

## IMPLICATIONS OF HYBRIDIZATION BETWEEN WHITE-TAILED DEER AND MULE DEER

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**ABSTRACT**—Frequency of interspecific hybridization between mule deer and white-tailed deer was investigated using ribosomal DNA and nucleotide sequences from the mitochondrial cytochrome *b* gene. Two of 15 individuals (collected by hunters) from northwestern Texas (Kent County) were identified as hybrids based on the ribosomal DNA marker. Sequence data from the cytochrome *b* gene indicated that 1 individual was the result of mating between a mule deer doe and a white-tailed deer buck, whereas the second individual resulted from mating between a white-tailed deer doe and a mule deer buck. These results indicate that hybridization between mule deer and white-tailed deer is not restricted to the Trans-Pecos region of Texas. Given the low levels of genetic divergence and frequency of hybridization, the validity of recognizing mule deer and white-tailed deer as distinct species is discussed. It is concluded that without the morphological and behavioral differences these 2 taxa could be considered subspecies rather than distinct species.

**RESUMEN**—La frecuencia de hibridación entre venados bura y venados cola blanca fue investigada usando ADN ribosomal, y secuencias de nucleótidos del gen citocromo *b* mitocondrial. Dos de 15 individuos (obtenidos a través de cazadores) provenientes del noroeste de Texas (condado de Kent) fueron identificados como híbridos basándose en el marcador ADN ribosomal. Los datos de las secuencias del gen citocromo *b* indicaron que un individuo fue el resultado de un apareamiento entre una hembra venado bura y un macho venado cola blanca, mientras que otro individuo fue el resultado de un apareamiento entre una hembra venado cola blanca y un macho venado bura. Estos resultados indican que la hibridación entre los venados bura y los venados cola blanca no está restringida a la región Trans-Pecos de Texas. Dado los bajos niveles de divergencia genética y frecuencia de hibridación, se discute la validez del reconocimiento de los 2 venados como especies distintas. Se concluye que sin las diferencias morfológicas y conductuales estos 2 grupos podrían ser considerados como subspecies y no especies distintas.

Hybridization between mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) has been well documented in various regions of North America (Cowan, 1962; Kramer, 1973; Wishart, 1980; Carr et al., 1986; Stubblefield et al., 1986; Cronin et al., 1988; Gavin and May, 1988; Cronin, 1991; Derr, 1991; Ballinger et al., 1992; Carr and Hughes, 1993; Cathey et al., 1998). In Texas, it has been hypothesized that hybridization between these 2 species has been a result of white-tailed deer expanding their range into the historical range of mule deer (Carr et al., 1986). This hypothesis is based on an encroachment of woody plant species (preferred habitat of white-tailed deer)

into the more open grassland habitat typically associated with mule deer (Wiggers and Beason, 1986). In addition, it has been inferred that the dynamics of hybridization are driven by behavioral and ecological factors instead of being limited by genetic sterility (Derr et al., 1991).

Carr et al. (1986) extensively studied hybridization between these 2 species in areas of western Texas generally referred to as the Trans-Pecos region. Their studies indicated that some specimens identified as mule deer, based on morphological appearance, had mitochondrial DNA normally associated with white-tailed deer. This finding was used as evidence

of natural hybridization. These authors further hypothesized that the direction of hybridization was a result of white-tailed deer does mating with mule deer bucks. However, Ballinger et al. (1992), Carr and Hughes (1993), and Cathey et al. (1998) provided evidence that a more likely scenario was hybridization between male white-tailed deer and female mule deer, with the white-tailed deer population eventually capturing the mitochondrial DNA genome of mule deer.

Similarly, Stubblefield et al. (1986) examined 319 individuals of mule deer and white-tailed deer from 5 counties in the Trans-Pecos region of Texas. Based on allozyme data from the albumin locus, they concluded that hybridization averaged 5.6% (range 0.0 to 13.8%) within the 5 counties. Additionally, hybridization varied greatly between populations, with hybridization as high as 24% within 1 population.

In this study, we examined sympatric populations of white-tailed deer and mule deer from Kent County, Texas, for evidence of hybridization. Available for study were 15 individuals collected by hunters during a single season at the above locality and 28 individuals from localities in Texas and Colorado. A nuclear marker, 28S ribosomal DNA (rDNA) region, was used to determine if individuals were either of a pure mule deer genotype, pure white-tailed deer genotype, or a mixed genotype. A mixed genotype was viewed to be a result of hybridization between the 2 species. In addition, DNA sequences from the maternally inherited mitochondrial cytochrome *b* gene were used to establish direction of hybridization for hybrid individuals.

**METHODS—Samples**—We obtained 43 muscle or liver samples from specimens of mule deer and white-tailed deer collected by hunters from 9 natural populations in Texas ( $n = 31$ ) and Colorado ( $n = 12$ ) during 1989. In addition, 2 individuals representing a pen-raised  $F_1$  hybrid and a white-tailed deer from South Carolina were included as positive controls. Initial identification of specimens was based on ear length, tail coloration, and antlers (if male). Specimen numbers, collection localities, and identification by the rDNA method are listed in Table 1.

**Ribosomal DNA Data**—Genomic DNA was isolated from 1 white-tailed deer, 2 mule deer, and the pen-raised  $F_1$  individual using the methods of Bingham and Rubin (1981) followed by a phenol/chloroform/

isoamyl alcohol extraction. Genomic DNAs were digested with a suite of 37 restriction enzymes following the guidelines of the manufacturer (New England Biolabs, Beverly, Massachusetts; Promega, Madison, Wisconsin; and Boehringer-Mannheim, Indianapolis, Indiana). Digested DNA fragments were electrophoresed on agarose gels and transferred to nylon membranes following Southern (1975). Radioactively labeled probes (labeled via random priming; Boehringer-Mannheim, Indianapolis, Indiana) were constructed from rDNA clones of the 18S (p2546) and 28S (pI19) genes (Arnheim, 1979). Membranes were hybridized to 18S and 28S ribosomal probes and placed against x-ray film. Four restriction enzymes (*Bam* HI, *Bgl* II, *Hinc* II, and *Stu* I) revealed variation in the 28S fragment between white-tailed deer and mule deer. The remaining samples were then digested with at least 1 of the 4 restriction enzymes and hybridized to the 28S probe.

**Cytochrome *b* Sequence Data**—Using the 28S restriction site data, 2 individuals were identified as hybrids. These individuals, in addition to 1 mule deer and 1 white-tailed deer (from the same locality), were examined by sequencing the first 425 base pairs (bp) of the mitochondrial cytochrome *b* gene. This sequencing was accomplished by extracting genomic DNA from frozen muscle samples (0.1 g) using the DNeasy Tissue Kit (Qiagen, Valencia, California). The entire cytochrome *b* gene (1,143 bp) was amplified using polymerase chain reaction (PCR) parameters modified from that described by Saiki et al. (1988): 1 initial cycle (95°C for 2 min); 35 cycles of 95°C denaturation (30 s), 45°C annealing (20 s), 72°C extension (1 min 40 s); and 1 final 72°C extension cycle (15 min). Primers utilized in the PCR reactions were H15149 and L14724 of Irwin et al. (1991). The resulting PCR product was purified using the QIAquick PCR purification kit (Qiagen, Valencia, California). The following 2 primers were used in cycle sequencing reactions to amplify the forward and reverse strands, respectively: LGL765 (Bickham et al., 1995) and H15149. Cycle sequencing was conducted using the ABI Prism Big Dye version 3 terminator ready reaction mix (PE Applied Biosystems, Foster City, California) and samples were analyzed on an ABI Prism 310 automated sequencer (PE Applied Biosystems, Foster City, California). Vector NTI 7.0 software (Informax, Inc., Bethesda, Maryland) was used to align and proof nucleotide sequences. All cytochrome *b* sequences obtained in this study were deposited in GenBank (accession numbers AF535863–AF535866).

**Data Analyses**—The cytochrome *b* sequence data generated herein were analyzed using likelihood methods and the HKY algorithm, identified by the MODLETEST program (Posada and Crandall, 2001) as the model best fitting the data. The heuristic search option in the software package PAUP\* (Swof-

TABLE 1—Identification of 44 individuals examined in this study based on gross morphology and 28S ribosomal DNA restriction patterns (*Bam* HI, *Bgl* II, *Hinc* II, and *Stu* I). W = genotype associated with white-tailed deer, M = genotype associated with mule deer, and H = genotype associated with white-tailed deer and mule deer (hybrid individual).

TK#	Morphology	<i>Bam</i> HI	<i>Bgl</i> II	<i>Hinc</i> II	<i>Stu</i> I	Locality
24397	W	H	H	H	H	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24398	W	W	W	W	W	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24399	W	—	W	W	W	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24400	W	—	—	W	W	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24401	W	W	W	W	W	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24403	W	W	W	—	—	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24405	W	W	W	—	—	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24406	W	W	W	W	W	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24407	W	H	—	H	H	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24408	W	W	—	—	—	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24409	W	W	—	—	W	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24410	W	W	—	—	—	Texas: Kent County, 20 mi S Jayton (Mesquite Grove Ranch)
24412	W	W	—	—	—	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24413	M	—	—	—	M	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24416	M	M	—	M	M	Texas: Kent County, 32 km S Jayton (Mesquite Grove Ranch)
24425	M	—	—	M	—	Texas: Terrell County, 64 km E Sanderson (Hodge Ranch)
25435	H	H	H	H	H	Texas: Pen-raised F <sub>1</sub> hybrid
25436	W	W	W	W	W	Texas: Hunt, AK10558
25437	W	—	W	W	W	Texas: Hunt, AK10560
25438	W	W	—	—	W	Texas: Pecos County (Puckett Ranch)
25440	W	W	W	W	W	South Carolina: Savannah River Plant
26440	M	M	—	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26441	M	M	M	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26442	M	M	—	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26443	M	—	—	M	—	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26444	M	M	M	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26446	M	M	—	M	—	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26447	M	—	—	M	—	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26449	M	M	M	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26450	M	—	M	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26452	M	M	M	M	M	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26453	M	M	M	M	—	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)
26454	M	M	—	M	—	Colorado: 56 km E Alamosa (Forbes-Trinchera Ranch)

TABLE 1—Continued.

TK#	Morphology	<i>Bam</i> HI	<i>Bgl</i> II	<i>Hinc</i> II	<i>Stu</i> I	Locality
26461	M	—	M	M	—	Texas: Brewster County, 8 km N Alpine (Kimble Ranch)
26462	M	—	—	M	—	Texas: Brewster County, 8 km N Alpine (Kimble Ranch)
26464	M	—	—	M	—	Texas: Brewster County, 8 km N Alpine (Kimble Ranch)
26465	M	—	—	M	—	Texas: Brewster County, 8 km N Alpine (Kimble Ranch)
26466	M	—	—	M	—	Texas: Brewster County, 8 km N Alpine (Kimble Ranch)
26467	M	M	—	M	—	Texas: Brewster County, 8 km N Alpine (Kimble Ranch)
26469	M	M	M	M	M	Texas: Hudspeth County, 4 km E Salt Flat (Chavez Ranch)
26471	M	—	—	M	—	Texas: Hudspeth County, 4 km E Salt Flat (Chavez Ranch)
27789	M	M	—	—	—	Texas: Moore County (Plum Creek Ranch)
27821	M	M	—	—	—	Texas: Brewster County, 32 km S Marathon (Combs Ranch)
27823	M	M	—	—	—	Texas: Brewster County, 32 km S Marathon (Combs Ranch)
27919	W	W	—	—	—	Texas: San Patricio County, Welder Wildlife Foundation

ford, 2002) was used to obtain a phylogenetic tree. *Cervus elaphus* (elk) was used as the outgroup, and sequences from a mule deer (L48402), black-tailed deer (*O. hemionus*; M98488), and white-tailed deer (L48406) obtained from GenBank were included as references.

**RESULTS**—Of the 44 individuals screened with the 28S rDNA probe, 2 (TK24397 and TK24407) displayed restriction patterns indicating that they possessed nuclear DNA of both mule deer and white-tailed deer. Both individuals were from the same population (Texas: Kent County, 32 km S Jayton). The remaining 13 individuals from this population were either pure mule deer ( $n = 2$ ) or white-tailed deer ( $n = 11$ ) based on results of the 28S rDNA gene.

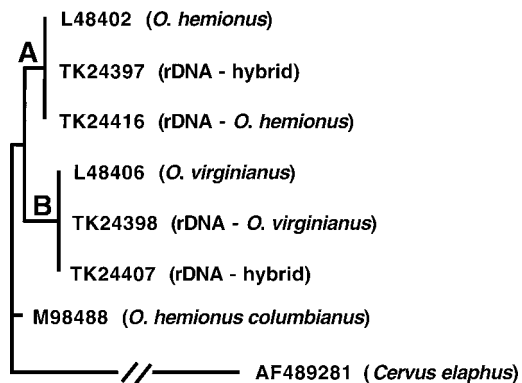


FIG. 1—Phylogenetic tree generated with DNA sequences from the cytochrome *b* gene. The tree obtained using likelihood methods contains a clade (A) representing taxa referable to mule deer and a clade (B) referable to white-tailed deer.

The likelihood analysis of cytochrome *b* sequences produced 2 clades (Fig. 1). The first clade (A) contained 3 sequences assigned to mule deer (TK24397, TK24416, and L48402) and the second clade (B) contained 3 sequences assigned to white-tailed deer (TK24398, TK24407, and L48406). The black-tailed deer sequence (M98488) was placed basal to the mule deer and white-tailed deer clades.

**DISCUSSION**—Two samples possessed rDNA banding patterns that did not correspond to the initial identification based on a morphological assessment. Individual TK24397, morphologically identified as a white-tailed deer, was a hybrid based on the 28S rDNA marker, and possessed mitochondrial DNA characteristic of mule deer. Likewise, individual TK24407, morphologically identified as a white-tailed deer, was a hybrid based on the 28S rDNA marker, but possessed mitochondrial DNA characteristic of white-tailed deer. Analysis of these results suggests that 1 individual (TK24397) was the result of a mating between a mule deer doe and a white-tailed deer buck, whereas the other (TK24407) resulted from a mating between a white-tailed deer doe and a mule deer buck.

Hybrid individuals were detected from only the Kent County, Texas locality. Overall frequency of hybrid individuals from this population was 13.3% (2 of 15). Both individuals appeared to represent  $F_1$ s based on comparison of the intensity of banding pattern with patterns obtained from the known  $F_1$  (pen-raised). However, it would be difficult to distin-

guish between  $F_1$  and backcross individuals given the techniques used in this study and the repetitive nature of the chromosomal distribution of the rDNA repeats.

Data generated from this study indicate that hybridization between mule deer and white-tailed deer in Texas is not restricted to the Trans-Pecos region but also occurs in portions of northwestern Texas. Mule deer and white-tailed deer occur sympatrically along the edge of the geological mesa known as the Llano Estacado. Although the Llano Estacado itself has not historically supported populations of deer, the edges or "caprock" provide suitable habitat for both species. Canyons, draws, and rolling hills are common along the caprock and presumably have provided a narrow band of suitable habitat in which the 2 species co-occur and have the potential to hybridize. Although the caprock provides a natural mechanism for mule deer to disperse into Texas from New Mexico or Colorado, the Texas Parks and Wildlife Department transplanted mule deer into the Palo Duro area during the 1950s. The latter event might be the most likely explanation for the occurrence of mule deer in this area, given that the expedition by United States Army Captains Marcy and McClellan into this area in 1852 provided observations of white-tailed deer but none of mule deer (Foreman, 1937).

Although the frequency of hybridization between mule deer and white-tailed deer might be high within certain populations (13.3%, this study; 24%, Stubblefield et al., 1986), we believe the 2 species behave as valid biological species. This especially is true if one follows the phylogenetic species concept of Cracraft (1983). Bradley and Baker (2001) argued that the magnitude of genetic differentiation between 2 taxa could be used as a reference point for recognition of species. In the example of mule deer and white-tailed deer, the 2 taxa differ by an average of 1.3%. This is substantially less than that reported by Bradley and Baker (2001) for sister species of rodents (mean = 9.6%) and bats (mean = 6.8%) and might indicate a relatively recent divergence time for the 2 species of deer. Alternatively, it might be that cervids exhibit a lower level of genetic divergence between sister species. Further complicating the interpretation of genetic divergence is the fact that, based on mitochondrial DNA sequences, mule deer are more closely related to white-

tailed deer than they are to black-tailed deer. Given that mule deer and black-tailed deer are considered to be conspecific, based on nuclear gene sequences, this introduces the arguments of lineage sorting, introgression, or a recent divergence of *O. virginianus* from *O. hemionus*. Cronin (1991) argued that lineage sorting (sensu Avise, 1994) is responsible for this phenomenon, whereas Carr et al. (1986) supported hybridization to explain the genetic similarity between mule deer and white-tailed deer. In a more extensive study, Carr and Hughes (1993) could not distinguish among the 3 alternatives. Although intriguing, these topics are beyond the scope of this study.

Recognition of 2 species is compatible with the strategies by state agencies and biologists for the management of deer herds. However, as pointed out by Jones et al. (1995), the presence of hybrids poses a dilemma for biologists and policy makers. Undoubtedly, hybrid individuals are collected as a result of hunter harvest. Because bag limits and times of hunting seasons vary, possession of a hybrid individual might pose an interesting situation for the hunter and law enforcement agents.

An overview is that mule deer and white-tailed deer are widely sympatric, with many areas of hybridization. Both species have areas of habitat preference where they exist in allopatry. Because these 2 species hybridize so extensively in some areas (e.g., 24% of population are hybrids), should these 2 currently recognized species of deer be reduced to subspecies? Clearly, mule deer behavior (e.g., gait, avoidance behavior) and phenotype (e.g., body form, color, antlers, ear size, length of metatarsal gland) are different from white-tailed deer. In our opinion, they represent biological species and the genetic integrity of each is maintained despite extensive hybridization over a widespread geographic area.

Before molecular biology, the prevailing view was that if 2 groups hybridized they represented subspecies, not species. With the advent of greater resolution of the genetic nature of individuals in populations, metapopulations, subspecies, and species, it becomes clear that even extensive hybridization does not necessarily mean introgression is occurring to a point where subspecies status is more appropriate than specific status. In Bradley and Baker (2001), the values of distinction of cytochrome

*b* sequences that generally indicate completion of the speciation process between sister species was reviewed, and the values that distinguish mule deer and white-tailed deer are at a level of populational or subspecific distinction. If these were nongame animals without the wealth of information on morphology, behavior, etc., we probably would recognize these 2 taxa as hybridizing subspecies, and we would underestimate the richness in this species complex.

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#### LITERATURE CITED

- ARNHEIM, N. 1979. Characterization of mouse ribosomal gene fragments purified by molecular cloning. *Gene* 7:83–96.
- AVISE, J. C. 1994. *Molecular markers, natural history, and evolution*. Chapman and Hall, New York.
- BALLINGER, S. W., L. H. BLANKENSHIP, J. W. BICKHAM, AND S. M. CARR. 1992. Allozyme and mitochondrial DNA analysis of a hybrid zone between white-tailed deer and mule deer (*Odocoileus*) in West Texas. *Biochemical Genetics* 30:1–11.
- BICKHAM, J. W., C. C. WOOD, AND J. C. PATTON. 1995. Biogeographic implications of cytochrome *b* sequences and allozymes in sockeye (*Onchorhynchus nerka*). *Journal of Heredity* 86:140–144.
- BINGHAM, P. R., AND G. M. RUBIN. 1981. Cloning of DNA sequences from the *white* locus of *D. melanogaster* by a novel and general method. *Cell* 25:693–704.
- BRADLEY, R. D., AND R. J. BAKER. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. *Journal of Mammalogy* 82:960–973.
- CARR, S. M., S. W. BALLINGER, J. N. DERR, L. H. BLANKENSHIP, AND J. W. BICKHAM. 1986. Mitochondrial DNA analysis of hybridization between sympatric white-tailed deer and mule deer in West Texas. *Proceedings of the National Academy of Science* 83:9576–9580.
- CARR, S. M., AND G. A. HUGHES. 1993. Direction of introgressive hybridization between species of North American deer (*Odocoileus*) as inferred from mitochondrial-cytochrome *b* sequences. *Journal of Mammalogy* 74:331–343.
- CATHEY, J. C., J. W. BICKHAM, AND J. C. PATTON. 1998. Introgressive hybridization and nonconcordant evolutionary history of maternal and paternal lineages in North American deer. *Evolution* 52:1224–1229.
- COWAN, I. M. 1962. Hybridization between the black-tailed deer and the white-tailed deer. *Journal of Mammalogy* 43:539–541.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. In: Johnston, R. F., editor. *Current ornithology*. Plenum Publishing Corporation, New York. Pp. 159–187.
- CRONIN, M. A. 1991. Mitochondrial and nuclear genetic relationships of deer (*Odocoileus* spp.) in western North America. *Canadian Journal of Zoology* 69:1270–1279.
- CRONIN, M. A., E. R. VYSE, AND D. G. CAMERON. 1988. Genetic relationships between mule deer and white-tailed deer in Montana. *Journal of Wildlife Management* 52:320–328.
- DERR, J. N. 1991. Genetic interactions between white-tailed and mule deer in the southwestern United States. *Journal of Wildlife Management* 55:228–237.
- DERR, J. N., D. W. HALE, D. L. ELLSWORTH, AND J. W. BICKHAM. 1991. Fertility in an F<sub>1</sub> male hybrid of white-tailed deer (*Odocoileus virginianus*) × mule deer (*O. hemionus*). *Journals of Reproduction and Fertility* 93:111–117.
- FOREMAN, G. 1937. *Adventure on Red River: report on the exploration of the Red River by Captain Randolph B. Marcy and Captain G. B. McClellan*. University of Oklahoma Press, Norman.
- GAVIN, T. A., AND B. MAY. 1988. Taxonomic status and genetic purity of Columbian white-tailed deer. *Journal of Wildlife Management* 52:1–10.
- IRWIN, D. M., T. D. KOCHER, AND A. C. WILSON. 1991. Evolution of the cytochrome *b* gene in mammals. *Journal of Molecular Evolution* 2:37–55.
- JONES, J. K., JR., R. D. BRADLEY, AND R. J. BAKER. 1995. Hybrid pocket gophers and some thoughts on the relationship of natural hybrids to the rules of nomenclature and the endangered species act. *Journal of Mammalogy* 76:43–49.
- KRAMER, A. 1973. Interspecific behavior and dispersion of two sympatric deer species. *Journal of Wildlife Management* 37:288–300.
- POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- SAIKI, R. K., D. H. GELFAND, S. STOFFEL, S. J. SCHARF, R. HIGUCHI, G. T. HORN, K. B. MULLIS, AND H. A. ERLICH. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* 239:487–491.
- SOUTHERN, E. M. 1975. Detection of specific sequences among DNA fragments separated by gel electrophoresis. *Journal of Molecular Biology* 98:503–517.
- STUBBLEFIELD, S. S., R. J. WARREN, AND B. R. MURPHY.

1986. Hybridization of free-ranging white-tailed and mule deer in Texas. *Journal of Wildlife Management* 50:688–690.
- SWOFFORD, D. L. 2002. PAUP\*: phylogenetic analysis using parsimony (\* and other methods), version 4. Sinauer Associates, Sunderland, Massachusetts.
- WIGGERS, E. P., AND S. L. BEASOM. 1986. Characterization of sympatric or adjacent habitats of 2 deer species in West Texas. *Journal of Wildlife Management* 50:129–134.
- WISHART, W. D. 1980. Hybrids of white-tailed and mule deer in Alberta. *Journal of Mammalogy* 61:716–720.
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