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GENETIC INTERACTIONS BETWEEN WHITE-TAILED AND MULE DEER IN THE SOUTHWESTERN UNITED STATES

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Abstract: I used protein electrophoresis to estimate the degree of genetic exchange between white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) from areas of sympatry throughout the southwestern United States. Allelic variation from 25 presumptive gene loci were assayed from 201 deer from 31 localities. Although interspecific hybridization has been previously documented with both nuclear and mitochondrial markers, most areas of sympatry in the Southwest displayed little evidence of nuclear gene introgression. Nevertheless, hybridization was evident from some localities with 2.0% of the white-tailed deer and 1.7% of the mule deer heterozygous at one of 2 diagnostic nuclear loci. Changing environmental conditions that provide a competitive advantage of 1 species over the other may result in ephemeral areas of hybridization. Studies designed to ascertain the ecological and concomitant behavioral changes in these areas could be used to predict and identify potential areas of genetic interaction between these 2 species.

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White-tailed and mule (or black-tailed) deer comprise the genus *Odocoileus* which is distributed throughout much of the New World from Alaska to South America. The range of white-tailed deer includes the north temperate habitats of Canada to tropical environments of Central and South America. The distribution of mule deer extends throughout the desert and mountainous regions of the western United States and Canada; whereas, black-tailed deer are found along the coast of the Pacific Northwest from California to Alaska. Ranges of the 2 species overlap in the western United States and southwestern Canada. Where white-tailed and mule deer occupy the same general area, they usually are ecologically segregated in their choice of habitats (Baker 1984).

Analyses of allele frequencies derived from protein electrophoresis indicate Columbian white-tailed deer (*O. v. leucurus*) and Columbian black-tailed deer (*O. h. columbianus*) share otherwise diagnostic alleles in low frequency (3%) at 3 presumptive gene loci in the Pacific Northwest (Gavin and May 1988). Different serum albumin alleles predominate in each species, and the distribution of these alleles has been used to infer interspecific hybridization. Stubblefield et al. (1986) estimated that 5.9% of the deer sampled in west Texas had hybrid ancestry. At the Longfellow Ranch in Pecos County, Texas, Ballinger (1987) found evidence of hybridization, based on albumin mobilities, from 24% of the deer sampled. In Montana, 2% of the individuals examined by Cronin et al. (1988) also shared albumin alleles that were otherwise diagnostic at this locus. These studies document the potential for hybridization in areas of sympatry; however, Stubblefield et al. (1986) and Cronin et al. (1988) only examined the products of 1 gene system, and Ballinger (1987) restricted his analysis to a single location.

Restriction endonuclease site mapping of mitochondrial deoxyribonucleic acid (mtDNA) also provides evidence of genetic interactions between the 2 species. Because mtDNA is maternally inherited and lacks recombination, this molecule can be considered a single haploid locus for population genetic analyses. As compared with allozyme data, white-tailed and mule deer in Montana have distinct but similar mtDNA haplotypes (Cronin et al. 1988). In contrast, Carr et al. (1986) and Ballinger (1987) found that white-tailed and mule deer shared a mtDNA haplotype on the Longfellow Ranch in west Texas, suggesting cytoplasmic gene flow. These studies also reveal that the sequence divergence of mtDNA haplotypes between white-tailed and mule deer is much less than the divergence between subspecies of *O. hemionus* (mule deer and black-tailed deer). One interpretation of this finding is historical introgression of mtDNA from white-tailed deer to mule deer, independent of black-tailed deer (Carr et al. 1986, Cronin et al. 1988, Derr 1990). These studies indicate the potential for nuclear and cytoplasmic gene flow between white-tailed and mule deer.

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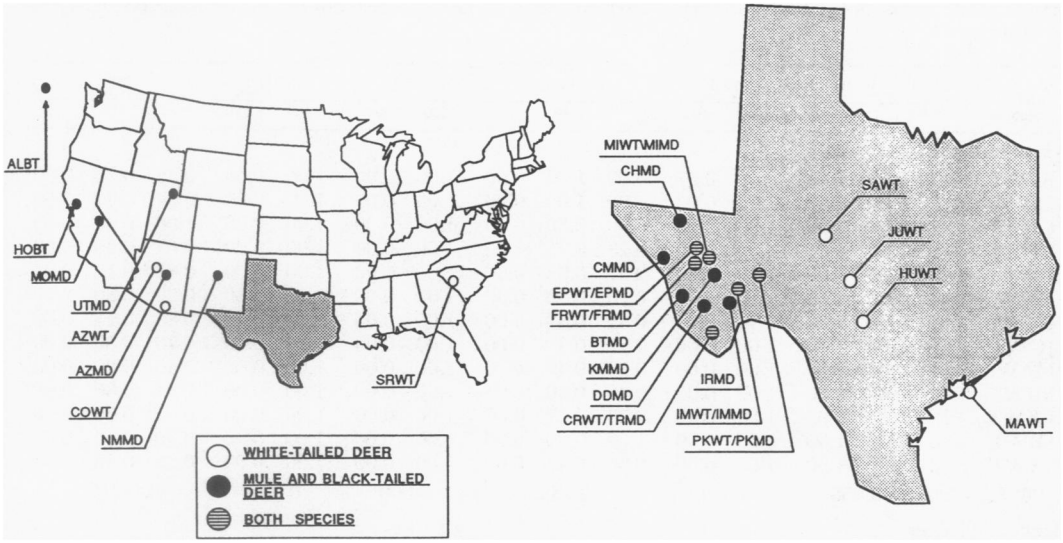

Fig. 1. Geographic distribution of the localities sampled for white-tailed, mule, and black-tailed deer. (See Appendix A for description of locations, abbreviations, and samples sizes.)

The goal of my study was to evaluate the extent of genetic interactions between the 2 species in the southwestern United States based on nuclear genetic markers and to compare this information to the mtDNA results of Carr et al. (1986). Subsequently, I estimated the effect of introgression, as demonstrated by cytoplasmic gene flow (mtDNA), on the integrity of the nuclear gene pools associated with white-tailed and mule deer.

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METHODS AND MATERIALS

Liver samples were obtained from 201 hunter-killed deer at 31 localities (Fig. 1) from 1984 to 1988. Species identification was made in the field using standard morphological characters (Wallmo 1981). Voucher tissues were deposited in the frozen tissue collection, Texas Cooperative Wildlife Collection, Texas A&M University, College Station. (See Appendix A for collection localities, abbreviations, and sample sizes.)

Tissue preparation and histochemical staining were conducted according to Selander et al. (1971) and Harris and Hopkinson (1976). Electrophoretic procedures were essentially those described by Selander et al. (1971). I assigned alleles numerical designations based on the mobilities of the protein products relative to the most common electromorph among samples of white-tailed deer (designated 100 if anodal or −100 if cathodal). (See Appendix B for buffer systems used, enzyme commission numbers [E.C.], and protein abbreviations.)

I used BIOSYS-1 (Swofford and Selander 1981) and BIOSTAT-1 (Pimentel and Smith 1986) to analyze allelic variation. Descriptive statistics included mean heterozygosity ($\bar{H}$), proportion of loci polymorphic (P), and the mean number of alleles per locus ($\bar{A}$). Statistical significance was addressed with a Mann-Whitney U nonparametric test. Deviation from Hardy-Weinberg equilibrium was tested with Fisher's exact test. Fixation indices (F_{st}) (Van Den Bussche et al. 1986) were calculated to measure genetic differentiation among populations within species.

Coefficients of genetic distance and identity (Nei 1972, Rogers 1972) were calculated for all pair-wise population comparisons of the 2 species. Previous genetic studies of white-tailed and mule deer have reported distance values calculated by the methods of both Nei (1972) and

Table 1. Allelic frequency and fixation indices for the polymorphic loci among populations of *Odocoileus* sampled. Localities are as in Figure 1.

Species and population	*n*	ACPH		ALB		GPD1			IDH1		MDH2		MP1		
		100	−100	100	103	100	145	86	100	94	−100	−140	100	118	82
White-tailed deer															
AZWT	7	0.00	1.00	0.93	0.07	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.75	0.25	0.00
COWT	8	0.00	1.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.64	0.36	0.00
CRWT	1	0.00	1.00	1.00	0.00	0.50	0.50	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
EPWT	8	0.00	1.00	1.00	0.00	0.25	0.75	0.00	1.00	0.00	1.00	0.00	0.67	0.33	0.00
FRWT	4	0.00	1.00	1.00	0.00	0.37	0.63	0.00	1.00	0.00	1.00	0.00	0.88	0.12	0.00
HUWT	5	0.00	1.00	1.00	0.00	0.70	0.30	0.00	1.00	0.00	1.00	0.00	0.20	0.80	0.00
IMWT	7	0.00	1.00	0.93	0.07	0.42	0.58	0.00	1.00	0.00	1.00	0.00	0.86	0.14	0.00
JUWT	5	0.00	1.00	1.00	0.00	0.70	0.30	0.00	1.00	0.00	1.00	0.00	0.70	0.30	0.00
MAWT	5	0.00	1.00	1.00	0.00	0.60	0.40	0.00	1.00	0.00	1.00	0.00	0.40	0.60	0.00
MIWT	14	0.00	1.00	1.00	0.00	0.46	0.50	0.04	1.00	0.00	1.00	0.00	0.64	0.36	0.00
PKWT	15	0.07	0.93	1.00	0.00	0.73	0.27	0.00	1.00	0.00	1.00	0.00	0.41	0.59	0.00
SRWT	5	0.00	1.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.90	0.10	0.00
SAWT	8	0.00	1.00	1.00	0.00	0.56	0.44	0.00	1.00	0.00	1.00	0.00	0.38	0.62	0.00
WT F_{ST}		0.058		0.054		0.289			0.000		0.000		0.212		
Black-tailed deer															
ALBT	1	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
HOBT	5	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
Mule deer															
AZMD	8	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.94	0.00	0.06
BTMD	10	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
CHMD	3	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.50	0.50	0.00
CMMD	3	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
DDMD	5	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
EPMD	9	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
FRMD	6	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.92	0.08	1.00	0.00	1.00	0.00	0.00
IMMD	7	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
IRMD	10	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
KMMD	5	1.00	0.00	0.10	0.90	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.60	0.30	0.10
MIMD	2	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
MOMD	10	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
NMMD	1	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
PKMD	11	1.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00
TRMD	6	1.00	0.00	0.08	0.92	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.90	0.10	0.00
UTMD	7	1.00	0.00	0.00	1.00	0.07	0.93	0.00	1.00	0.00	0.93	0.07	0.93	0.07	0.00
MD F_{ST}		0.000		0.071		0.057			0.066		0.057		0.295		

Rogers (1972). For comparison with published values, I calculated both estimates of genetic distance. I also examined phenetic relationships among populations with the unweighted pair group matrix analysis (UPGMA) algorithm of Sneath and Sokal (1973).

RESULTS

Allelic Variation.—The products of 25 presumptive gene loci were assessed in a preliminary survey of 15 white-tailed deer, 10 mule deer, and 5 black-tailed deer. Ten loci were polymorphic, including eight for white-tailed deer and eight for mule deer (Table 1). Animals from all populations were surveyed for allelic variation at each polymorphic locus; however, due to variation in tissue quality, only 94.6% of this data matrix was complete. Two of the polymorphic loci among all populations deviated from Hardy-Weinberg equilibrium. White-tailed deer from the Eppenhauer Ranch (EPWT) had a heterozygote deficiency for MPI (P = 0.03), and mule deer from the Brite Ranch (BTMD) had a heterozygote excess at PGD (P = 0.045). Observed mean heterozygosity ($\bar{H}$) was 0.056 ± 0.026 (SE) for white-tailed deer and 0.037 ± 0.022 for mule and black-tailed deer. A Mann-Whitney U 2-sample test failed to reject the null hypothesis of equivalent observed heterozygosity values between the 2 species ($P < 0.01$). The difference in mean number of alleles per locus ($\bar{A}$) for white-tailed deer (1.52) and mule and black-tailed deer (1.40) was not significant ($P < 0.01$). The proportion of loci

Table 1. Extended.

PEPD			PEPE		PGD				SDH				
100	94	88	100	96	100	118	109	73	−100	−120	−105	−92	−84
1.00	0.00	0.00	1.00	0.00	0.79	0.00	0.00	0.21	1.00	0.00	0.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.71	0.00	0.00	0.00	0.29
1.00	0.00	0.00	1.00	0.00	0.88	0.00	0.00	0.12	0.75	0.00	0.25	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.40	0.00	0.10	0.50	0.50	0.00	0.00	0.00	0.50
1.00	0.00	0.00	1.00	0.00	0.79	0.00	0.00	0.21	0.80	0.00	0.00	0.00	0.20
1.00	0.00	0.00	1.00	0.00	0.75	0.25	0.00	0.00	0.50	0.50	0.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00	0.30
1.00	0.00	0.00	1.00	0.00	0.96	0.00	0.00	0.04	0.83	0.00	0.08	0.00	0.09
1.00	0.00	0.00	1.00	0.00	0.96	0.00	0.00	0.04	0.60	0.00	0.05	0.00	0.35
1.00	0.00	0.00	1.00	0.00	0.90	0.00	0.00	0.10	1.00	0.00	0.00	0.00	0.00
0.94	0.06	0.00	0.94	0.06	0.94	0.00	0.00	0.06	0.71	0.00	0.00	0.00	0.29
	0.049			0.049			0.220				0.189		
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
1.00	0.00	0.00	1.00	0.00	0.44	0.06	0.00	0.50	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.55	0.00	0.00	0.45	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.17	0.00	0.00	0.83	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.67	0.00	0.00	0.33	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.25	0.00	0.00	0.75	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.67	0.00	0.00	0.33	0.25	0.00	0.75	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.25	0.00	0.00	0.75	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.29	0.00	0.00	0.71	0.86	0.00	0.14	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.15	0.00	0.00	0.85	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.70	0.00	0.00	0.30	0.25	0.00	0.75	0.00	0.00
1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.39	0.00	0.00	0.61	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.27	0.00	0.00	0.73	0.00	0.00	1.00	0.00	0.00
1.00	0.00	0.00	1.00	0.00	0.25	0.00	0.00	0.75	0.00	0.00	1.00	0.00	0.00
0.93	0.00	0.07	1.00	0.00	0.25	0.00	0.00	0.75	0.00	0.00	1.00	0.00	0.00
	0.057			0.000			0.243				0.573		

polymorphic (P) was the same for both species (32.0%).

Profound differences in allozymic frequencies distinguished populations of white-tailed deer from those of mule and black-tailed deer. The products of 2 presumptive loci, ACPH and ALB, displayed nearly fixed allelic differences between samples of the 2 species. All white-tailed deer at the ACPH locus, except for 1 individual (PKWT), were homozygous for the ACPH −100 allelle, and all mule and black-tailed deer were homozygous for the ACPH 100 allele. For ALB, 2 of the 92 white-tailed deer sampled (from AZWT and IMWT) were heterozygous for the ALB 100/103 alleles. All remaining white-tailed deer were homozygous for the ALB 100 allele. Two of the 103 mule deer sampled (from TRMD and KMMD) were heterozygous (100/103) at the ALB locus; whereas, all others were homozygous for the ALB 103 allele. Each of the 6 black-tailed deer examined were homozygous for the ALB 103 allele.

Not all sympatric localities exhibit evidence of genetic interaction. For example, both species had fixed ACPH and ALB allelic differences on the Friends Ranch (FRWT/FRMD, $n = 10$) and the McIvior Ranch (MITW/MIMD, $n = 16$). From sympatric localities both species displayed similar effects of introgression with 3 of 64 (2.0%) white-tailed deer and 2 of 86 (1.7%) mule deer heterozygous at one of the 2 marker nuclear loci.

Allele frequency differences at 4 other presumptive loci provided additional evidence of

Table 2. Coefficients of genetic distance and identity among and between samples of *Odocoileus virginianus* (white-tailed deer) and *O. hemionus* (black-tailed and mule deer).

Coefficient and comparison	Range	$\bar{x}$
Distance (Rogers 1972)		
Populations		
White-tailed deer	0.011–0.086	0.043
Mule deer	0.000–0.071	0.030
Between species	0.102–0.206	0.160
Taxa		
White-tailed vs. mule deer		0.161
White-tailed vs. black-tailed deer		0.149
Mule vs. black-tailed deer		0.052
Distance (Nei 1972)		
Populations		
White-tailed deer	0.001–0.050	0.017
Mule deer	0.000–0.056	0.017
Between species	0.089–0.200	0.135
Taxa		
White-tailed vs. mule deer		0.137
White-tailed vs. black-tailed deer		0.130
Mule vs. black-tailed deer		0.031
Identity (Nei 1972)		
Populations		
White-tailed deer	0.951–0.999	0.982
Mule deer	0.948–1.000	0.983
Between species	0.915–0.806	0.873

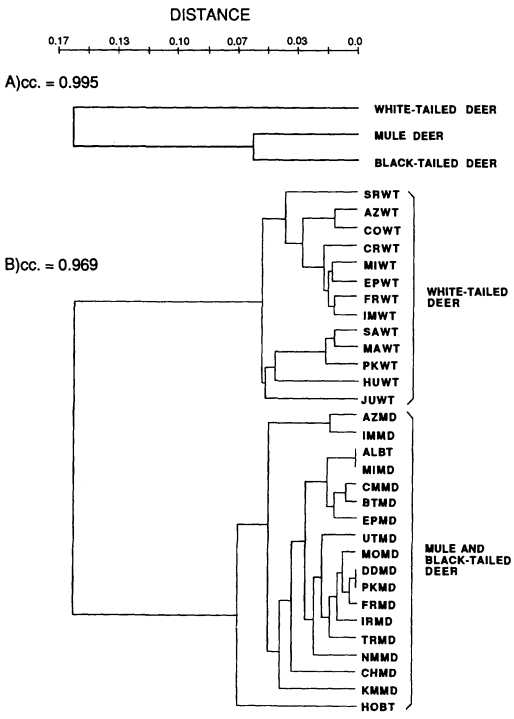

Fig. 2. Clustering of distance values among (A) white-tailed, mule, and black-tailed deer and (B) for each locality examined. (See Appendix A for description of locations, abbreviations, and samples sizes.)

genetic divergence. White-tailed deer allele frequencies were almost equally split between the GPD1 allele 100 (0.465) and GPD1 allele 145 (0.529), whereas all mule deer except one (0.995) and all black-tailed deer had the GPD1 145 allele. Similar allele frequencies occurred at the MPI locus where white-tailed deer displayed both the MPI 100 allele and the MPI 118 allele in roughly equal frequencies (0.596 and 0.404, respectively), whereas mule and black-tailed deer predominately had the MPI 100 allele (0.950). Only two of the 4 alleles resolved from the PGD locus were common in either species. The PGD 100 allele was the most common allele from white-tailed deer (0.886), whereas the PGD 73 allele was the most frequently encountered allele at this locus from mule deer (0.619). All black-tailed deer had the PGD 100 allele. Of the 5 alleles determined at the SDH locus, SDH −100 was the most common allele in white-tailed deer (0.766), and the SDH −105 was the most frequent allele from mule deer (0.815). One SDH allele (SDH −92) was unique to California black-tailed deer (HOBT).

Efforts to resolve an additional enzyme, galactosaminidase (E.C. 3.2.1.53), reported as species-specific by Gavin and May (1988), proved unsuccessful. These authors reported 2 alleles at this locus from the Pacific Northwest, one of which was unique to white-tailed deer; the other was restricted to mule and black-tailed deer.

Genetic Distance.—Estimates of mean genetic distance between species were 0.135 (Nei 1972) and 0.160 (Rogers 1972). Mean identity values (Nei 1972) among populations were similar for both white-tailed and mule deer; I = 0.982 and I = 0.983, respectively (Table 2). Cluster analysis constructed from the coefficients of genetic distance (Table 2) grouped white-tailed, mule, and black-tailed deer, which is consistent with their current taxonomic relationship (Fig. 2A). In the phenogram clustering individual populations of the 2 species (Fig. 2B), samples of white-tailed deer clustered at values <0.052, and mule and black-tailed deer clustered at values <0.065. The 2 major subdivisions, representing both species groups, form the terminal

assemblage at the mean interspecific distance of 0.160.

Quantitative evidence of divergence between species also reveals marked differences. Nei's (1972) genetic distance between white-tailed and mule deer (D = 0.135, based on 25 loci) was identical to the value reported by Gavin and May (1988) based on 35 loci and was also similar to that reported by Baccus et al. (1983) (Nei's D = 0.149; based on 19 loci). Ballinger (1987) reported a Nei's D = 0.050 and Rogers' D = 0.086 from the Longfellow Ranch in west Texas. These reduced distance values, compared with the above published reports, were interpreted as the result of introgressive hybridization at that location. Although the relationship between genetic distance and taxonomic categories are quite variable, the values observed between white-tailed and mule deer fall within the range of those reported from other intrageneric comparisons of mammalian taxa (Avise and Aquadro 1982). The estimates of genetic distance between mule and black-tailed deer (D = 0.031) are higher than those previously reported (Nei's D = 0.018) (Gavin and May 1988).

Phenetic clustering of distance values revealed evidence of biogeographic structuring among some white-tailed deer populations (Fig. 2). For example, the first major white-tailed deer assemblage (in Fig. 2B) includes the 2 Arizona white-tailed deer localities (AZWT and COWT), all west Texas white-tailed deer localities (CRWT, MIWT, EPWT, FRWT, and IMWT) except PKWT, and the most geographically distant white-tailed deer population, SRWT, from South Carolina. White-tailed deer from the PKWT locality clustered with the remaining non-west Texas populations forming the second major white-tailed deer assemblage. Conversely, little geographic structure is evident across mule deer populations. Notable exceptions include the placement of black-tailed deer from California (HOBT), which connects to all other mule deer at values <0.048, and mule deer from Arizona (AZMD) and 1 Texas locality (IMMD) that associate with remaining mule deer populations at values <0.042. The 1 black-tailed deer sampled from Alaska (ALBT) clustered among samples of mule deer and was indistinguishable from the west Texas locality MIMD. Estimates of differentiation among deer populations and biogeographic structuring should be viewed with caution because population decimation and subsequent efforts of reintroduction may strongly influence these values (Kennedy et al. 1987).

DISCUSSION

Reports detailing various aspects of hybridization between these 2 deer species are not uncommon (Whitehead 1972, Day 1980, Wishart 1980). Three studies from captive populations indicate at least some degree of hybrid fertility (Nichols and Murrey 1973, Wishart et al. 1988, Derr 1990). Although results from controlled experiments may not always reflect phenomena from natural populations, these studies substantiate fertility through 2 generations and document no structural genetic differences that preclude fertility in *O. virginianus–O. hemionus* hybrids.

I detected no F1 hybrids from the 31 populations sampled. This is based on the assumption that parentals would be homozygous for alternate alleles at the ACPH and ALB loci, and the resultant F1 hybrids would be heterozygous at both of these loci. The observation of individuals heterozygous at one of these loci (Table 1) indicates that they may be the products of subsequent generations of backcrossing. Gavin and May (1988) also report finding only backcross hybrids among populations of white-tailed, black-tailed, and mule deer in the Pacific Northwest. One interpretation of these results is that F1 hybrids in natural populations are rare, whereas animals with hybrid ancestry (backcross progeny) are more common. However, as discussed by Cronin et al. (1988), it is not possible to determine if rare heterozygotes are the result of introgressive hybridization or simply the retention of ancestral alleles. Nevertheless, the most reasonable explanation is introgression in cases where (1) the frequency of heterozygotes is higher among sympatric as compared with allopatric populations, and (2) an independent data set supplies additional evidence of gene exchange among sympatric populations (e.g., mtDNA) (Carr et al. 1986, Ballinger 1987, Derr 1990).

The frequency of animals heterozygous at the ALB locus (2–3%) is similar to those reported from Montana (2% heterozygotes from both species [Cronin et al. 1988]), the Pacific Northwest (2% white-tailed deer and 4% mule deer heterozygotes [Gavin and May 1988]) and west Texas (5.9% heterozygotes, both species [Stubblefield et al. 1986]) but less than those reported by Ballinger (1987) (12.5 and 24% ALB hetero-

zygotes, respectively, for white-tailed and mule deer). Moreover, 3 of the 46 mule deer Ballinger (1987) sampled from the Longfellow Ranch were homozygous for the ALB 100 allele. Large populations of both species occur on the Longfellow Ranch primarily due to restricted hunting and the availability of large tracts of suitable habitat. The Longfellow Ranch also includes ecotone areas between typical habitat of white-tailed and mule deer that are extensively used by both species (L. H. Blankenship, Uvalde, Tex., pers. commun.). These factors may contribute to the high incidence of hybridization Ballinger (1987) reported from this ranch.

Other reports representing >2,000 white-tailed deer from throughout the eastern and central United States (Baccus et al. 1983, Smith et al. 1984, Sheffield et al. 1985, Kennedy et al. 1987, Breshears et al. 1988) found only 2 ALB heterozygotes (from Mich.) (Manlove 1979). From mule deer populations in Colorado, Scribner et al. (1990) reported that 2.9% of the animals they examined were heterozygous for ALB. The only comparable information on ACPH allelic variation from sympatric populations is that of Gavin and May (1988). These authors reported that 2% of the white-tailed deer and no mule deer were heterozygous at this locus. Other studies reported 2 ACPH alleles from white-tailed deer populations (Hillestad 1984, Smith et al. 1984, Kennedy et al. 1987), but neither appeared to be the same as the common allele (ACPH −100) found in mule deer. In my study, all allopatric populations of both species had fixed allelic differences at the ALB and ACPH loci. Except for the Longfellow Ranch (Ballinger 1987) and possibly the Iron Mountain Ranch (Stubblefield et al. 1986), white-tailed and mule deer from sympatric localities in west Texas, Montana, and the Pacific Northwest share rare alleles at these 2 loci in roughly equal frequencies.

Based on the similarity of their mtDNA haplotypes, differential cytoplasmic introgression in the past may have established white-tailed deer mtDNA among mule deer populations (Carr et al. 1986, Ballinger 1987, Cronin et al. 1988, Derr 1990). This historical aspect of interspecific genetic exchange is not readily apparent from the allozymic data. In spite of the mtDNA introgression, the 2 species have coexisted over extended areas with little or, in many areas, no evidence of extensive nuclear introgression. Although the genetic structure of local populations may be altered, overall, hybridization does not seem to present a significant threat to the nuclear gene pools, hence the genetic integrity of either species.

Natural hybridization between fully differentiated and morphologically distinct species is not uncommon. Although local populations may be disrupted, the genetic integrity of the parental species is rarely threatened (Carson et al. 1989). Observations such as these led Paterson (1985), and more recently Templeton (1989), to argue that the gene pool of a species is distinct from others primarily by the positive forces of strong balancing selection that operate within each species to maintain its own optimal reproductive mode. The coherence of a gene pool, therefore, is a much better basis for the characterization of a species than reproductive isolation. Accordingly, although white-tailed and mule deer share identical mtDNA haplotypes in some areas, the nuclear genomes of both species clearly represent discrete genetic entities and are the result of independent evolutionary lineages.

What conditions contribute to the disruption of this "coherent gene pool" and allow hybridization in some geographic areas and not others? One possible explanation is that environmental factors in many areas of the Southwest have played an important role in providing reproductive contact. In west Texas, white-tailed deer have expanded their range into typical mule deer habitat primarily because of ecological changes related to domestic livestock production (Baker 1984). In other areas of the West, the desert chaparral of Arizona for example, environmental factors that favor mule deer have allowed that species to inhabit areas that were once the sole domain of white-tailed deer (Anthony and Smith 1977). All individuals I identified with protein electrophoresis as having hybrid ancestry (i.e., heterozygotes at either the ACPH or ALB loci) were from localities that include ecotonal areas between suitable habitat for both species. Studies designed to ascertain the ecological and concomitant behavioral changes in these areas may allow for the prediction or identification of potential areas of genetic interaction.

These changing environmental conditions that allow 1 species to move into the range of the other may provide temporary areas of hybridization. No stable zone of hybridization, in the traditional sense, is evident. Hybrid zone models proposed by Endler (1977), Moore (1977), and Barton and Hewitt (1981, 1985) differ in their

interpretation of the role of environmental factors and the effect of selection on the maintenance of these zones. However, each defines hybrid zones as clines that may be characterized from samples collected along linear transects across the zone (Harrison and Rand 1989). Hybridization between white-tailed and mule deer occurs in a mosaic of independent and isolated pockets that are strongly associated with ecological parameters. Nontraditional hybrid zones of this fashion have been reported for other closely related species (Howard 1986, Sperling 1987, Harrison and Rand 1989). These mosaic hybrid zones may have gone unnoticed because the patterns of variation are not as striking as the steep clines and clear discontinuities that characterize the more traditional zones (Harrison and Rand 1989). Moreover, nontraditional hybrid zones may be ephemeral, existing for 1 or a few generations, and may be sporadically distributed throughout an area of sympatry.

LITERATURE CITED

ANTHONY, R. G., AND N. S. SMITH. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. Ecol. Monogr. 47: 255–277.

AVISE, J. C., AND C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates. Pages 151–185 *in* M. K. Hecht, B. Wallace, and G. Prance, eds. Evolutionary biology. Plenum Press, New York, N.Y.

BACCUS, R., N. RYMAN, M. H. SMITH, C. REUTERWALL, AND D. CAMERON. 1983. Genetic variability and differentiation of large grazing mammals. J. Mammal. 64:109–120.

BAKER, R. H. 1984. Origin, classification and distribution. Pages 1–18 *in* L. K. Halls, ed. Whitetailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

BALLINGER, S. W. 1987. Allozymic and mitochondrial DNA analysis of sympatric white-tailed and mule deer in west Texas. M.S. Thesis, Texas A&M Univ., College Station. 48pp.

BARTON, N. H., AND G. M. HEWITT. 1981. Hybrid zones and speciation. Pages 109–145 *in* W. R. Atchley and D. S. Woodruff, eds. Evolution and speciation: essays in honour of M. J. D. White. Cambridge Univ. Press, U.K.

———, AND ———. 1985. Analysis of hybrid zones. Annu. Rev. Ecol. Syst. 16:113–148.

BRESHEARS, D. D., M. H. SMITH, E. G. COTHRAN, AND P. E. JOHNS. 1988. Genetic variability in white-tailed deer. Heredity 60:139–146.

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. Proc. Natl. Acad. Sci. USA. 83: 9576–9580.

CARSON, H. L., K. Y. KANESHIRO, AND F. C. VAL. 1989. Natural hybridization between the sympatric Hawaiian species *Drosophila silvestris* and *Drosophila heteroneura*. Evolution 3:190–203.

CLAYTON, J. W., AND D. N. TRETIAK. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Can. 29:1169–1172.

CRONIN, M. A., E. R. VYSE, AND D. G. CAMERON. 1988. Genetic relationships between mule deer and white-tailed deer in Montana. J. Wildl. Manage. 52:320–328.

DAY, G. I. 1980. Characteristics and measurements of captive hybrid deer in Arizona. Southwest. Nat. 52:320–328.

DERR, J. N. 1990. Genetic interactions between two species of North American deer, *Odocoileus virginianus* and *O. hemionus*. Ph.D. Thesis, Texas A&M Univ., College Station. 111pp.

ENDLER, J. A. 1977. Geographic variation, speciation and clines. Princeton Univ. Press, N.J. 246pp.

GAVIN, T. A., AND B. MAY. 1988. Taxonomic status and genetic purity of Columbian white-tailed deer. J. Wildl. Manage. 52:1–10.

HARRIS, H., AND D. H. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. Am. Elsevier, New York, N.Y.

HARRISON, R. G., AND D. M. RAND. 1989. Mosaic hybrid zones and the nature of species boundaries. Pages 111–133 *in* D. Otta and J. L. Endler, eds. Speciation and its consequences. Sinauer Assoc., Sunderland, Mass.

HILLESTAD, H. O. 1984. Stocking and genetic variability of white-tailed deer in the southeastern United States. Ph.D. Thesis, Univ. Georgia, Athens. 112pp.

HOWARD, D. J. 1986. A zone of overlap and hybridization between two ground cricket species. Evolution 40:34–43.

KENNEDY, P. K., M. L. KENNEDY, AND M. L. BECK. 1987. Genetic variability in white-tailed deer (*Odocoileus virginianus*) and its relationship to environmental parameters and herd origin (Cervidae). Genetica 74:189–201.

MANLOVE, M. N. 1979. Genetic similarity among contiguous and isolated populations of white-tailed deer in Michigan. M.S. Thesis, Michigan State Univ., East Lansing. 26pp.

MOORE, W. S. 1977. An analysis of narrow hybrid zones in vertebrates. Quart. Rev. Biol. 52:263–278.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

NICHOLS, R., AND J. MURREY. 1973. Black-tailed deer–white-tailed deer breeding study. Final Rep. W-46. Tenn. Game and Fish Comm., Nashville. 13pp.

PATERSON, H. E. H. 1985. The recognition concept of species. Pages 21–29 *in* E. S. Vrba, ed. Species and speciation. Transvaal Mus. Monogr. No. 4, Pretoria, South Africa.

PIMENTEL, R. A., AND J. D. SMITH. 1986. BIOSTAT I: univariate statistical toolbox. Sigma Soft Inc., Placentia, Calif.

RIDGWAY, G. J., S. U. SHERBURNE, AND R. D. LEWIS. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99:147–151.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics. VII. Univ. Texas Publ. 7213:145–153.

SCRIBNER, K. T., M. H. SMITH, R. A. GARROTT, AND L. H. CARPENTER. 1990. Temporal, spatial, and age specific changes in genotype composition of mule deer. J. Mammal. 72:126–137.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Stud. in Genetics. VI. Univ. Texas Publ. 7103:49–90.

SHEFFIELD, S. R., R. P. MORGAN II, G. A. FELDHAMER, AND D. M. HARMAN. 1985. Genetic variation in white-tailed deer (*Odocoileus virginianus*) populations in western Maryland. J. Mammal. 66:243–255.

SMITH, M. H., R. BACCUS, H. O. HILLESTAD, AND M. N. MANLOVE. 1984. Population genetics. Pages 119–128 *in* L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. Freeman, San Francisco, Calif. 573pp.

SPERLING, F. A. H. 1987. Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae). Quaestiones Entomologicae. 23:198–315.

STUBBLEFIELD, S. S., R. J. WARREN, AND B. R. MURPHY. 1986. Hybridization of free-ranging white-tailed and mule deer in Texas. J. Wildl. Manage. 50:688–690.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72: 281–283.

TEMPLETON, A. R. 1989. The meaning of species and speciation: a genetic perspective. Pages 3–27 *in* D. Otta and J. L. Endler, eds. Speciation and its consequences. Sinauer Assoc., Sunderland, Mass.

VAN DEN BUSSCHE, R. A., M. J. HAMILTON, AND R. K. CHESSER. 1986. Problems of estimating gene diversity among populations. Texas J. Sci. 38: 281–287.

WALLMO, O. C. 1981. Mule and black-tailed deer distribution and habitats. Pages 1–25 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

WHITEHEAD, C. J. 1972. A preliminary report on white-tailed deer and black-tailed deer crossbreeding studies in Tennessee. Proc. Ann. Conf. Southeast Assoc. Game and Fish Comm. 25:65–69.

WISHART, W. D. 1980. Hybrids of white-tailed and mule deer in Alberta. J. Mammal. 61:716–720.

———, F. HRUDKA, S. M. SCHMUTZ, AND P. F. FLOOD. 1988. Observations on spermatogenesis, sperm phenotype, and fertility in white-tailed × mule deer hybrids and a yak cow hybrid. Can. J. Zool. 66:1664–1671.

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APPENDIX A

Collection Localities, Abbreviations, and Sample Sizes of Animals Examined

White-tailed Deer.—Total 92. ARIZONA: Cochise Co., Fort Huachuca, [COWT] (8); Yavapai Co., [AZWT] (7). SOUTH CAROLINA: Aiken Co., Savannah River Plant, [SRWT] (5). TEXAS: Brewster Co., Iron Mountain Ranch, [IMWT] (7); Terlingula Ranch [CRWT] (1); Calhoun Co., Matagorda Island [MAWT] (5); Jeff Davis Co., Eppenhauer Ranch, [EPWT] (8); Friends Ranch, [FRWT] (4); McIvior Ranch [MIWT] (14); Kerr Co., Hunt [HUWT] (5); Kimble Co., Junction, [JUWT] (5); Pecos Co., Puckett Ranch, [PKWT] (15); Tom Green Co., San Angelo, [SAWT] (8).

Mule Deer.—Total 103. ARIZONA: Coconino Co., [AZMD] (8). NEW MEXICO: Otero Co., [NMMD] (1). CALIFORNIA: Mono Co., [MOMD] (10). TEXAS: Brewster Co., Double Diamond Ranch, [DDMD] (5); Kimball Ranch, [KMMD] (5); Ike Roberts Ranch, [IRMD] (10); Iron Mountain Ranch, [IMMD] (7); Terlingula Ranch [TRMD] (6); Jeff Davis Co., Clay Miller Ranch, [CMMD] (3); Eppenhauer Ranch [EPMD] (9); Friends Ranch, [FRMD] (6); McIvior Ranch [MIMD] (2); Hudspeth Co., Camilo Chavez Ranch, [CHMD] (3); Pecos Co., Puckett Ranch, [PKMD] (11); Presidio Co., Brite Ranch, [BTMD] (10). UTAH: Rich Co., [UTMD] (7).

Black-tailed Deer.—Total 6. ALASKA: Sitka, [ALBT] (1). CALIFORNIA: Mendocino Co., Hopland Field Station, [HOBT] (5).

APPENDIX B

Electrophoretic Buffer Systems, Enzyme Commission Numbers (E.C.), and Protein Abbreviations Used

Horizontal Electrophoresis.—(1) Ridgway et al. (1970) pH 8.0/8.5, glycerol-3-phosphate dehydrogenase (E.C. 1.1.1.8; GPD1), lactate dehydrogenase (E.C. 1.1.1.27; LDH1), glucose phosphate isomerase (E.C. 5.3.1.9; GPI), peptidase (E.C. 3.4.11 or 3.4.13; (L-leucyl-L-alanine) PEPB, (L-leuclyglycylglycine) PEPD, and (L-leucyl-L-proline) PEPE).

Vertical Electrophoresis.—(2) continuous tris-citrate I, pH 6.7–6.3, (Selander et al. 1971), malic enzyme (E.C. 1.1.1.40; ME), aminopeptidase (E.C. 3.4.11.1; AP); (3) continuous tris-citrate

pH 7.0, (Selander et al. 1971), isocitrate dehydrogenase (E.C. 1.1.1.42; IDH1, IDH2), phosphoglucomutase (E.C. 5.4.2.2; PGM1, PGM2), hexokinase (E.C. 2.7.1.1; HK), glucose dehydrogenase (E.C. 1.1.1.47; GDH); (4) continuous tris-citrate II pH 8.0, (Selander et al. 1971), aspartate aminotransferase (E.C. 2.6.1.1; AAT), superoxide dismutase (E.C. 1.15.1.1; SOD1, SOD2), catalase (E.C. 1.11.1.6; CAT); (5) amino propyl morphine, pH 6.1 (Clayton and Tretiak 1972), acid phosphatase (E.C. 3.1.3.2; ACPH), albumin (ALB), phosphogluconate dehydrogenase (E.C. 1.1.1.43; PGD), malate dehydrogenase (E.C. 1.1.1.37; MDH1, MDH2), sorbitol dehydrogenase (E.C. 1.1.1.14; SDH) and mannose phosphate isomerase (E.C. 5.3.1.8; MPI).

ENERGETIC CONSIDERATIONS AND HABITAT QUALITY FOR ELK IN ARID GRASSLANDS AND CONIFEROUS FORESTS

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Abstract: I used static modeling to explore the recent success of elk (*Cervus elaphus*) colonizing the arid shrub-steppe of Washington. Forage-based estimates of metabolizable energy available to elk in the shrub-steppe were compared to energy available in 2 mesic forest communities that historically have served as more typical summer elk habitat. Although precipitation and primary productivity were substantially lower in the shrub-steppe, the estimated calories available in shrub-steppe forage over a 300-km^2 area were 271 and 86%, respectively, of lodgepole pine (*Pinus contorta*) and cedar-hemlock (*Thuja-Tsuga*) forests of similar size. Low intercommunity variability in forage production, lack of a significant nonforage overstory, and the large size and relative abundance of foraging areas in the shrub-steppe mitigated reduced primary production. In the shrub-steppe, 92% of the habitat represented potential foraging habitat as determined by minimum forage biomass, whereas only 10 and 40% of the forested habitats, respectively, could be considered prime foraging areas. Whereas forage energy was concentrated in openings within conifer forests, it was more uniformly dispersed over the habitat mosaic in the shrub-steppe. These results provide a bioenergetic framework for understanding the recent success of elk colonizing the arid shrub-steppe of Washington and are consistent with observed patterns of movement and habitat use for elk in shrub-steppe habitat.

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Individual growth, reproductive, and survival rates of elk colonizing the arid shrub-steppe of Washington have exceeded those for many elk populations occupying more mesic summer habitats (McCorquodale et al. 1988, 1989*a*). This is surprising because the summer environment occupied by steppe elk is arid, treeless, and relatively unproductive compared to more mesic elk habitats. Elk use of arid steppe habitats for summer range is also historically atypical (Murie 1951, Mack and Thompson 1982, Skovlin 1982).

Hypothetically, as community productivity decreases with increasing aridity, nutrient and energy intake rates by large herbivores should decline and negatively affect growth and reproduction. This contrasts with observations made for elk in the shrub-steppe. The absence of significant summer thermal cover and the rapid forage desiccation typical of arid environments should also reduce the value of these areas to summering elk. Clearly, conventional views of habitat quality for elk do not adequately explain their success in Washington's shrub-steppe. Accordingly, McCorquodale et al. (1989*b*) hypothesized that the effects of low primary productivity in the shrub-steppe have been offset by the relatively high availability of foraging areas and low intercommunity variation in forage production.

To test this hypothesis, I used static modeling to compare the metabolizable energy available to elk during spring and summer in the shrub-steppe versus 2 more typical elk habitats. Spring–summer habitat was compared because (1) growth and reproductive costs accrue mainly during this time; (2) growth rates and reproductive success are the best measures of habitat

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Literature Cited

Ecological Relationships between Mule Deer and White-Tailed Deer in Southeastern Arizona

Robert G. Anthony; Norman S. Smith

Ecological Monographs, Vol. 47, No. 3. (Summer, 1977), pp. 255-277.

Stable URL:

http://links.jstor.org/sici?sici=0012-9615%28197722%2947%3A3%3C255%3AERBMDA%3E2.0.CO%3B2-S

Genetic Variability and Differentiation of Large Grazing Mammals

Ramone Baccus; Nils Ryman; Michael H. Smith; Christina Reuterwall; David Cameron

Journal of Mammalogy, Vol. 64, No. 1. (Feb., 1983), pp. 109-120.

Stable URL:

http://links.jstor.org/sici?sici=0022-2372%28198302%2964%3A1%3C109%3AGVADOL%3E2.0.CO%3B2-U

Analysis of Hybrid Zones

N. H. Barton; G. M. Hewitt

Annual Review of Ecology and Systematics, Vol. 16. (1985), pp. 113-148.

Stable URL:

http://links.jstor.org/sici?sici=0066-4162%281985%2916%3C113%3AAAOHZ%3E2.0.CO%3B2-V

LINKED CITATIONS

Mitochondrial DNA Analysis of Hybridization between Sympatric White-Tailed Deer and Mule Deer in West Texas

Steven M. Carr; Scott W. Ballinger; James N. Derr; Lytle H. Blankenship; John W. Bickham

Proceedings of the National Academy of Sciences of the United States of America, Vol. 83, No. 24. (Dec. 15, 1986), pp. 9576-9580.

Stable URL:

http://links.jstor.org/sici?sici=0027-8424%2819861215%2983%3A24%3C9576%3AMDAOHB%3E2.0.CO%3B2-3

Natural Hybridization between the Sympatric Hawaiian Species Drosophila silvestris and Drosophila heteroneura

H. L. Carson; K. Y. Kaneshiro; F. C. Val

Evolution, Vol. 43, No. 1. (Jan., 1989), pp. 190-203.

Stable URL:

http://links.jstor.org/sici?sici=0014-3820%28198901%2943%3A1%3C190%3ANHBTSH%3E2.0.CO%3B2-2

Genetic Relationships between Mule Deer and White-Tailed Deer in Montana

Matthew A. Cronin; Ernest R. Vyse; David G. Cameron

The Journal of Wildlife Management, Vol. 52, No. 2. (Apr., 1988), pp. 320-328.

Stable URL:

http://links.jstor.org/sici?sici=0022-541X%28198804%2952%3A2%3C320%3AGRBMDA%3E2.0.CO%3B2-J

Characteristics and Measurements of Captive Hybrid Deer in Arizona

Gerald I. Day

The Southwestern Naturalist, Vol. 25, No. 3. (Nov. 14, 1980), pp. 434-438.

Stable URL:

http://links.jstor.org/sici?sici=0038-4909%2819801114%2925%3A3%3C434%3ACAMOCH%3E2.0.CO%3B2-M

Taxonomic Status and Genetic Purity of Columbian White-Tailed Deer

Thomas A. Gavin; Bernie May

The Journal of Wildlife Management, Vol. 52, No. 1. (Jan., 1988), pp. 1-10.

Stable URL:

http://links.jstor.org/sici?sici=0022-541X%28198801%2952%3A1%3C1%3ATSAGPO%3E2.0.CO%3B2-N

A Zone of Overlap and Hybridization Between Two Ground Cricket Species

Daniel J. Howard

Evolution, Vol. 40, No. 1. (Jan., 1986), pp. 34-43.

Stable URL:

http://links.jstor.org/sici?sici=0014-3820%28198601%2940%3A1%3C34%3AAZOOAH%3E2.0.CO%3B2-Q

LINKED CITATIONS

An Evaluation of Narrow Hybrid Zones in Vertebrates
William S. Moore
The Quarterly Review of Biology, Vol. 52, No. 3. (Sep., 1977), pp. 263-277.
Stable URL:
http://links.jstor.org/sici?sici=0033-5770%28197709%2952%3A3%3C263%3AAEONHZ%3E2.0.CO%3B2-P

Genetic Distance between Populations
Masatoshi Nei
The American Naturalist, Vol. 106, No. 949. (May - Jun., 1972), pp. 283-292.
Stable URL:
http://links.jstor.org/sici?sici=0003-0147%28197205%2F06%29106%3A949%3C283%3AGDBP%3E2.0.CO%3B2-U

Temporal, Spatial, and Age-Specific Changes in Genotypic Composition of Mule Deer
Kim T. Scribner; Michael H. Smith; Robert A. Garrott; Len H. Carpenter
Journal of Mammalogy, Vol. 72, No. 1. (Feb., 1991), pp. 126-137.
Stable URL:
http://links.jstor.org/sici?sici=0022-2372%28199102%2972%3A1%3C126%3ATSAACI%3E2.0.CO%3B2-K

Genetic Variation in White-Tailed Deer (Odocoileus virginianus) Populations in Western Maryland
Steven R. Sheffield; Raymond P. Morgan, II; George A. Feldhamer; Dan M. Harman
Journal of Mammalogy, Vol. 66, No. 2. (May, 1985), pp. 243-255.
Stable URL:
http://links.jstor.org/sici?sici=0022-2372%28198505%2966%3A2%3C243%3AGVIWD%28%3E2.0.CO%3B2-H

Hybridization of Free-Ranging White-Tailed and Mule Deer in Texas
Suzy S. Stubblefield; Robert J. Warren; Brian R. Murphy
The Journal of Wildlife Management, Vol. 50, No. 4. (Oct., 1986), pp. 688-690.
Stable URL:
http://links.jstor.org/sici?sici=0022-541X%28198610%2950%3A4%3C688%3AHOFWAM%3E2.0.CO%3B2-M

Hybrids of White-Tailed and Mule Deer in Alberta
William D. Wishart
Journal of Mammalogy, Vol. 61, No. 4. (Nov., 1980), pp. 716-720.
Stable URL:
http://links.jstor.org/sici?sici=0022-2372%28198011%2961%3A4%3C716%3AHOWAMD%3E2.0.CO%3B2-V