100317	321	335	157	166	204	204	213	223	146	146	Ι	М	А
100318	333	333	168	168	204	217	219	221	144	146	Ι	М	А
100337	337	337	157	166	204	217	204	217	142	142	III	М	А

ТК	Nm	ia01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
100338	329	337	149	168	239	239	213	213	146	154	III	М	А
100339	317	329	130	153	219	219	219	219	142	163	III	F	А
100340	335	341	168	168	206	247	187	237	142	156	III	F	А
100341	337	337	130	166	219	219	204	230	146	148	III	М	А
100342	323	329	130	132	204	204	204	204	142	144	III	М	SA
100343	329	333	130	168	219	223	206	240	142	154	III	М	SA
100344	321	335	148	163	213	223	242	246	146	163	III	М	SA
100345	335	339	130	172	213	213	234	239	142	144	III	F	SA
100346	329	339	130	149	237	237	213	213	142	146	III	М	J
100347	321	333	168	168	204	223	211	246	144	152	III	М	SA
100348	317	327	130	130	213	219	204	242	142	146	III	F	SA
100349	329	329	129	129	210	226	181	181	142	142	II	М	А
100350	325	325	164	170	213	215	204	249	144	146	II	М	А
100351	331	341	129	129	213	227	237	240	142	144	II	F	А
100352	321	335	130	168	213	217	206	240	144	148	II	F	А
100380	329	333	130	168	204	237	213	221	142	144	Ι	М	А
100381	325	343	168	168	206	223	230	232	144	144	Ι	F	А
100382	329	329	130	159	210	245	213	213	142	144	Ι	F	А
100383	333	341	159	174	245	247	230	245	142	142	Ι	М	SA
100384	321	329	130	161	204	241	240	244	142	144	Ι	М	J
100385	333	341	130	166	204	241	221	221	142	144	Ι	М	SA
100386	329	333	130	130	235	235	245	249	142	144	Ι	F	А
100395	329	333	130	130	213	229	235	237	142	144	II	F	А
100396	335	339	130	130	213	221	217	235	142	146	II	М	А
100397	321	335	130	149	213	215	234	240	142	144	II	М	SA
100398	325	333	129	130	213	223	230	232	146	146	II	F	А
100399	321	325	130	161	221	223	185	239	142	146	II	М	А
100400	321	335	130	161	213	215	239	250	142	144	II	F	А
100401	325	333	130	149	213	221	239	249	142	161	II	М	SA
100402	325	327	161	170	219	226	206	230	142	156	II	М	J
100403	325	325	130	168	217	223	237	251	142	142	II	F	А
100404	321	337	130	168	186	204	204	225	144	144	III	F	А
100405	321	339	168	168	213	217	185	234	142	144	III	М	SA
100406	333	335	130	130	219	223	219	223	142	156	III	F	А
100407	317	335	129	129	204	213	206	242	142	144	III	М	А
100408	321	321	170	170	213	219	235	240	146	146	III	F	А
100409	327	333	130	130	204	226	196	245	142	144	III	М	J

TK	Nm	a01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
100410	337	341	130	168	219	219	234	237	144	152	III	F	SA
100411	333	337	130	168	237	247	204	219	144	152	III	F	А
100412	327	329	130	168	229	240	230	240	144	154	III	F	А
100413	325	333	130	149	215	217	185	234	142	146	III	М	SA
100414	335	335	149	157	217	229	204	231	142	144	III	F	А
100445	329	341	159	168	235	240	181	204	142	142	Ι	F	А
100446	329	341	130	159	213	223	206	242	142	146	Ι	F	А
100447	335	335	130	157	213	226	237	242	144	144	Ι	М	J
100448	321	335	164	166	213	217	237	249	142	142	Ι	F	А
100449	333	337	168	168	213	219	185	204	142	142	Ι	F	А
100450	325	333	166	172	215	217	204	204	142	142	II	М	А
100451	329	333	161	168	213	227	181	204	142	144	II	М	SA
100452	321	339	130	164	210	221	204	204	142	142	II	F	SA
100453	331	337	130	153	204	235	219	223	144	163	III	М	J
100454	335	337	130	130	215	223	204	239	142	144	III	М	J
100455	321	321	168	168	204	226	231	245	144	146	III	F	SA
100517	335	335	159	168	213	217	187	217	142	142	Ι	F	А
100518	321	329	164	172	213	213	185	185	142	142	Ι	F	А
100519	321	341	130	159	213	221	213	221	144	146	Ι	М	А
100520	313	331	159	166	213	219	204	217	142	144	Ι	М	J
100521	329	335	130	168	234	241	206	211	142	142	Ι	М	SA
100522	329	329	130	172	217	219	204	239	142	163	II	М	А
100523	323	331	161	172	221	226	204	204	142	144	II	F	SA
100524	325	331	130	130	213	219	187	217	142	144	II	М	SA
100525	329	339	164	170	219	221	206	249	142	150	II	F	А
100526	327	329	130	130	219	219	204	235	142	144	II	F	А
100527	337	339	130	174	213	217	204	204	146	161	II	F	J
100528	329	333	130	149	219	229	204	204	142	144	III	М	А
100529	313	331	130	153	219	221	200	230	142	154	III	F	А
100530	323	327	149	149	204	217	180	206	142	144	III	F	SA
100531	321	341	130	130	223	226	206	211	142	144	III	F	J
100532	335	341	149	168	215	219	217	242	144	163	III	F	SA
100533	317	329	149	153	215	221	217	232	144	154	III	М	А
100534	333	339	130	168	219	226	200	230	144	144	III	F	А
100535	333	341	130	161	215	219	180	206	146	156	III	М	J
100536	313	341	168	170	215	215	189	249	142	142	III	М	А
100546	329	339	130	130	213	221	242	245	142	144	Ι	F	J

TK	Nm	a01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
100582	335	335	130	159	213	226	181	217	142	144	Ι	F	А
100583	337	337	130	166	215	219	230	237	144	144	Ι	М	А
100584	329	329	130	161	213	221	234	234	144	144	Ι	М	SA
100585	321	333	130	166	215	219	206	242	142	146	Ι	F	А
100586	335	343	130	172	210	217	235	245	142	148	Ι	М	SA
100587	335	339	130	172	210	221	242	246	142	142	Ι	F	SA
100588	341	341	130	166	215	217	185	235	142	146	II	F	А
100589	331	333	130	130	213	227	234	239	142	144	II	F	А
100590	331	339	168	168	215	223	217	235	142	142	II	М	J
100591	329	329	130	130	221	221	239	239	142	142	II	F	А
100592	317	335	149	153	221	229	235	242	142	142	III	М	А
100593	339	341	130	149	215	226	204	230	144	144	III	F	А
100594	327	327	130	149	204	204	234	249	142	144	III	М	А
100595	331	333	153	168	204	223	234	250	142	144	III	М	А
100596	335	339	130	168	223	223	189	206	142	142	III	F	J
100597	331	339	130	130	204	213	185	250	142	142	III	F	SA
100598	331	341	164	168	219	219	179	249	142	154	III	М	J
100599	335	335	130	157	217	223	206	242	142	142	III	F	А
100600	335	335	130	168	210	226	204	239	142	144	III	М	А
100601	317	335	149	168	219	221	204	206	142	156	III	М	J
100606	329	333	130	149	213	219	231	239	142	146	II	М	SA
100607	325	339	130	157	213	221	217	232	144	144	II	F	А
100608	321	337	160	174	217	217	208	247	142	161	II	F	SA
100609	325	331	130	161	213	217	234	240	142	142	II	F	SA
100643	329	333	130	170	213	221	196	211	142	161	Ι	М	SA
100644	321	321	130	130	213	221	180	242	142	142	II	F	А
100716	339	341	168	168	213	221	204	230	144	144	III	М	А
100717	325	331	130	130	217	219	187	194	142	144	II	М	А
100718	331	333	130	157	215	219	236	240	144	167	II	М	А
100719	335	337	151	160	219	219	237	242	142	142	II	М	А
100720	325	337	130	172	215	221	194	231	142	144	II	М	А
100721	323	335	157	164	213	223	204	206	142	146	II	М	А
100722	325	337	157	170	215	221	206	217	142	144	II	F	А
100723	323	331	157	168	213	223	204	204	142	146	II	М	SA
100724	321	333	130	168	221	227	234	246	142	142	II	М	А
100725	325	333	130	176	204	215	185	245	142	146	III	F	А
100726	323	335	130	132	215	219	231	249	142	167	III	F	А

TK	Nm	na01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
100757	325	329	130	174	213	217	204	242	142	146	Ι	М	А
100758	321	333	130	143	217	217	242	252	142	167	II	F	SA
100761	321	325	130	130	215	226	185	249	142	142	III	М	SA
100762	317	333	155	166	219	219	236	237	142	144	Ι	М	А
100763	329	343	130	168	204	219	215	240	142	144	Ι	F	А
100764	335	337	130	168	215	219	206	237	142	142	II	М	А
100765	323	325	130	164	213	219	217	245	144	146	II	F	А
100766	313	325	130	130	217	223	200	234	144	146	II	М	А
100767	331	331	130	181	217	227	234	245	142	144	II	М	SA
100768	325	331	130	149	217	223	194	200	144	146	II	F	А
100769	321	341	161	172	217	219	234	237	142	144	II	F	SA
100770	329	339	168	168	213	217	194	246	161	163	II	F	SA
100771	313	341	168	168	215	223	204	232	146	150	II	М	А
100772	329	341	130	159	204	219	206	245	142	167	II	F	А
100814	329	341	130	157	217	219	206	240	142	146	Ι	F	А
100815	335	335	157	159	213	223	204	204	142	142	Ι	F	А
100816	329	337	132	166	206	219	230	237	142	144	Ι	М	А
100817	337	339	130	130	217	227	242	242	142	154	II	F	А
100818	329	337	130	149	215	226	240	240	142	146	II	М	SA
100819	335	335	164	164	210	210	206	237	146	171	II	М	SA
100820	333	341	130	164	217	226	235	246	140	142	II	М	SA
100821	335	339	149	149	215	219	246	249	142	163	III	М	SA
100840	329	337	130	130	215	219	237	240	142	144	Ι	F	А
100841	333	337	130	130	219	221	245	252	142	142	Ι	М	А
100842	321	335	159	168	213	217	213	235	142	146	Ι	М	А
100843	337	337	130	132	206	215	237	240	142	167	Ι	М	А
100844	321	333	157	159	219	219	217	235	142	146	Ι	М	А
100845	329	341	130	168	221	229	237	240	142	144	Ι	F	А
100846	325	325	130	149	215	217	194	217	142	142	II	F	А
100847	325	341	130	166	213	219	185	217	142	144	II	М	А
100848	321	335	130	164	210	219	204	237	146	146	II	F	А
100849	337	339	168	170	213	215	235	246	142	142	II	F	А
100850	329	341	132	168	217	221	240	245	142	144	II	F	А
100851	335	339	130	168	217	223	185	204	142	144	III	F	А
100859	331	337	149	172	213	223	217	217	142	142	II	М	SA
100860	325	341	130	151	204	215	217	244	142	142	III	F	А
100861	333	341	130	168	221	223	189	246	142	156	III	F	А

ТК	Nm	ia01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
100900	335	337	132	166	204	219	206	231	142	142	III	М	SA
100901	329	341	161	161	204	219	234	249	142	144	III	М	SA
100902	333	339	130	149	204	226	237	250	144	144	III	М	А
100903	335	335	168	168	213	226	185	185	144	146	III	F	SA
100904	321	321	130	168	204	210	185	185	144	146	III	М	А
100905	333	335	130	130	217	229	185	250	142	144	III	М	SA
100906	313	331	130	153	213	221	185	185	142	146	III	М	А
100907	323	329	159	164	217	226	217	245	142	142	II	М	J
100908	321	341	168	168	210	221	204	234	142	146	Ι	F	А
100909	321	335	172	174	219	219	237	249	144	144	Ι	М	SA
100910	331	335	157	159	213	213	204	237	142	142	Ι	F	SA
100929	325	333	159	166	219	221	217	234	144	144	II	М	А
100930	329	337	149	172	221	223	217	217	142	144	II	F	А
100931	335	337	130	157	217	229	206	242	144	163	III	F	А
100957	321	333	149	168	217	219	194	204	142	144	Ι	F	J
100958	329	341	130	132	213	223	240	242	161	161	Ι	F	J
100959	329	343	130	149	206	213	242	246	142	142	Ι	F	SA
100960	323	331	149	164	223	223	206	217	142	142	II	М	J
100961	337	341	130	168	221	223	217	242	142	144	II	М	J
100962	337	337	130	161	204	221	187	242	142	142	II	F	J
100963	331	337	130	172	221	221	187	242	142	144	II	F	J
100964	325	325	168	168	213	223	187	217	142	142	II	F	J
100965	339	339	130	149	215	219	194	256	142	146	III	F	А
100966	337	337	149	168	219	219	206	242	142	144	III	F	SA
100967	329	335	132	149	223	223	249	250	142	146	III	F	SA
100968	335	339	130	130	213	219	231	236	142	142	III	F	J
100969	333	339	130	130	223	223	189	240	142	142	III	М	А
100970	321	329	130	170	219	223	204	250	144	146	III	F	А
100971	329	333	130	130	213	219	240	249	142	144	III	F	J
102264	335	335	157	159	213	219	204	204	142	142	Ι	F	SA
102265	339	341	159	168	210	223	185	196	142	144	Ι	F	J
102266	321	339	130	130	221	221	234	239	142	144	Ι	М	А
102267	313	333	166	172	215	219	194	204	142	144	Ι	F	А
102268	325	329	130	157	217	221	217	217	142	144	II	F	SA
102269	325	341	157	166	219	221	185	239	142	144	II	F	SA
102270	321	321	161	168	204	217	235	237	142	146	II	F	J
102271	325	337	130	130	215	221	194	231	142	144	II	F	J

TK	Nm	a01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
102272	325	329	130	157	215	215	217	217	142	144	II	F	J
102273	329	335	168	168	213	223	228	236	142	144	II	М	А
102274	329	333	130	168	219	221	206	239	142	167	II	F	А
102275	333	339	128	130	221	221	239	246	161	163	II	F	SA
102276	337	337	130	168	219	221	240	245	142	144	II	М	А
102277	327	341	149	149	204	226	204	206	142	144	III	F	J
102278	337	337	130	130	213	223	235	240	165	165	III	F	SA
102304	321	329	164	168	213	219	204	204	142	142	Ι	F	J
102305	341	341	168	168	210	217	204	213	142	146	Ι	F	J
102306	333	335	149	172	215	217	194	204	142	142	Ι	F	J
102307	329	341	130	168	223	226	228	242	144	150	II	F	А
102308	335	339	130	164	219	221	235	235	146	150	II	М	А
102309	325	329	130	130	217	217	235	240	142	142	II	F	SA
102310	315	333	130	130	219	221	206	217	142	146	II	М	SA
102311	313	325	130	130	217	221	232	234	144	146	II	F	SA
102312	331	337	130	130	219	219	185	203	142	146	III	F	SA
102313	339	339	130	161	219	229	244	249	142	144	III	М	J
102315	321	335	168	168	210	213	185	185	144	146	III	F	J
102316	339	339	130	149	213	213	234	240	140	140	III	F	J
102317	333	335	132	168	215	226	239	246	142	144	III	F	J
102318	333	333	130	149	213	223	192	240	142	163	III	М	А
102319	329	339	130	168	213	221	240	246	142	165	III	F	J
102320	333	337	130	149	213	223	180	242	142	144	III	F	А
102335	329	343	145	166	206	219	237	240	142	142	Ι	М	SA
102336	335	339	130	145	204	215	215	240	142	142	Ι	М	SA
102337	331	333	149	159	204	223	217	246	142	150	II	М	SA
102338	323	335	130	164	219	226	183	183	142	142	II	М	SA
102339	337	339	130	130	213	223	180	189	142	142	III	М	SA
102340	333	341	149	168	223	223	192	246	142	156	III	F	SA
102502	333	335	130	168	213	221	213	237	142	142	Ι	М	А
102503	315	337	130	130	204	219	217	249	142	144	II	F	А
102504	329	337	130	168	213	223	217	217	142	144	II	F	А
102505	321	329	168	174	217	217	206	239	142	142	II	М	А
102506	335	337	130	130	219	226	246	249	142	144	II	М	SA
102507	337	337	153	157	219	223	237	240	142	144	II	М	А
102508	331	335	130	172	213	227	234	252	142	144	II	М	А
102509	337	339	130	149	223	223	240	242	146	167	III	F	SA

ТК	Nm	ia01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
102612	329	341	130	174	219	219	204	217	144	161	II	F	SA
102613	335	339	130	130	204	215	204	239	144	161	Ι	М	А
102614	321	335	130	168	213	217	204	231	142	142	Ι	F	А
102615	333	339	130	172	221	223	240	244	142	161	Ι	F	SA
102616	333	335	161	166	221	221	240	249	144	144	Ι	F	А
102617	341	341	130	166	213	229	213	245	142	144	Ι	F	А
102618	329	337	130	130	219	221	217	249	142	142	II	М	А
102619	335	339	130	130	223	229	204	249	142	142	III	М	SA
102683	329	335	130	166	219	221	206	237	142	144	Ι	М	SA
102684	329	341	164	168	217	226	228	235	142	144	II	М	SA
102685	339	341	161	170	204	219	185	244	144	146	III	М	SA
102686	329	339	130	130	213	221	230	249	142	144	III	F	А
102759	325	329	130	159	213	219	240	250	142	144	Ι	М	J
102760	327	329	130	145	219	219	187	234	144	152	Ι	М	SA
102761	335	341	132	172	219	223	204	240	144	161	Ι	F	J
102762	321	325	130	164	219	226	204	217	142	142	II	М	А
102763	335	337	128	164	221	221	206	239	159	163	II	F	А
102764	327	337	130	151	219	226	236	245	142	144	II	М	А
102765	325	337	164	172	219	221	217	217	144	144	II	М	А
102766	333	339	130	130	213	229	249	250	142	142	III	М	А
102767	339	339	130	157	213	215	204	204	142	142	III	М	J
102768	321	329	130	130	213	213	206	230	142	142	III	F	J
102808	341	341	130	157	219	226	228	240	142	144	II	М	SA
102809	333	333	130	149	215	229	249	250	142	146	III	F	SA
102849	321	335	151	157	213	219	232	239	142	142	Ι	F	J
102850	321	329	130	172	219	223	204	242	146	161	Ι	М	SA
102851	329	329	149	168	213	217	234	234	144	161	Ι	М	SA
102852	329	339	149	172	210	217	240	242	142	161	Ι	М	J
102853	339	341	130	164	213	227	242	246	142	142	II	М	J
102854	339	341	161	164	213	217	204	242	142	142	II	М	J
102855	333	341	164	168	213	213	234	245	142	142	II	F	J
102856	325	341	130	130	221	226	249	250	142	144	II	М	J
102857	325	331	130	166	213	221	249	250	142	144	II	М	SA
102858	325	327	149	151	204	215	204	215	142	142	III	F	SA
102859	331	339	130	130	219	219	194	250	142	146	III	М	SA
102860	325	329	130	130	204	223	242	245	142	142	III	F	SA
102861	333	339	130	161	213	223	249	250	142	144	III	F	SA

TK	Nm	a01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
102862	329	333	130	149	213	223	217	249	142	142	III	М	А
103041	313	343	166	168	204	219	204	215	142	144	Ι	F	А
103042	329	333	130	168	213	221	192	235	142	142	Ι	М	А
103043	317	343	145	161	215	223	234	237	142	144	Ι	М	А
103044	321	341	130	172	213	223	230	230	142	142	II	F	А
103045	323	333	159	164	219	219	217	249	142	142	II	F	SA
103046	317	341	159	168	204	219	208	242	142	142	II	М	SA
103047	329	333	161	168	210	213	204	242	144	148	II	F	SA
103048	329	335	164	176	221	223	217	230	142	146	II	F	А
103049	317	339	130	151	217	221	234	235	142	146	II	F	J
103050	337	341	130	151	213	219	204	240	144	146	II	М	А
103051	331	331	164	181	217	221	237	240	142	142	II	F	SA
103052	325	335	130	157	219	221	185	185	142	150	II	М	J
103053	329	341	130	172	213	215	217	230	142	144	II	М	А
103054	325	335	157	164	217	221	179	217	144	146	II	М	А
103055	321	335	130	130	213	219	179	206	142	142	III	М	А
103139	329	335	130	166	206	215	237	240	142	144	Ι	F	А
103140	325	339	130	145	219	221	211	246	142	144	Ι	F	SA
103141	329	335	130	166	206	215	200	235	144	144	Ι	F	J
103142	321	329	168	168	213	219	206	245	142	142	Ι	F	А
103143	335	335	157	166	213	219	204	204	142	142	Ι	М	J
103144	325	339	130	145	221	223	235	245	142	142	Ι	F	А
103145	329	331	130	166	217	219	211	246	142	146	Ι	М	SA
103146	333	343	130	130	213	221	239	239	142	146	Ι	М	SA
103147	339	341	130	130	213	213	206	239	142	144	Ι	F	А
103149	331	335	168	168	217	219	204	211	142	146	Ι	М	А
103150	321	329	130	159	206	213	237	246	142	142	Ι	F	SA
103151	321	341	161	166	226	226	204	242	142	144	III	F	А
103152	321	335	130	166	219	226	217	235	142	152	III	М	А
103153	317	333	161	172	213	223	192	204	146	161	III	F	SA
103154	329	329	130	168	213	213	192	204	146	154	III	М	J
103155	321	329	149	170	223	223	235	237	142	144	III	F	J
103156	333	339	130	161	221	227	187	217	142	142	II	М	SA
103157	329	333	130	164	217	219	181	181	142	167	II	М	А
103158	333	335	161	164	221	227	215	217	144	146	II	М	SA
103159	333	335	161	164	221	227	240	242	144	146	II	F	SA
103160	333	335	161	164	221	227	194	217	142	144	II	М	SA

TK	Nm	a01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
103161	327	331	130	172	219	219	245	247	142	146	II	F	А
103162	339	341	130	168	213	217	185	232	142	144	II	М	SA
103163	335	337	157	164	217	221	240	245	142	146	II	М	SA
103164	325	331	168	168	213	223	240	244	144	146	II	F	А
103165	325	329	149	157	215	215	217	254	142	144	II	F	SA
103166	325	337	168	168	204	213	185	215	142	142	II	F	SA
103167	317	325	157	170	219	221	185	217	142	144	II	F	А
103168	323	337	157	164	213	215	237	237	144	144	II	М	SA
103169	333	341	130	157	213	219	235	235	144	146	II	М	J
103170	317	337	130	157	204	221	200	235	142	142	II	F	J
103171	329	335	130	168	204	219	204	237	150	161	II	М	А
103172	317	323	130	170	221	221	185	217	142	142	II	М	А
103173	321	321	130	130	204	217	237	237	142	142	II	F	А
103174	317	335	157	164	219	219	235	235	142	146	II	F	J
103175	329	343	130	130	213	221	234	239	142	146	Ι	F	А
103238	333	339	168	168	213	213	235	250	142	142	II	F	J
103264	327	339	145	166	219	219	217	242	142	148	Ι	М	SA
103265	333	333	130	168	213	226	200	245	142	146	Ι	F	А
103266	339	339	130	168	219	221	206	246	144	144	Ι	М	J
103267	339	339	130	130	219	221	234	239	142	144	Ι	F	А
103268	333	339	159	164	219	221	185	242	144	150	II	F	А
103269	337	341	130	130	213	223	215	217	144	144	II	F	J
103270	313	329	166	170	204	219	200	245	142	146	II	F	J
103271	335	337	130	130	219	226	189	236	142	144	II	F	А
103272	325	335	130	166	217	219	187	234	138	144	II	М	SA
103273	313	335	168	168	217	219	204	242	150	161	II	М	А
103274	321	337	168	168	204	213	240	242	142	148	II	F	А
103275	325	337	157	159	210	221	237	237	142	144	II	М	SA
103276	315	337	128	149	215	221	189	239	142	159	II	F	J
103277	327	339	145	168	217	219	187	234	144	152	Ι	F	А
103278	337	337	149	153	213	213	236	239	142	144	III	М	А
103279	329	331	168	168	219	221	194	217	146	163	III	М	А
123771	339	341	130	130	204	213	237	240	161	161	Ι	F	J
123772	321	333	157	159	213	213	211	215	142	146	Ι	F	А
123773	329	333	130	166	221	221	204	234	142	142	Ι	F	А
123774	329	343	130	168	219	223	236	239	144	146	Ι	F	А
123775	321	333	159	172	213	219	194	217	144	146	Ι	F	А

TK	Nm	na01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
123776	329	339	130	149	217	217	234	234	144	161	Ι	М	А
123777	321	329	130	161	215	221	206	240	142	144	Ι	М	А
123778	337	343	130	130	213	221	204	234	142	142	Ι	М	SA
123779	341	341	130	168	210	229	196	245	142	144	Ι	F	SA
123780	341	341	157	159	213	219	239	242	142	146	Ι	F	SA
123781	329	329	130	168	215	219	215	240	144	163	Ι	М	SA
123782	329	329	145	168	219	226	192	215	146	163	Ι	М	SA
123783	321	333	157	172	213	219	194	204	146	146	Ι	М	J
123784	321	321	130	168	219	223	204	242	142	144	II	F	А
123785	331	339	130	130	213	219	239	242	142	142	II	F	А
123786	337	341	130	168	213	219	215	217	142	144	II	М	А
123787	315	341	166	170	217	219	240	242	150	161	II	F	SA
123788	329	329	159	168	217	221	185	244	142	142	II	F	А
123789	311	327	130	159	217	219	217	234	142	144	II	М	SA
123790	325	333	130	168	215	219	180	204	142	142	II	М	А
123791	329	339	168	168	221	223	236	239	142	142	II	F	А
123792	337	337	168	176	215	219	240	242	142	154	II	F	J
123793	321	329	130	149	219	223	185	244	142	146	III	F	А
123794	341	341	130	130	223	223	240	242	142	142	III	F	J
123795	337	337	130	130	213	219	180	204	146	154	III	F	А
123796	317	329	149	168	213	229	236	249	142	154	III	F	SA
123797	329	329	130	166	213	226	234	242	142	142	III	F	SA
123798	337	341	149	170	213	223	211	217	142	146	III	М	А
123799	329	337	130	130	213	221	211	217	142	142	Ι	F	SA
123817	339	339	130	145	204	215	237	240	144	163	Ι	М	SA
123848	321	335	159	161	219	221	204	234	144	150	II	М	А
123902	323	325	149	161	215	217	237	246	142	144	II	М	А
123966	321	325	157	166	213	219	217	237	146	146	Ι	М	SA
123967	333	335	157	166	213	219	217	240	146	146	Ι	F	J
123968	333	335	161	168	213	219	237	237	142	161	II	М	А
123969	317	335	166	174	221	227	206	230	142	163	II	F	А
123970	331	341	130	168	213	217	237	246	142	144	II	F	А
123971	321	325	130	168	213	213	249	250	142	144	II	М	J
123972	315	333	130	130	213	223	203	242	142	144	II	М	J
123973	325	341	130	170	219	219	240	242	142	146	II	М	J
123974	339	339	130	130	219	221	206	230	142	144	III	F	А
123975	321	339	149	168	213	215	204	239	144	146	III	F	SA

TK	Nm	na01	Nm	a04	Nm	ia06	Nm	a10	Nm	a11	Web	Sex	Age
123976	337	339	130	130	226	229	249	250	142	144	III	М	А
123977	331	337	130	168	219	219	203	242	142	144	III	F	А
123978	329	329	130	130	223	223	240	242	142	142	III	F	J
124101	339	339	149	166	215	217	204	204	142	146	Ι	F	SA
124102	313	335	130	130	219	221	234	239	144	144	Ι	F	SA
124103	321	339	161	168	213	217	204	234	142	142	Ι	F	SA
124104	329	331	161	168	219	226	237	246	144	152	III	М	А
124105	321	333	130	130	204	217	242	245	142	142	II	F	SA
124106	325	333	130	168	204	213	206	206	144	167	II	М	А
124240	319	337	130	161	213	215	206	230	142	144	III	М	А
124241	323	337	130	149	213	213	204	239	142	146	III	F	SA
124242	317	329	130	168	213	221	204	211	142	142	Ι	М	А
124243	329	333	130	168	219	229	204	213	142	159	Ι	F	А
124244	321	333	166	168	219	221	215	235	142	163	Ι	М	А
124245	321	329	159	166	213	219	187	242	142	152	Ι	F	А
124246	329	333	130	145	217	219	206	234	144	148	Ι	М	SA
124247	327	339	130	172	213	221	187	215	144	144	II	М	А
124248	325	337	130	130	204	210	179	239	142	142	II	М	А
124249	327	333	157	172	219	219	215	242	142	144	II	F	J
124250	331	337	130	130	221	226	230	230	144	148	II	М	А
124342	339	339	130	168	215	219	204	234	142	142	Ι	F	А
124343	329	343	130	159	213	221	239	240	142	144	Ι	М	SA
124344	325	329	130	168	213	226	230	247	142	142	II	М	А
124345	325	339	130	170	210	227	194	208	142	163	II	F	А
124346	317	319	157	170	213	219	185	217	144	150	II	М	А
124347	325	329	130	174	217	219	206	217	142	167	II	F	А
124401	329	337	149	168	210	217	196	196	142	142	Ι	М	J
124402	339	341	130	130	213	221	204	242	161	163	Ι	М	J
124403	335	341	164	168	217	226	235	240	142	144	II	F	J
124404	329	333	164	168	223	226	228	245	142	150	II	М	SA
124405	333	341	159	172	213	219	187	217	142	167	II	F	J
124406	325	333	130	161	204	213	180	244	144	154	III	F	J
124407	329	341	130	130	213	219	204	244	142	154	III	F	SA
124489	329	341	130	172	213	226	211	230	142	142	Ι	М	А
124490	335	339	145	166	204	210	204	240	142	163	Ι	М	А
124491	321	341	168	172	204	213	185	211	142	142	Ι	F	SA
124492	329	333	130	168	206	213	204	237	142	144	Ι	F	J

TK	Nm	na01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
124493	329	329	166	170	213	215	211	235	142	142	Ι	F	А
124494	339	341	164	172	213	219	187	217	142	156	II	М	J
124495	325	333	130	161	213	219	185	196	142	144	III	F	А
124496	321	331	130	130	204	221	206	234	142	142	III	F	А
124497	329	341	130	168	213	219	185	204	146	146	III	М	J
124498	329	341	149	166	213	223	242	246	144	146	Ι	М	SA
124568	333	337	130	130	219	223	236	240	142	142	III	М	J
124569	321	337	168	168	213	223	236	245	146	156	III	М	А
124570	329	341	149	164	215	221	240	242	144	163	III	F	J
124571	331	331	130	159	217	219	185	249	142	150	II	F	J
124572	323	329	130	145	219	223	239	240	142	142	Ι	F	А
124573	325	339	159	166	213	213	211	213	142	146	Ι	F	А
124574	333	335	130	170	204	219	230	239	142	154	Ι	F	А
124611	329	339	168	168	206	215	204	240	142	144	Ι	М	SA
124612	329	343	130	170	204	219	239	240	144	154	Ι	М	А
124613	325	329	130	130	215	217	204	204	142	142	Ι	М	А
124614	329	335	130	161	217	221	204	239	142	142	Ι	М	А
124615	321	329	130	130	213	217	204	240	161	163	Ι	М	SA
124616	335	339	164	166	204	217	245	246	142	161	II	F	А
124617	335	341	130	130	215	221	217	230	142	144	II	F	А
124618	325	337	130	172	219	226	204	217	142	144	II	F	SA
124619	321	331	130	161	210	217	200	228	144	171	II	F	А
124620	315	341	130	164	213	215	208	242	142	146	II	М	А
124621	333	337	130	130	219	219	217	235	142	150	II	F	А
124622	331	335	130	166	215	219	215	217	142	144	II	М	J
124623	329	337	130	161	215	226	204	204	142	142	II	F	А
124624	329	329	166	174	219	227	204	242	161	163	II	F	А
124625	331	341	128	149	210	223	240	249	142	144	III	М	А
124626	335	339	149	166	223	223	245	246	142	146	III	F	А
124627	333	335	157	172	213	217	189	242	142	154	III	М	А
124797	329	337	130	130	219	223	236	240	142	142	III	М	SA
124798	331	337	149	149	215	223	242	245	142	154	III	F	SA
124799	335	337	149	168	215	219	204	240	142	163	III	М	А
124800	329	339	130	168	221	229	204	242	142	144	III	М	SA
124801	331	339	161	172	219	226	180	180	144	152	III	М	J
124802	317	341	130	149	219	223	204	246	142	154	III	F	А
124803	331	335	130	149	219	223	194	194	142	142	III	М	А

ТК	Nm	ia01	Nm	a04	Nm	a06	Nm	a10	Nm	a11	Web	Sex	Age
124804	321	331	130	130	219	226	196	196	142	144	III	F	SA
124805	329	343	145	168	213	215	234	249	142	142	Ι	М	А
124806	321	331	130	130	206	217	206	249	142	159	II	F	А
124807	315	333	130	168	213	213	237	242	142	159	II	F	SA
124808	317	341	159	164	219	219	235	246	142	144	II	F	SA
124809	325	329	151	168	217	217	206	235	142	142	II	F	А
124810	329	335	130	130	217	219	234	235	142	142	II	F	А
124811	329	331	130	172	215	219	187	215	142	142	II	F	А
124812	333	339	130	130	215	227	237	240	142	159	II	М	А
124937	329	333	130	130	221	221	192	228	142	159	Ι	F	А
124938	335	339	145	166	215	223	239	240	142	152	Ι	М	SA
124939	321	329	172	172	217	217	211	249	142	142	Ι	F	А
124940	333	333	130	168	215	221	192	204	142	144	Ι	М	SA
124941	329	329	168	168	213	221	204	228	142	142	Ι	М	А
124942	321	335	157	157	213	213	194	204	142	142	Ι	F	SA
124943	339	343	130	170	204	219	230	239	142	144	Ι	F	А
124944	333	339	130	130	213	213	217	235	142	144	II	М	SA
124945	329	341	159	168	204	213	187	249	142	144	II	F	SA
124946	333	335	130	168	204	217	245	246	142	159	II	М	SA
124947	325	329	130	130	215	217	215	217	144	144	II	F	А
124948	329	329	130	153	204	226	234	234	142	142	III	М	J
124949	329	341	149	157	213	219	206	230	142	144	III	М	А
124950	329	337	166	168	204	215	234	237	146	148	III	F	А
124951	329	339	130	130	213	219	194	230	142	146	III	М	J
124952	323	339	130	130	215	223	206	242	142	142	III	F	SA
131050	339	339	130	168	204	226	230	230	142	154	Ι	F	А
131051	325	329	130	168	213	219	213	240	144	146	II	F	А
131052	333	335	130	130	217	226	240	242	142	144	II	F	А
131053	337	339	130	170	206	219	234	242	142	148	II	М	А
131054	329	339	130	151	217	221	206	231	142	144	II	F	J
131055	333	339	130	149	213	221	226	235	142	144	II	М	А
131056	321	331	130	130	213	219	204	234	142	142	II	F	А
131057	325	337	128	174	221	221	189	237	142	163	II	F	А
131058	335	339	130	132	223	229	242	249	142	146	III	F	SA
131059	335	339	130	132	223	229	244	249	142	146	III	F	А

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