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Taxonomic and Conservation Status of the Pecos River Muskrat

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Abstract

Ondatra zibethicus (Common Muskrat) is comprised of 16 morphologically defined subspecies distributed across most of temperate North America. Due to current conservation concerns, the status of the Pecos River muskrat (*O. z. ripensis*) was evaluated using DNA sequences obtained from the mitochondrial cytochrome-*b* gene. Tissue and toe clip samples of museum vouchers and wild caught specimens (n = 29) from localities in Texas, New Mexico, and Louisiana, with a focus on populations representative of the parapatrically distributed *O. z. ripensis* and *O. z. osoyooensis*, were examined. Phylogenetic analyses including maximum likelihood, Bayesian inference, and statistical parsimony were used to determine relationships among individuals and populations. Two monophyletic clades were obtained that exhibited low sequence divergence (0.0061%), however, they were distinguished by a substitution at amino acid residue 237. Results indicate that populations on the Rio Grande were likely separated into northern and southern groups by a biogeographic barrier (e.g., Elephant Butte Reservoir). Low sequence divergence among clades refuted a clear taxonomic separation of *O. z. ripensis* and *O. z. osoyooensis*. Instead, it appears that one genetically and perhaps phenotypically variable subspecies is present along southern portions of the Rio Grande and Pecos River drainages. Although habitat degradation remains a serious threat to *O. z. ripensis*, there appears to be less urgency than previously thought to manage this taxon as a unique subspecies, especially given the genetic data aligning muskrats from the Pecos River with populations along the Rio Grande.

Key words: conservation, muskrat, *Ondatra zibethicus*, Pecos River, Rio Grande, subspecies

Introduction

With the advent of modern genetic analyses (e.g., DNA sequence analyses) taxonomists have developed better methods of resolving evolutionary relationships among closely related species. There are various species concepts (i.e., Biological Species Concept—Dobzhansky 1937, Mayr 1942; Morphological Species Concept—Cronquist 1978; Phylogenetic Species Concept—Cracraft 1983; and Genetic Species Concept—Bradley and Baker 2001; Baker and Bradley 2006) through which taxonomists can use genetic data to examine biological diversity and ultimately define species delineations. Therefore, the interpretation of species delineations may form the basis for regulations placed on anthropogenic industries. Further, the definition of

a species and subspecies, and the subsequent protection by law, has been an exhaustive topic of disagreement in science, especially since the addition of molecular data (Zink et al. 2000; Issac et al. 2004; Harris and Froufe 2005; Mallet et al. 2005; Haig et al. 2006).

Fundamentally related to these scenarios (see Frankham et al. 2012) is the taxonomic and conservation status of the Pecos River Muskrat (*Ondatra zibethicus ripensis*). This taxon was described by Bailey (1905) with a historical distribution that included the Pecos River and Rio Grande River watersheds (Willner et al. 1980). Based on limited museum records, and a previous survey conducted by Texas Parks and Wildlife personnel (Swepston 1981), the Pecos River muskrat is thought to have historically occurred along the entirety of the Rio Grande and Pecos Rivers and their subsequent watersheds in New Mexico and southwestern Texas. Based on a survey by Swepston (1981), the most recent records of *O. z. ripensis* include six specimens collected in 1980 from Reeves County, Texas (five from Balmorhea [30.9839°N, 103.7422°W] and one from 9.17 km southwest of Orla [31.8245°N, 103.9089°W]). An inspection of museum records indicate that an additional specimen was collected in 1991, from south-central New Mexico (14.16 km north of the Texas border [32.2155°N, 104.2904°W]).

No contemporary records exist from the Big Bend region of the Rio Grande and it may be that those populations have been extirpated (Holmes 1970; Schmidly 2004). Hafner et al. (1998) suggested that modern reduction in the flow of the Rio Grande River between El Paso and Presidio, Texas, drastically modified suitable muskrat habitat and may have reduced muskrat populations along the Lower Rio Grande. However, Schmidly (2002) noted that during the biological survey of Texas (Bailey 1905) no muskrats were collected or observed in El Paso County, Texas, suggesting that the Big Bend populations may have been the result of recent colonization in the early 20th century. Other observations from the Trans-Pecos Region, such as the degradation of riparian habitat and water quality, give rise to the assumption of possible extirpation along the entire Pecos River in Texas (Schmidly 2002, 2004; Gregory et al. 2013). For example, muskrats were unable to adapt to the formation of the San Solomon Ciénega in 1996 and subsequently were extirpated from the Balmorhea, Texas region (Garrett 2004). Further competitive exclusion resulting from the presence of the highly invasive nutria (*Myocastor coypus*) forced the muskrat from Lake Amistad (29.4503°N, 101.0578°W), and nutrias may pose a serious threat to extant populations statewide (LoBello 1976; Schmidly and Ditton 1978).

Relative to this region and this study, Hollister (1911) concluded that *O. z. ripensis* was a taxon distinct from its neighboring subspecies (*O. z. pallidus* and *O. z. osyooensis*). Hollister (1911) noted that *O. z. ripensis* differed from *O. z. pallidus* in having a smaller skull, more inflated bullae, narrower nasals, a lighter rostrum, and from *O. z. osyooensis* by possessing a darker pelage. *O. z. ripensis* is parapatric with *O. z. osoyooensis* with *O. z. ripensis* being distributed south of a line that extends east-west near Albuquerque, New Mexico, and transects both the Pecos River and the Rio Grande. Therefore, the headwaters of these rivers contain the range of *O. z. osoyooensis* and downstream populations of muskrats are within the range of *O. z. ripensis*. Due to the interdigitation of the Pecos and Rio Grande watersheds, a clear dispersal barrier separating these subspecies has not been documented, and given numerous dams, reservoirs, and stretches of disconnected habitat, it is plausible that genetic introgression between these taxa has occurred historically or may be happening in contemporary times.

An investigation into the taxonomic status of *O. z. ripensis* has not been conducted since Hollister's (1911). Further, limited genetic data exist for the *Ondatra* (Zachos et al. 2007; Laurence et al. 2011, 2013; Mychajliw and Harrison 2014); thereby little data exists that would provide an overall view of genetic variation in this species. Given the reduction in population numbers and restriction in overall distribution, there is a need to assess levels of genetic variation within surviving populations and to determine if *O. z. ripensis* is genetically distinguishable from *O. z. osoyooensis* (see Hafner et al. 1998). The mitochondrial cytochrome-*b* gene (Cyt-*b*) was chosen due to its proven usefulness in phylogeographic studies (Irwin et al. 1991; Graybeal 1993; Farias et al. 2001) and the advantage of using mtDNA over nuclear genes is the ability to detect differences between populations with small sample sizes, as generally is the case with threatened species (Moritz 1994). Therefore, the goals of this study were: 1) use DNA sequences from the mitochondrial Cyt-*b* gene to evaluate genetic variation within *O. z ripensis*; 2)

determine the taxonomic status of *O. z. ripensis*; 3) examine distributional delineations of *O. z ripensis* as depicted by Hall (1981); and 4) provide information to address management implications. To accomplish these goals, historical subspecies designations were used as a null model to evaluate genetic variation across the geographic landscape of the Pecos and Rio Grande drainages.

MATERIALS AND METHODS

Sampling.—Efforts were made to sample as many populations as possible (Fig. 1; Appendix) from the historically recognized ranges of *O. z. ripensis* and *O. z. osyooensis*. A representative from southeastern Louisiana (LSUMZ28303) and a representative from eastern Texas (SRSU2188) were used as references to assess levels of genetic variability throughout New Mexico and Texas. In total, 29 specimens, of which 9 represented *O. z. osyooensis*, 18 represented *O. z. ripensis*, and 2 represented *O. z. rivalicius* (outgroup), were examined.

DNA isolation.—To augment sampling from the historical distribution of *O. z. ripensis*, toe clips were obtained from 14 museum voucher specimens (archived at the natural history collections at University of Texas El Paso and Sul Ross State University; see Appendix). Toe clips were taken from the medial region of either the II, III, or IV phalanx or from either pedis and were prepared following ancient DNA extraction protocols outlined in Campos and Gilbert (2012), Fulton et al. (2012), Bradley and Mauldin (2016), and McDonough et al. (2018). The samples were cleaned prior to DNA extraction to decontaminate any DNA residuals from other voucher specimens housed in museum drawers and collections. All utensils were sterilized with bleach, autoclaved, and moved directly into a vent hood. The top layer of epithelial cells on each sample was considered contaminated and consequently scraped off. Each sample (entire toe) was placed in 0.25–0.5% diluted bleach and then rinsed with ddH_20 to ensure removal of bleach. Samples were then placed in sterilized reaction tubes containing ddH_20 on a shaker for three days with water being changed daily. Samples were rehydrated in 1mL of Tris-EDTA buffer solution for 24 hours, rinsed with 70% ETOH and ddH_20, hydrated again in 1mL of TE solution for 24 hours, and finally rinsed with 0.5 M EDTA to wash away inhibitors. Samples were then minced to remove nail and hair residues, leaving the uncontaminated, DNA rich, nail quick and toe pad. A Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, California) was utilized for the remaining extraction methods. To avoid the risk of contamination, DNA was extracted in a vent hood in a non-PCR laboratory. For contemporary samples, whole genomic DNA was extracted from approximately 0.1 g of frozen or ethanol preserved tissue (liver, heart, or muscle) using the Qiagen DNeasy blood and tissue kit.

PCR amplification and DNA sequencing.—PCR methods followed the polymerase chain reaction method (Saiki et al. 1988). For DNA obtained from toe clips, a ~700 bp fragment was amplified using primer 400F (Tiemann-Boege et al. 2000) and a primer (OzBRev, Mychajliw et al. 2014) designed specifically for muskrats. PCR reactions used the Phire II Hot Start DNA polymerase (Finnzymes Thermo Scientific, Rockford, Illinois) and the following parameters: initial denaturation at 98° C for 1 min 45 sec, followed by 38 cycles of denaturation at 98° C for 20 sec, annealing at 50° C for 20 sec, and extension at 72° C for 20 sec, with a final extension at 72°C for 1 min. For DNA obtained from tissue samples, two primers LGL765 forward (Bickham et al. 1995) and LGL766 reverse (Bickham et al. 2004) were used and the following PCR parameters: initial denaturation at 94° C for 2 min, followed by 35 cycles of denaturation at 94° C for 40 sec, annealing at 51° C for 45 sec, and extension at 73° C for 1 min 20 sec, with a final extension at 73° C for 10 min.

PCR products from both the toe and tissue methods were then purified with a QIAquick PCR Purification Kit (Qiagen, Valencia, California). Internal primers for cycle sequencing included: the 2 PCR primers, 700H (Peppers and Bradley 2000), and 400F (Edwards et al. 2001). Sequencing reactions were purified using sephadex columns (Princeton Separation, Adelphia, New Jersey), centrifuged, dehydrated, and then suspended in formamide. Purified products were sequenced with an ABI 3130-Avant automated sequencer and ABI Prism Big Dye version 3.1 terminator technology (Applied Biosystems, Foster City,

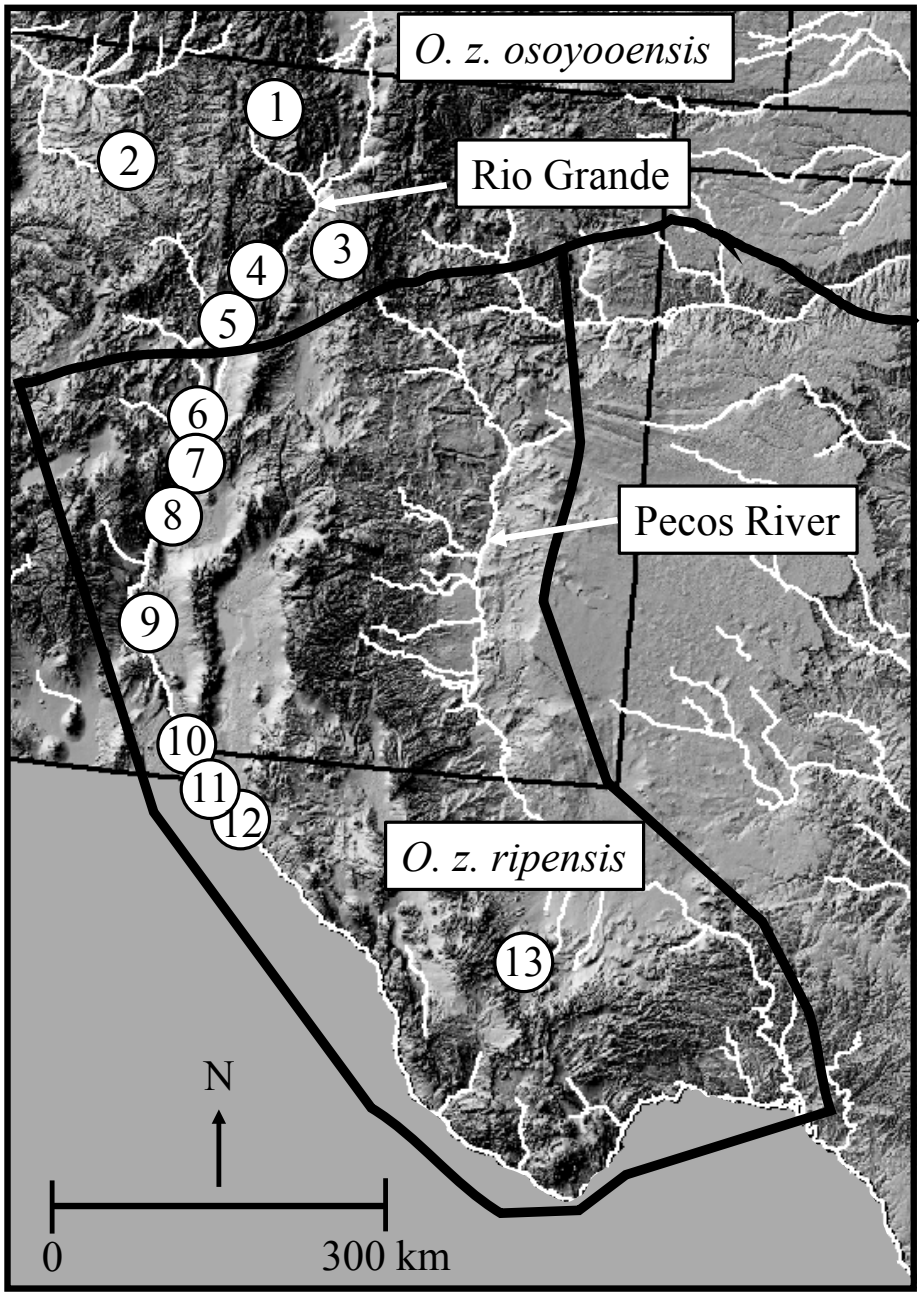

Figure 1. Map (redrawn based on Hall 1981) depicting the distribution of the two subspecies (*Ondatra zibethicus osoyooensis* and *O. z. ripensis*) present in New Mexico and western Texas. Sampling locations utilized in this study are depicted by black numbers placed in white circles and correspond to localities listed in the Appendix. The Pecos River and Rio Grande are indicated by white arrows.

California). Resulting sequences were aligned to a previously sequenced cytochrome-*b* gene in its entirety of *O. zibethicus* obtained from GenBank (KC563206), and proofed using Sequencher 4.0 software (Gene Codes, Ann Arbor, Michigan); chromatograms were examined visually to verify all base changes. All Cyt-*b* sequences obtained in this study were deposited in GenBank, and accession numbers are listed in the Appendix.

Data analyses.—Maximum likelihood models were examined using MODELTEST (Posada 2008) in order to determine the model of DNA evolution best fitting the data. The Akaike information criterion (AIC) identified the Generalized Time Reversible (GTR) model as being the most appropriate model for this dataset. Compared to other models, the GTR generated significantly better likelihood scores (-lnL = 2293.4575) and included the following parameters: base frequencies (A = 0.3115, C = 0.2780, G = 0.1290, and T = 0.2816) and rates of substitution (A–C = 2.6134, A–G = 4.3132, A–T = 1.3965, C–G = 1.0395, C–T = 9.1070, and G–T = 1.00). Nodal support was estimated using the bootstrap analysis method (Felsenstein 1985) with 1,000 iterations.

A Bayesian inference model (MRBAYES; Huelsenbeck and Ronquist 2001) was used in a likelihood framework and to generate clade probability values (CPV) that could be used as being indicative of nodal support. The southeastern Louisiana sample (*O. z. rivalicius*, LSUMZ28303) was selected as the outgroup. The GTR+I+G model with a site-specific gamma distribution was used with the following options: 4 Markov-chains, 10 million generations, and sample frequency = every 1,000th generation. The first 1,000 trees were discarded after a visual inspection and the remaining trees were used to construct a 50% majority rule consensus tree.

Genetic distances between selected taxa were calculated with the Kimura 2-parameter model of evolution (Kimura 1980). Following criteria outlined in Bradley and Baker (2001) and Baker and Bradley (2006), those values were used to assess the levels of genetic divergence among *Ondatra* subspecies.

A statistical parsimony analysis was used to illustrate relationships among haplotypes representing the DNA sequences. In this analysis, a minimum spanning haplotype network was generated in TCS v1.21 (Clement et al. 2000) with a 95% joining probability and a 9-step connection limit from a near seamless 482 bp segment (bp 512–993) of 22 Cyt-*b* sequences. The sequences were designated as either members of *O. z. ripensis* or *O. z. osoyooensis* (based on morphological identification) and were depicted in the network as proportions of each haplotype.

RESULTS

Likelihood and Bayesian analyses (Fig. 2) produced similar topologies that showed strong support for two major clades (A, CPV = 0.99 and B, CPV = 1.00). Clade A contained mostly samples from the more northern portion of the study area (Localities 1 and 3–9; Fig. 1) and Clade B contained samples generally from the more southern portion of the study area (Localities 2 and 10–12). The single sample representing the Pecos River drainage (Locality 13) was sister to the unsupported clade containing all other samples (Clade A + Clade B). There were two obvious exceptions to these patterns. First, individuals from near Blanco, New Mexico, (Locality 2) were placed within the southern clade (B), that locality being the second most northern sampling point. Second, individuals (Localities 6–9) historically assigned to *O. z. ripensis* (based on Hall's 1981 assessment) were included in the northern clade (A).

Genetic distances revealed relatively low levels of sequence divergence among all individuals (Table 1). Comparison between members of the northern clade (A) and the southern clade (B) yielded the largest genetic divergence (0.0061). The sample from Balmorhea, Texas (Locality 13), appeared to be identical to samples from Port Arthur, Texas, and Pierre Part, Louisiana; although the Balmorhea, Texas, sample was only 483 bp in length and the short sequence may have influenced phylogenetic affiliation. For additional comparisons, samples were further placed into a western group (all ingroup samples, e.g. Localities 1–12) and an eastern group represented by the two individuals of

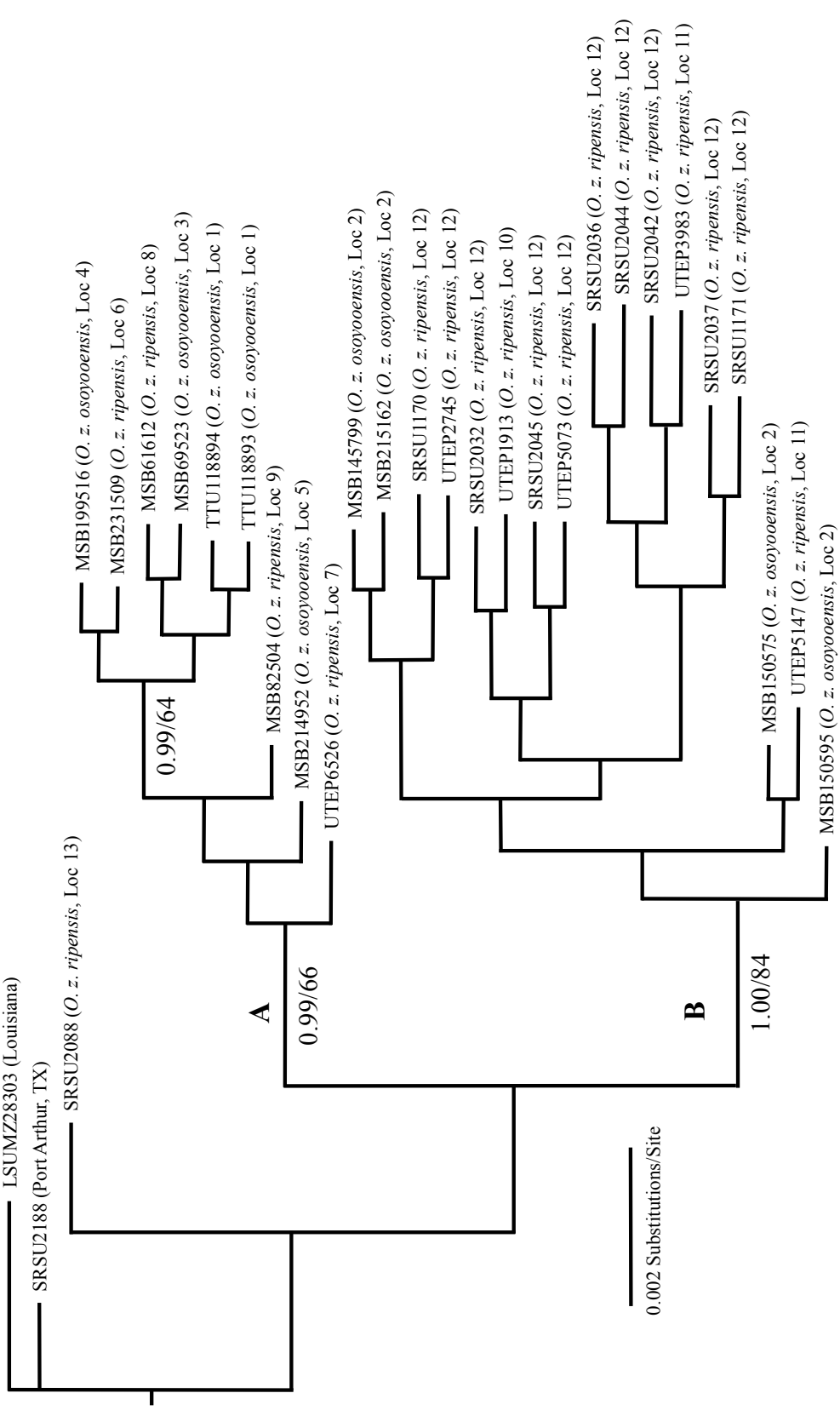

Figure 2. Phylogenetic tree obtained from maximum likelihood analysis (MrBayes, Huelsenbeck and Ronquist 2001) using the GTR+I+G model of evolution and DNA sequences obtained from the mitochondrial cytochrome-*b* gene. Letters A and B refer to major clades as identified in the text. Posterior probability values (> 0.95) are to the left of the slash (/) and bootstrap support values > 65% are indicated to the right of the slash. Localities and specimen numbers are explained in Table 1 and the Appendix.

Table 1. Average genetic distances estimated for selected comparisons of samples of *Ondrata zibethicus* using the Kimura 2-parameter model of evolution (Kimura 1980) and DNA sequences obtained from the mitochondrial cytochrome-*b* gene. Composition of northern and southern clades are referenced in the text; the western group contains all samples west of the Pecos River (northern and southern clades); whereas the eastern group was comprised of representatives of *O. z. rivalicius* (samples from Port Arthur, Texas, SRSU 2188, and Pierre Part, Louisiana, LSUMZ 28303). The sample from Balmorhea, Texas (SRSU 2088) was excluded given its genetic similarity to members of the eastern clade.

Locality	Balmorhea	Northern	Southern	Eastern	Western
Balmorhea	----	0.0035	0.0045	0.0000	0.0042
Northern	----	----	0.0061	0.0042	0.0023
Southern	----	----	----	0.0039	0.0032
Eastern	----	----	----	----	0.0040
Western	----	----	----	----	----

O. z. rivalicius (SRSU 2188 and LSUMZ 28303) and SRSU2088 from Balmorhea, Texas (Loc 13); this comparison revealed a genetic distance of 0.0040 (Table 1). Using a substitution rate of 0.028/site/1,000,000 years (i.e., 2.8% divergence per million years; see Arbogast and Slowinski [1998]), the largest genetic divergence rate observed in this study (0.0061) would translate into a separation of clades A and B approximately 217,857 years ago.

Three nucleotide substitutions were evident in the DNA sequence alignment (positions 618, 710, and 711), which distinguished the two clades. Nucleotide substitutions at 2nd and 3rd codon positions (710 and 711) of codon 237 gave rise to an amino acid difference between clades A and B (Table 2). Members of the southern clade (B) possessed a threonine at amino acid 237, whereas, individuals in the northern clade (A) and all other samples (LSUMZ28303, SRSU2188, and SRSU2088) possessed a methionine at amino acid 237. Although analyses of nucleotide sequences failed to resolve the phylogenetic relationship of the sample from Balmorhea, Texas (SRSU2088; Locality 13), the fact that it possessed a methionine at amino acid 237 suggests that it may be affiliated with members of the northern clade (Localities 1 and 3–9).

Results of the statistical parsimony analysis and minimum spanning haplotype network (TCS v1.21; Clement et al. 2000) indicated seven unique haplotypes (A–G; Fig. 3, Table 2). Haplotype B was represented by 10 individuals, haplotype D by six individuals, haplotype A by two individuals, and the remaining haplotypes were represented by a single individual. The ancestral haplotype (B) with the greatest frequency of samples (10) was nearly equally comprised of samples from the northernmost part of New Mexico and the southernmost part of Texas. The sample from Balmorhea, Texas (SRSU2088), exhibited a unique haplotype (G).

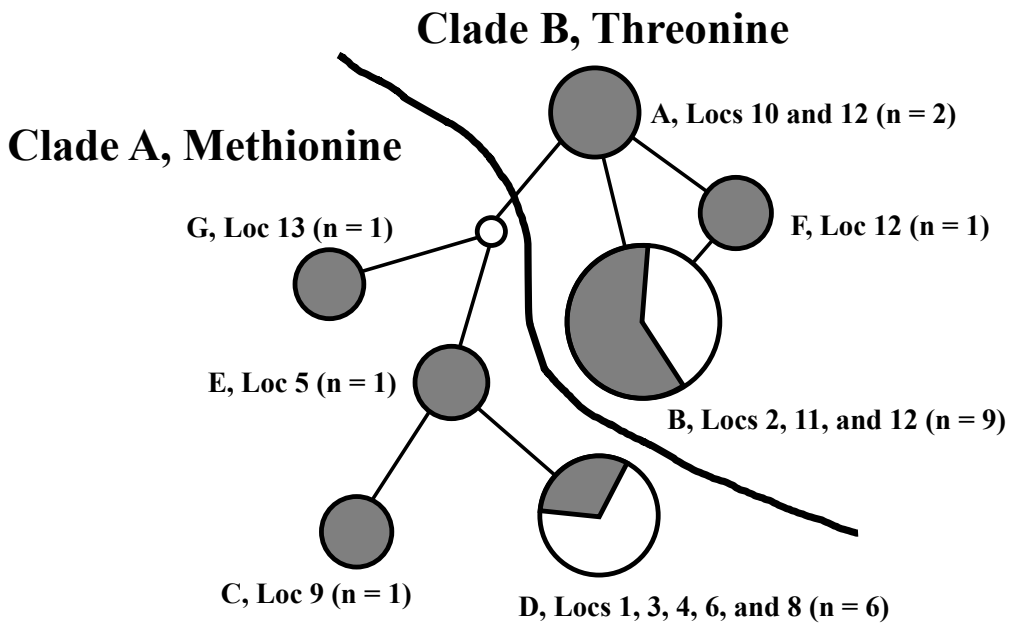

Figure 3. TCS haplotype network for the seven mitochondrial cytochrome-*b* haplotypes (A–G) obtained in this study. A minimum spanning haplotype network generated in TCS v1.21 (Clement et al. 2000) with a 95% joining probability and a 9-step connection limit from a near seamless 482 bp segment (bp 512–993) of 22 cytochrome-*b* sequences was used to illustrate relationships among haplotypes. The circle size was proportional to the number of individuals possessing a particular haplotype and each node represents a 1 bp change in nucleotide sequence. Haplotype B was represented by 10 individuals, haplotype D by 6 individuals, haplotype A by 2 individuals, and the remaining haplotypes were represented by a single individual. The open circle represents a probable missing haplotype. Dark grey represents the percentage of individuals from the putative range of *Ondatra zibethicus ripensis*, and white represents individuals from the putative range of *O. z. osoyooensis*.

Table 2. The TCS statistical parsimony network generated seven unique cytochrome-*b* haplotypes (A–G). Sample ID and Locality refer to specimens and collecting sites (see Appendix). Regions are defined as follows: Upper Rio Grande corresponds to the section of the Pecos River north of Albuquerque, NM; Middle Rio Grande corresponds to the section of river South of Albuquerque, NM, and north of Elephant Butte Reservoir; and the Lower Rio Grande corresponds to the section of the river south of Elephant Butte Reservoir. Amino acids (AA) detected at codon position 237 are abbreviated Thr (Threonine) and Met (Methionine).

Sample ID	Haplotype	Taxon	Locality	Region	AA
UTEP1913	A	*O. z. ripensis*	10	Lower Rio Grande	Thr
SRSU1170	A	*O. z. ripensis*	12	Lower Rio Grande	Thr
MSB145799	B	*O. z. osoyooensis*	2	San Juan River	Thr
MSB150595	B	*O. z. osoyooensis*	2	San Juan River	Thr
MSB150575	B	*O. z. osoyooensis*	2	San Juan River	Thr
MSB215162	B	*O. z. osoyooensis*	2	San Juan River	Thr
UTEP5147	B	*O. z. ripensis*	11	Lower Rio Grande	Thr
UTEP1171	B	*O. z. ripensis*	12	Lower Rio Grande	Thr
SRSU2032	B	*O. z. ripensis*	12	Lower Rio Grande	Thr
SRSU2045	B	*O. z. ripensis*	12	Lower Rio Grande	Thr
UTEP5073	B	*O. z. ripensis*	12	Lower Rio Grande	Thr
MSB82504	C	*O. z. ripensis*	9	Middle Rio Grande	Met
TTU118894	D	*O. z. osoyooensis*	1	Upper Rio Grande	Met
TTU118893	D	*O. z. osoyooensis*	1	Upper Rio Grande	Met
MSB69523	D	*O. z. osoyooensis*	3	Upper Rio Grande	Met
MSB199516	D	*O. z. osoyooensis*	4	Middle Rio Grande	Met
MSB231509	D	*O. z. ripensis*	6	Middle Rio Grande	Met
MSB61612	D	*O. z. ripensis*	8	Middle Rio Grande	Met
MSB214952	E	*O. z. ripensis*	5	Middle Rio Grande	Met
SRSU2037	F	*O. z. ripensis*	12	Lower Rio Grande	Thr
SRSU2088	G	*O. z. ripensis*	13	Lower Pecos	Met

DISCUSSION

Results of the molecular analyses indicate some evidence of phylogeographic patterns among muskrats sampled in New Mexico and western Texas. Two clades were recovered (A and B) that primarily depicted a northern group and a southern group. The most notable exception involved samples collected near Blanco, New Mexico (Locality 2), which were included in the southern clade (B) despite this locality being the second most northern sampling point. This finding may be indicative of an anthropogenic translocation of *O. z. ripensis* representatives to northern New Mexico; however, communication with the collector of these individuals (Zane Dohner, pers. comm.) provided no resolution. The inclusion of samples (Localities 6–9) normally assigned to *O. z. ripensis* into the northern clade (A) is interesting and may represent the need for a re-interpretation of the geographic separation between *O. z. ripensis* and *O. z. osoyooensis*, if the distinction between these two subspecies is valid. Finally, the single representative from the Pecos River drainage (Locality 13) was not included in either the northern (A) or southern (B) clades; instead it was unresolved (positioned basally and unsupported by Bootstrap or CPV) relative to clades A and B.

Average sequence divergence values between clades A and B (Table 1) were approximately an order of magnitude less than the benchmark values (2–5%) typically recovered in comparisons of subspecies as discussed in Bradley and Baker (2001) and Baker and Bradley (2006). As might be expected, samples from Louisiana (LSUMZ28303) and east Texas (SRSU2188), representative of *O. z. rivalicius*, were genetically divergent (0.0040) from muskrat samples from western Texas and New Mexico; however, the greatest genetic divergence (0.0061) actually occurred between the northern and southern clades (A and B). Despite this small level of differentiation, patterns of genetic divergence did not support previously recognized taxonomic divisions.

Although the variation among DNA sequences was low, there was a diagnostic difference among amino acids that mimicked the results of the phylogenetic relationship among localities (Fig. 2). Members of the northern clade (A) and all other samples (LSUMZ28303, SRSU2188, and SRSU2088) possessed a methionine at amino acid 237, whereas members of the southern clade (B) possessed a threonine at amino acid 237. This observation also supports the findings of the haplotype network and suggests that, genetically, the sample from the Pecos River drainage (Balmorhea, Texas, SRSU2088; Locality 13) may be affiliated with members of the northern portions of the Rio Grande (Localities 1 and 3–9). Martin and Palumbi's (1993) synopsis of the translated protein for mammalian Cyt-*b* would seem to indicate that the amino acid substitution at site 237 occurs in a highly variable region. Further, their data indicate that typically there are approximately 1.4 amino acid replacements per million years; which would indicate a much older divergence among members of clades A and B than depicted by the sequence data (217,857 years ago) presented herein.

Taxonomic implications.—The low levels of sequence divergence in the Cyt-*b* dataset obtained herein suggests that *O. z. ripensis* and *O. z. osoyooensis* are, essentially, genetically identical and perhaps should be synonymized. However, this would ignore the findings based on morphological data (Hollister 1911) and ignore the possibility of anthropogenic movement of muskrats resulting in a homogenization of genetic backgrounds. A phylogenetic investigation including the *O. z. cinnamominus* and *O. z. pallidus* subspecies may be warranted due to the proximity of their distributions relative to *O. z. ripensis* and *O. z. osoyooensis*.

Although the findings of the DNA sequence analyses, haplotype network, and distribution of the methionine versus threonine data do not support the historic delineations of *O. z. ripensis* and *O. z. osoyooensis*, there may be a natural division of populations of muskrats that occur along the Rio Grande near the Elephant Butte Reservoir. Elephant Butte Reservoir frequently discharges water for irrigation purposes (Texas Water Development Board 2015) causing a variable depth that may act as a biogeographic barrier to gene flow between populations in northern New Mexico and populations in southern New Mexico and the Trans-Pecos region of Texas. Mychajliw and Harrison (2014) and Laurence et al. (2011) discuss the formation of bottlenecks and their potential impact on contemporary populations of muskrats; and it may

be that the Elephant Butte Reservoir acts as such a barrier. Alternatively, the reduction in the impact of natural flood cycles due to water impoundment and drought may have hindered the advancement of the *O. z. osoyooensis* subspecies southward due to the fragmentation of connected palustrine marshes and flooded woodlands providing suitable temporary home ranges. Further investigations are warranted, with a focus on detecting natural genetic breaks along in the vicinity of the Elephant Butte Reservoir, and additional samples are required from throughout this region to provide a more robust interpretation of the molecular results and systematic implications.

Conservation status.—There is a general consensus that more information needs to be obtained and assessed for *O. z. ripensis* (J. Evans, Texas Parks and Wildlife Department, personal communication). The status of *O. z. ripensis* has varied by listing authority: sensitive (New Mexico Department of Game and Fish 2014), not listed (United States Fish and Wildlife Service 2018), S2 subspecies (International Union for Conservation of Nature; Cassola 2016), and unlisted by others (Texas Parks and Wildlife Department 2015). *O. z. ripensis* was considered as a category 2, trend U (U.S. Fish and Wildlife Service 1996) but currently it is not listed by the U.S. Fish and Wildlife Service (2018). Further, the muskrat scored "vulnerable" to climate change on the Middle Rio Grande due to inherent riparian habitat degradation caused by drought (Friggens et. al 2013; Finch and Tainter 1995).

The economic importance of the muskrat has changed drastically over the past 3–5 decades due to lower fur prices (U.S. Department of Agriculture 2011a, b) and the decline in the number of trappers in Texas and New Mexico. Data from the U.S. Department of Agriculture indicates that the impact of fur harvest on muskrat populations was negligible statewide (U.S. Department of Agriculture 2011a, b). Consequently, the public perception of the muskrat has gone from being socioeconomically important in the fur trade to being stigmatized as an agricultural pest (U.S. Department of Agriculture 2011a, b). The most recently available harvest numbers are from the 2000–2001 trapping season and based on the reports from 17 trappers, it appears that 255 individuals were taken from the Trans-Pecos region (J. Evans, Texas Parks and Wildlife, unpublished data). However, this number may be underrepresented due to lack in reporting from nuisance abatement. There are no current publications on population distribution or density estimates in the Trans-Pecos to compare with the 2000–2001 harvest rates.

Management implications.—Results presented herein suggests that there may be less urgency to manage *O. z. ripensis* as a unique subspecies given the low level of genetic variation between *O. z. ripensis* and *O. z. osoyooensis*. In fact, it may be that the two subspecies should be synonymized. However, based on data presented herein, the El Paso County, Texas, and Doña Ana County, New Mexico, populations may be isolated from those to the more northern areas of New Mexico; consequently, genetic introgression with populations north of Elephant Butte Reservoir may be inhibited. Additional studies are needed to assess the conservation status of *O. z. ripensis* and *O. z. osoyooensis* in southwestern Texas and the eastern half of New Mexico. Extensive fieldwork is needed to determine if populations currently occupy the lower drainages of the Rio Grande and Pecos Rivers. Further, if individuals exist in these areas, modern molecular genetic methods (Moritz 1999 and 2002; Palsboll 2006; Rubinoff 2006) should be employed to assess remaining genetic variation among populations. If sustainable populations are no longer present in this region, then a broader study is needed, including not only more contemporary samples, but also historical museum specimens to identify source/stock populations for translocation efforts.

Although *O. zibethicus* may not be restricted directly to a water-body, it is dependent upon the limited hydrographic network (Allen and Hoffman 1984) provided by the Rio Grande and Pecos River. Loss in functionality of the historical flood regime along the Pecos River and Rio Grande has caused a large ecological impact, hindering the viability and continuity of the bosque ecosystem (Crawford et al. 1996). Given that irreversible, unsuitable habitat changes are occurring rapidly on these waterways (Holmes 1970; Schmidly 2002, 2004; Gregory et. al 2013) sustainable populations of muskrats may depend on integrated ecological restoration of waterways. Consequently, current demography statistics should be evaluated to direct restoration efforts. Necessary practices might include: improved hydrology/hydrography through the modification of water release regimes to promote

river sinuosity (U.S. Geologic Survey 2001; Fullerton and Batts 2003; U.S. Army Corps of Engineers 2004, 2008, 2011), soil restoration, restoration of native plant communities supported by community stewardship programs (Rodriguez and Lougheed 2010), strict enforcement of discharge permits (El Paso Water Utilities Public Service Board 2015), restoration of the fluvial process, treatment of invasive species, reduction of fuel loads (brush clearing) to avoid catastrophic wildfires (Crawford et al. 1993, 1996), provide natural pollution buffering (Crawford et al.1993, 1996; Fullerton and Batts 2003; U.S. Fish and Wildlife Service 2010), and development of urban habitat as an alternative habitat (Cotner and Schooley 2011).

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APPENDIX

For each specimen, the collection locality, museum catalogue number (abbreviations for museum acronyms follow Hafner et al. 1997), and GenBank accession number are provided in parentheses. Abbreviations are as follows: Museum of Texas Tech University (TTU); Centennial Museum, University of Texas at El Paso (UTEP); James Scudday Vertebrate Collection, Sul Ross State University (SRSU); the Museum of Southwestern Biology, University of New Mexico (MSB); and the Museum of Natural Science, Louisiana State University (LSUMZ). Localities are shown in Figure 1 and taxonomic designations follow Hall (1981).

Ondatra zibethicus osyooensis.—New Mexico: Bernalillo County; Albuquerque (Locality 4; MSB199516, KT376451); Rio Arriba County; Chama (Locality 1; TTU118893, KT376465; TTU118894, KT376464); San Juan County; Blanco, 1.6 km NE of Blanco, Zane Dohner property (Locality 2; MSB145799, KT376444; MSB150575, KT376450; MSB150595, KT376449; MSB215162, KT376454); Santa Fe County; Santa Fe (Locality 3; MSB69523, KT376456); Valencia County; Isleta Marsh (Locality 5; MSB214952, KT376453).

Ondontra zibethicus ripensis.—New Mexico: Doña Ana County; 3.21 km W. Canutillo Rio Grande drainage (Locality 10; UTEP1913, KT376467); Socorro County; Socorro (Locality 7; UTEP6526, KT376466); Socorro, Bosque del Apache Wildlife Refuge, Unit 24A (Locality 9; MSB82504, KT376441); 12.87 km S of San Marcial (Locality 8; MSB61612, KT376455); and Valencia County; Belen, ditch along Escobedo Rd and railroad tracks (Locality 6; MSB231509, KT376452);. Texas: El Paso County; 4.82 km NW of Clint (Locality 12; SRSU1170, KT376443); 3.21 km E of Clint (Locality 12; SRSU1171, KT376445); 3.21 km SE of Clint (Locality 12; SRSU2032, KT376457; SRSU2036, KT376458; SRSU2037, KT376459; SRSU2042, KT376442; SRSU2044, KT376460); 2.73 km S of Clint (Locality 12; SRSU2045, KT376461); North of Fabens (Locality 12; UTEP2745, KT376447); West of Fabens (Locality 12; UTEP5073, KT376468); El Paso, Junction Buford and Robin on Horizon Blvd. (Locality 11; UTEP3983, KT376448); El Paso (Locality 11; UTEP5147, KT376446); and Reeves County; Balmorhea State Park (Locality 13; SRSU2088, KT376462).

Ondontra zibethicus rivalicius.—Louisiana: Assumption Parish; Vicinity of Pierre Part (locality not shown; LSUMZ28303, KT456547). Texas: Jefferson County; Port Arthur (locality not shown; SRSU2188, KT376463).

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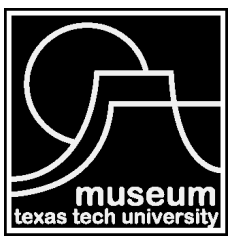

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