

## College of Agriculture

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August 28, 1995

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Dear Valerie,

Here is the report on my analysis of the genetic data from the White River Area horses. Please look it over and contact me with questions or comments. Also, please let me know if there are any aspects of the genetics of the herd that you or your colleagues think were not covered in sufficient detail. Thanks for your patience.

Sincerely yours,

E. Gus Cothran, Ph.D.

Director

Equine Blood Typing Research Laboratory

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enclosure

# Genetic analysis of the feral horses of the White River Resource Area of Colorado

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Maintaining populations of feral horses on public lands frequently requires that the populations be kept small to ensure preservation of the habitat. Unfortunately, small population size can frequently lead to the loss of genetic variability and inbreeding. Loss of genetic variation threatens long term adaptability while inbreeding can result in reduced viability or fertility. It is possible to manage populations so that the effects of small population size upon genetic variability can be minimized. The first step in building an effective management plan is the assessment of current levels of genetic variation in the population. In this report I present the genetic analysis of the feral horse population of the White River Resource Area (WRRA) Wild Horse Herd Area of the Bureau of Land Management.

### **METHODS**

In August of 1992, 12 samples from the Barcus Creek area were obtained. In July of 1993, 14 samples from Barcus Creek and 18 samples from 84 Mesa area were obtained. An additional 11 samples from Barcus Creek plus 16 samples from the Square S Well Area were obtained in August of 1993. In October of 1993, 15 samples from he West Fork of Spring Creek were collected. In August of 1994, samples were obtained from additional areas as follows: 9 from Hammond, 11 from Greasewood, 15 from Little Duck Creek, and five from Spring Creek. The total number of horses sampled was 126. Seventeen genetic marker systems were analyzed. Seven systems were red blood cell alloantigen loci (the A, C, D, K, P, Q and U horse blood groups) tested by standard serological methods of agglutination and compliment mediated hemolysis. The other 10 systems were biochemical polymorphisms detected by electrophoretic techniques. These systems were Albumín (Al), Alpha-1-beta Głycoprotein (A1B), serum Cholenesterase (Es), Vitamin D Binding Protein (Gc), Glucose Phosphate Isomerase (GPI), alpha

Hemoglobin (Hb), Phosphoglucomutase (PGM), Phosphogluconate Dehydrogenase (PGD), Protease Inhibitor (Pi), and Transferrin (Tf).

A variety of genetic variability measures were calculated from the gene marker data. The measures were observed heterozygosity (Ho) which is the actual number of loci heterozygous per individual and is based upon biochemical loci only; expected heterozygosity (He) which is the predicted number of heterozygous loci based upon gene frequencies, it was calculated for biochemical and all marker systems; unbiased He (Hu) which is He corrected for sample size; effective number of alleles (ENA) which is a measure of marker system diversity; total number of variants (TNV); and estimated inbreeding level (Fis) which is calculated as 1-Ho/He. Genetic structure of the total population was examined by analysis of F-statistics.

Genetic markers also can provide some information about ancestry in some cases. Genetic resemblance to domestic horse breeds was calculated using Roger's 1972 genetic similarity coefficient S. Genetic relationships also were estimated by construction of a genetic tree diagram (dendogram) by use of a restricted maximum likelihood (RML) procedure.

### RESULTS AND DISCUSSION

The primary genetic variability measures of the sampling areas of the WRRA are given in Table 1. The mean values for these same measures for domestic horse breeds also are shown in the Table. In most cases (not considering Fis), values of genetic variation of the WRRA horses were less than that for domestic horse breeds. The exceptions were the expected heterozygosity measures (He and Hu) for the 84 Mesa and West Fork populations.

The most basic measure of genetic diversity is the total number of genetic variants (TNV).

TNV for the WRRA horses was quite low compared to the average for domestic horses. Even

the largest value (Barcus Creek) is considerably lower than the domestic mean. However, this is somewhat misleading. TNV is strongly influenced by sample size in horse populations and this trend is evident for the WRRA sampling areas. Also, if the entire WRRA is considered as a single population, TNV would be higher than the domestic mean as 73 variants were observed overall.

A more informative measure of genic diversity of a population than TNV is ENA. ENA measures the number of alleles per gene locus that actually contribute to overall genetic variation. It is not inflated by rare variants that may occur only once or twice in a population as TNV is. ENA is influenced by sample size but not to the degree that TNV is. ENA for the WRRA samples also was well below that for domestic breeds. The highest values were for the West Fork and 84 Mesa samples. Note that the West Fork sample had one of the lowest values for TNV. The main observation is that ENA for the WRRA herds is low for horses and that this is not due to small sample size of the separate populations.

Expected heterozygosity measures (He and Hu) gave similar results to ENA. The unbiased measure (Hu) is probably better as a comparative measure as most of the sample sizes were small. Again, these measures indicated a lower level of populational genetic variability then that found in domestic breeds. However, the West Fork and 84 Mesa populations did have He and Hu measures that were greater than the mean for horse breeds. Overall, all populational measures of genetic diversity of the WRRA populations were low compared to genetic diversity of domestic horse breeds. However, these measures for the WRRA horses were greater than the means for feral horse populations.

Individual genetic variation (Ho) also was lower for the WRRA populations than for the domestic horse mean. Only the West Fork population had an Ho value near the domestic breed

mean while the Little Duck Creek population had an extremely low value of Ho. Ho in horses is not statistically associated with sample size. Thus the Ho values of the WRRA populations support the relatively low values of genetic variation indicated by the other measures.

The ratio of observed and expected heterozygosities (Ho/He) theoretically is related to inbreeding level and the statistic Fis uses this relationship to provide a relative measure of inbreeding level in a population. The Fis values for the WRRA populations give mixed results. Four of the values were positive indicating some inbreeding while four were negative indicating an absence of inbreeding. The populations with the positive inbreeding values were those with the highest expected heterozygosities. The Fis values for the Square S and West Fork populations essentially were not different from zero. The other six populations had Fis values, both positive and negative, that were fairly high. There is a statistically significant trend for values of Fis of feral horse populations to be positively associated with both sample size and population size. This means the largest values of Fis (positive values) tend to be associated with the larger sample or population sizes. There is no such pattern shown by the WRRA samples.

Although Fis is considered as an estimate of inbreeding, this does depend upon a number of assumptions about the populations which frequently may not be met. This is most likely the case for the WRRA horses because of the wide variation in Fis values in horses likely derived from the same founding population and in the same geographic area. In this case, Fis is simply a comparison of Ho to He, where positive values of Fis represent cases where He is greater than Ho and vice versa. The three populations with the highest Fis values all show some evidence of recent introductions into the population (this will be discussed in more detail below). If individuals from a population with different gene frequencies are introduced into another

population, this will inflate values of He. This could be the case for the Barcus Creek, Little Duck Creek and 84 Mesa populations. For the three populations with high negative values of Fis, Greasewood, Hammond and Spring Creek, a recent reduction in breeding population size could be the cause of the excess of Ho relative to He.

As indicated above, although these samples are from populations that are very close to each other geographically, each population is genetically distinctive. By this I mean that each population has a characteristic set of gene markers that is different from each other sample. For example, the Square S sample has a very high frequency of the Es-L variant seen elsewhere in only two individuals of the 84 Mesa herd. The West Fork herd has a very high frequency of the Es-F marker, only seen in three other individuals not in that sample. The patterns of marker distribution suggest genetic subdivision of the total population. The marker distributions also potentially could be used to track movements between populations, although this would not be simple. Also, there were several markers, for example the Hb-A2 variant, that occurred in several of the sample populations but only as a single copy. Such variants may represent markers in the original population from which the entire herd is derived. These markers are now widely distributed but at low frequency and may be examples of genetic variants that will eventually be lost.

Genetic subdivision of populations can be measured by use of F-statistics, primarily Fst (the standardized variance in allele frequency). Fst was calculated for all pairwise comparisons of WRRA samples (Table 2). Fst for all populations also were calculated as was a comparison the WRRA herd to the Little Bookcliffs population from near Grand Junction, CO. All comparisons yielded statistically significant Fst values. The overall Fst value was 0.131. This indicates that

approximately 13% of the total variability in gene frequencies was accounted for by among sample variation, which does indicate genetic substructuring of the total herd. Surprisingly, the within WRRA Fst was greater than the WRRA/Little Bookcliffs Fst (0.125). This indicates that there was greater differentiation among the WRRA subpopulations than between the WRRA and Little Bookcliffs herds.

Genetic association among the WRRA samples also was assessed by genetic similarity (Table 3) and cluster analysis using the RLM procedure (Figure 1). The genetic similarity matrix clearly shows the within group similarity (the diagonal) is much greater than among groups similarity. Mean within group similarity was 0.840 compared to among group similarity of 0.793. Among group similarity is fairly accurately depicted in Figure 1. The tree reveals that there is not a strict geographic basis to relationship. One major cluster consisted of the eastern most populations (Greasewood, Barcus Creek, Square S, and Little Duck Creek). The other two clusters contained the South Western most populations (West Fork and 84 Mesa) and the two most northwestern populations (Spring Creek and Hammond). Based upon geographic distance, it would be expected that populations such as 84 Mesa, Little Duck Creek and Square S or Spring Creek, Hammond and Greasewood would have clustered together. The observed cluster may be due to ecological or physical barriers to dispersal that I have no information about or could perhaps be due to sampling biases.

The primary conclusions from the analysis of genetic variability of the WRRA horse herd are that significant genetic subdivision of the herd exists and that, in general, genetic variation within subdivisions is relatively low. However, within the entire WRRA genetic diversity is fairly high. From a management standpoint, this is an almost ideal situation. Population subdivision

with limited inbreeding within subdivisions and occasional exchange of individual among subdivisions is one of the best strategies for the long term maintenance of genetic variability. The subdivision of the WRRA population with the levels of dispersal that now appear to exist should be sufficient to maintain genetic variation within the area for many generations even if relatively small numbers of individuals are maintained within subdivisions. If additional interchange of individuals appears to be needed in the future, transfer of one or two two-year old females every three to five years would be the most efficient strategy. Patterns of exchange between populations should be randomized to minimized the rate of homogenization of the gene pool.

Analysis of gene markers also can provide some information about the origins or ancestry of populations. Qualitative appraisal of the variants present indicate some evidence of Spanish ancestry, however, only a small number of animals carry markers indicative of Spanish ancestry with the exception of the Pi-V allele. This allele is primarily found in New World horses of Iberian descent and may have been a marker for the type of horse brought over by the early Spanish explorers, conquerors and colonists. There also is some suggestion of draft horse influence but this is much less clear. Other specific breed affiliations cannot be determined at this point.

Quantitative measures of resemblance are given by genetic similarity coefficient (Table 4) and cluster analysis (Figure 2). Mean values of genetic similarity of the WRRA populations to the major groupings of domestic breeds shows that four of the populations have their highest S with the gaited North American breeds and one each with Thoroughbred type, Arabian type and Draft horse groups. The high similarity to the gaited North American breeds is difficult to interpret. These breeds have an important, old Spanish component to their ancestry, probably the Spanish

Jennet. However, these breeds also were the types of breeds that could have contributed to the feral populations within the last century. The high frequency of the Pi-V marker is more likely from old Spanish type horses as it is rarely seen in the gaited North American breeds. There also were two individuals with clear cut Spanish markers not found in the gaited North American breeds.

The RML cluster analysis also gave ambiguous results. Six of the eight WRRA populations grouped essentially together within the cluster that contained most of the Arabian type breeds. These in turn grouped with the Morgan horse and Standardbreds. The remaining two populations grouped with Turkoman (an oriental breed which is closely related to the Arabian types) but the cluster is within the grouping that contains the remaining gaited North American breeds. The Turkoman and the Akhal-Teke (another oriental breed with Arabian affinities) show a high similarity to the gaited North American breeds, thus the overall pattern supports the high similarity of the WRRA herd to these breeds. Overall the results of the analysis suggest that the WRRA horses certainly have a component of Spanish ancestry that probably is not recent. However, the WRRA horses appear to be primarily derived from North American breeds. One final point is that the WRRA horses appear to have a close relationship to the Little Bookcliffs population although they do not cluster close to each other in Figure 2.

Table 1. Measures of genetic variation of the WRRA feral horse populations and the mean of these measures for domestic horse breeeds.

SAMPLE	N	Но	He	Hu	TNV	ENA	Fis
BARCUS CREEK	37	0.311	0.348	0.353	56	1.972	0.107
GREASEWOOD	11	0.345	0.287	0.301	41	1.752	-0.202
HAMMOND	9	0.322	0,286	0.303	38	1.817	-0.127
LITTLE DUCK CREEK	15	0.287	0.327	0.338	47	1.873	0.123
84 MESA	18	0.340	0,383	0.395	54	2.046	0.112
SPRING CREEK	5	0.300	0.248	0.276	30	1.664	-0.210
SQUARE SWELL	16	0.313	0.304	0.313	44	1,917	-0.029
WEST FORK SPRING CREEK	15	0.371	0.392	0.405	43	2.127	0.053
DOMESTIC HORSE MEAN	87	0.373	0.364	0.371	64	2.391	-0.025

Table 2. Measure of standardized variance of allele frequencies (Fst) between each population from the WRRA (above the diagonal) and the chi-square with 84 degrees of freedom for each Fst (below the diagonal).

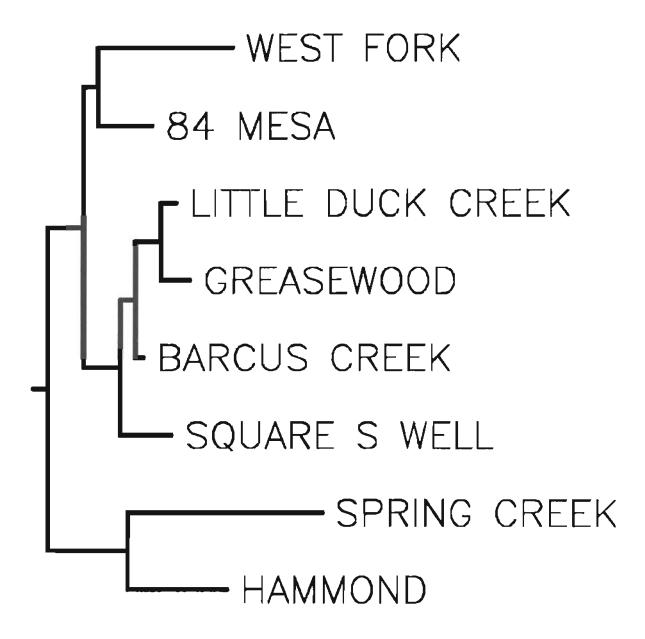
	BC	MS	SS	WF	HA	GS	LD	SC
BARCUS CREEK - BC	-	.0621	.0358	.0926	.0629	.0163	.0176	.0395
84 MESA - MS	1038	-	.0855	.0173	.0995	.0695	.0783	.0526
SQUARE'S WELL - SS	643	813	-	.111	.1075	.0820	.0855	.0859
WEST FORK - WF	1189	837	903	-	.0934	.1265	.1208	.1289
HAMMONĎ≈HA	1113	919	1038	818	-	.0917	.0722	.1330
GREASEWOOD - GS	218	669	792	904	717	-	.0172	.1189
LITTLE DUCK CREEK - LD	279	1049	851	1109	814	215	-	.1096
SPRING CREEK - SC	944	609	889	806	702	906	1037	-

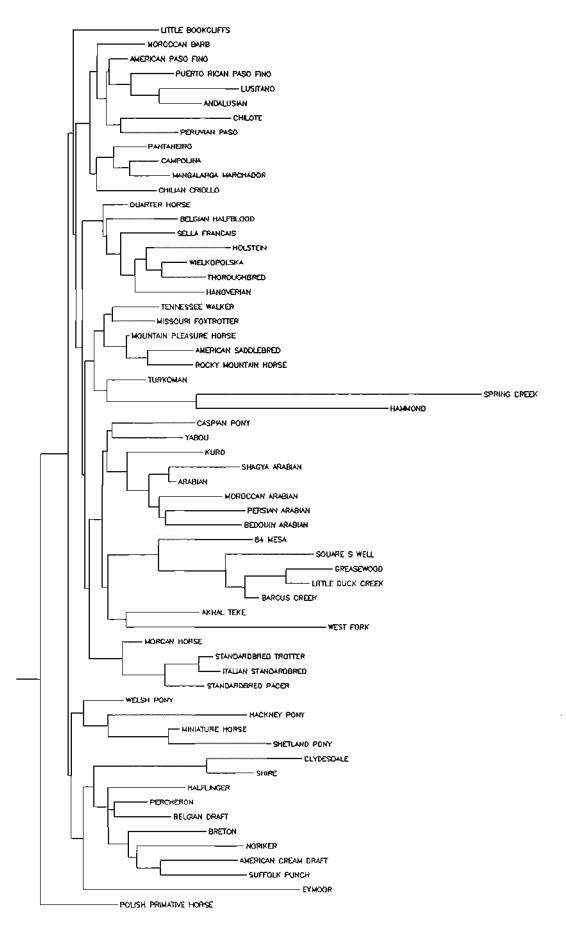
Table 3. Mean Rogers genetic similarity of individual horses within each population (on the diagonal) and between each WRRA population.

	BC.	GS	ΉA	LD	MS	SC	SS	WF
BARCUS CREEK	829	.819	.804	.816	.794	.806	.816	.766
GREASEWOOD		.852	.787	.826	.796	.794	.809	.762
HAMMOND			877	.802	.789	.812	.798	.786
LITTLE DUCK CREEK	Š			.815	.787	.792	.798	.760
84-MESA					.816	.814	.788	.755
SPRING CREEK					GOLVANSKOCH SIGNAVA	.882	.795	.757
SQUARE S WELL							844	.769
WEST FORK								808

Table 4. Mean Rogers genetic similarity for each WRRA population compared to major groups of domestic horse breeds.

	BC	GS	HA	$\mathbf{L}\mathbf{D}$	MS	SC	SS	WF
Thoroughbred type breeds	.747	.782	.731	.786	.752	.701	.780	.751
Arabian type breeds	.797	785	739	.792	.776	.728	.788	.734
Old World Iberian breeds	.786	.770	.738	.772	.776	.734	.780	.717
New World Iberian breeds	.755	.740	.731	.748	.749	.721	.701	.705
Gaited North American breeds	.808	.783	.738	.804	.786	.711	.789	.744
Heavy Draft Horse breeds	.729	.702	.752	.727	.758	.713	.718	.724
Pony breeds	.761	.734	.738	.754	.754	.704	.747	.712





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ab-d-f-	Į,	Į.	Į.	1 HP	-f-	d-f-	d-f-	f-		-ff-1	-f-	Ę.	ا ا	L L	
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cd-	-de	bcde	cde-g	-bcg	cde-g	cg-	cdgh	-bcdgh-		-bcdgh-	bcde	dgh	-de-gh	bcd-	
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-bcdgh <b></b>	-de-gh	1	1		Ì		h	ከ		<u></u> р	   	h	ከ	h	
ä	m-0	m-o	m-0	m	O-W	<b>™</b>	<b>™</b>	Ħ		m	M-0	m	m-0	<u></u> M	
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0	-C-	0	5	a-cd	-cd	<u>С</u>	-cd	-cd		0	a-cd	1	С П	-C-	
}	1	   		1	1 1	1	<u>-</u> ط-	<u>-</u> d-			<u> </u>	-bc	0	<u>-</u> d-	
i	ı	ı	i	ı	i	,	i	i		i	i	1	1	í	

Appendix 2. Summaries of complete genetic variability measures for each population of WRRA horses.

		94	= 3.29	TOTAL	ALLELES !	AVE #	= 3.429	ALLELES BG	AVE # AL	00	EC = 3.2	ES ELEC	ALLELES	AVE #
	.0021	 	.390	 			1.972	 	               	.364	 	 	56	MEAN
 		 	,           	 	 	4 1 1 1 1	 	1 1 1 1 1 1 1	 	i H i i	ALL LOC	S FOR		MEAN
 	.0021	 	.443	 	1 E I I I		2.297	 		.387		(   	24	MEAN
1 1 1 1 1		 		         				1 1 1 1 1 1 1	LOCI	GROUP	BLOOD (	S FOR	VALUE	MEAN
	.0031	1 1 1 1 1 1		       		 	. 22			8	 	         	   2 	 pdu
	.0012		.518				4			.511			ω	დხვ
	.0003		œ				. 05			7			4	pdq
	.0026						. 15			ω			2	Kbg
	.0017		9				.19						œ	Dbg
	.0014		S				.06			S			N	СЬЗ
	.0030	!					1.878						ω	Abg
.119	.0021	16.218	353	54	16.132	.107	1.745	1.485	37.	.348	.0181	.311	32	MEAN
						.046			LOCI	IICAL	втоснем	SFOR	VALUES	MEAN
.238		. 10		21	N	N	.31	4	u	.700	.0069	4	7	Ţď
.196	$\vdash$	.41	7	ω	σ	$\infty$	9	8		9	90	7	ω	픙
.000	0	0	0	0	0	0	.00	0		0	00	0	۲	GPI
006	1	0	S	ב	1	2	ഗ	0		$^{\circ}$	01	$\mathfrak{S}$	2	PGM
155	.0033	.885	.257	1	1.075	170	1.340	.273	37.	.254	.0058	.297	2	PGD
050	$\sim$	9	$\sim$	1	S	9	. 14	$\vdash$		2	03	$\omega$	N	GC.
015	0	0	0	ᆸ	W	$\sim$	. 99	$\vdash$		9	9	$\vdash$	N	Αl
. 548	W	$\vdash$	ω	15	$\boldsymbol{\sigma}$	4	ω	7		W	.0051	4	σ	Es
7	W		$\sim$	ᆫ	σ	ထ		α		2	9	ഗ	8	AlB
0	$\omega$		w	10	S		.12	9		$\omega$	.0067	9	ហ	Tf
Fisub	VAR	X3	Heub	df	X2	Fis	ENA	×	N	Не	VAR	НО	#ALs	Locus
 	 	 	! ! !	1	             	         		1		:       				

AVE # 1	MEAN	MEAN	MEAN	MEAN V	pdn form	<b>Sq</b> ŏ	Pdq	Kbg	Dbg	Cbg	Abg	MEAN	MEAN V	Pí	Нb	GPI	PGM	PGD	ရင	Al	ES	A1B	Τf	Locus
ALLELES	41	VALUES	18	VALUES	1	ω	4	N	4	1	ω	23	VALUES	 	w	1	2	2	2	2	<b>-</b>	2	ယ	#ALs
Data St		FOR	 	FOR								.345	FOR	.818	.727	.000	.273	.273	.091	.364	.000	.273	.636	Но
= 2.3		ALL LOCI	 	BLOOD G	1 1 1 1 1							.0282	втоснем	.0149	.0198	.0000	.0198	.0198	.0083	.0231	.0000	.0198	.0231	VAR
00 A	.298	H           	.312	ROUP LO	.000	.550	.546	.090	.607	.000	.393	.287		.714	.490	.000	.235	. 235	.086	.397	.000	.235	.483	He
AVE # AL				LOCI								11.	LOCI	11.	11.	11.	11.	11.	11.	11.	11.	11.	11.	       \( \( \) \( \)
ALLELES BG		 										1.285		.167	1.264	.000	.067	.067	.003	.031	.000	.067		×
= 2.571	1.752		1.959		.00	2.221	. 20	.09	. 54	. 0	1.648	1.608	AVE F	•	•		•	1.307	•		•	1.307	1,935	ENA
AVE #												202	140	146	-,484	.000	-,161	161	057	.084	.000	161	318	Fis
ALLELES '												4.887		W	7	0	$\infty$	.284	W	7	0	.284		X2
TOTAL											1	21		10	ω	0	ㅂ	۲	卢	1	0	1	u	df
= 2.412	.330		.370		0	7	7	9	$\omega$	.000	۱ ۲	.301		4	1	0	4	.246	9	$\vdash$	0	4	0	Heub
2											! ! ! !	3.296		9	$\vdash$	0	$\sim$	.128	0	7	0	$\sim$	ω	X3
	.0060		.0056		00	90	80	90	9	.0000	11		ᅜ 1	21	05	00	10	.0108	90	07	0	10	0	VAR
											       	147	097	094	417	.000	108	108	009	.126	.000	108	258	i 🚝

AVE #	MEAN	MEAN	MEAN	MEAN	bqn bqo	Pbg	Kbg	Dbg	Cbg	Abg	MEAN	MEAN	Pi	# F	Id5	PGD	ရင်	Al	ES	A1B	Tf	Locus
ALLELES	38	VALUES	19	VALUES	4 4    -	ω	1	ហ	2	ယ	19	VALUES	ωι	N I	→ ⊦	بر د	2	2	2	ᆸ	4	3 #ALS
ES ELEC		FOR	         	S FOR	         						.322	FOR	778	. 444	000	. 000	.556	.667	.111	.000	. 667	HO.
= 1.		ALL LOCK		BLOOD G	! ! ! !						.0547	вгоснемі	.0216	.0309	0000	.0000	.0309	.0278	.0123	.0000	.0278	VAR
900 AVE	.322	H H	.373	GROUP LOC	.647	535	.000	.745	.380	.304	.286	ICAL LOCI	.641	. 444	000	.000	.475	.494	.106	.000	.698	. не не
*				CI	1 1 1 1 1 1						9.	CI	     9	9 9	٥.	o	9.	9.	9.	9.	9.	
ALLELES BG			[ [ ] ] ]	!   	 						.418		10	0	$\circ$	.000	2	4	0	0	$\vdash$	
= 2.714	1.817		1.997	 	1.000	. 15	0	. 92	.61	1.436	1.691	AVE F	2.799	. 7		1.000	. 9	• 9	1.118		3.309	ENA
AVE #											127	074	213	001	. 000	.000	170	350	048	.000	.045	Fis
ALLELES TOTAL				 							1.807		.410	0	$\circ$	$\circ$	S	0	2	0	$\vdash$	X2
COTAL											13		Ι ω ι	ц,	<b>o</b> c	0	1	1	1	0	6	df
2.23	œ		. 438		. 685	6	0	$\infty$	0	N	.303		7	7	0 0	.000	0	$\sim$	$\vdash$	0	w	Heub
<b>υ</b>				[ ] ] ] ] ]							1.083		.192	.027	. 000	.000	.098	.678	.001	.000	.086	X3
	.0038		.0063	_	.0065	80	00	02	9	16	.0020	AVE F	01	05			02	00	80	00	00	VAR
				1 1 1 1 1 1							1.065		4	<b>5</b> 1	0 0	.000	0			0	9	Fisub

# LITTLE DUCK CREEK

#ALS HO VAR HE N X ENA 5 .533 .0178 .630 15222 2.714 2 .133 .0083 .320 15. 1.633 1.471 2 .067 .0044 .064 15002 1.068 2 .533 .0178 .444 15270 1.799 2 .400 .0171 .320 15165 1.385 2 .133 .0083 .125 15106 1.143 1 .000 .0000 .000 15000 1.000 3 .333 .0159 .485 15711 1.951 6 .400 .0171 .602 15711 1.951 6 .400 .0171 .602 15739 1.652 27 .287 .0389 .327 15739 1.652 3 .33 .0159 .467 2.100 5 .066 4 .400 .709 .066 4 .400 .709 .066 2 .247 2 .287 .0389 .327 15739 1.652 3 .3400 .467 .247 2 .2190 VALUES FOR BLOOD GROUP LOCI VALUES FOR ALL LOCI VALUES FOR ALL LOCI
VAR He N X ENA 3 .0178 .630 15222 2.71 3 .0083 .320 15. 1.633 1.47 7 .0044 .064 15002 1.06 3 .0178 .444 15270 1.79 0 .0171 .320 15165 1.38 3 .0083 .125 15000 1.47 0 .0000 .000 15000 1.00 3 .0159 .485 15711 1.95 0 .0171 .602 15. 1.017 2.51 R BIOCHEMICAL LOCI AV 1.000 .609 .327 15739 1.65 1.000 .609 .709 .467 .101 2.10 R BLOOD GROUP LOCI 3.375 2.19
VAR He N X ENA 3 .0178 .630 15222 2.71 3 .0083 .320 15. 1.633 1.47 7 .0044 .064 15002 1.06 3 .0178 .444 15270 1.79 0 .0171 .320 15165 1.38 3 .0083 .125 15008 1.14 0 .0000 .000 15000 1.00 3 .0159 .485 15711 1.95 0 .0171 .602 15. 1.017 2.51 R BIOCHEMICAL LOCI AV 7 .0389 .327 15739 1.65 .709 .669 .066 .709 .066 .709 .467 .187 3 .44 1.87 3 .44 1.87 3 .44 1.87
VAR He N X ENA  3 .0178 .630 15222 2.71  3 .0083 .320 15. 1.633 1.47  7 .0044 .064 15002 1.06  3 .0171 .320 15270 1.79  0 .0171 .320 15165 1.38  3 .0083 .125 15000 1.47  0 .0171 .602 15711 1.95  0 .0171 .602 15. 1.017 2.51  R BIOCHEMICAL LOCI Av
VAR He N X ENA  3 .0178 .630 15222 2.71  3 .0083 .320 15633 1.47  7 .0044 .064 15002 1.06  3 .0178 .444 15270 1.79  0 .0171 .320 15300 1.47  3 .0083 .125 15000 1.00  3 .0159 .485 15000 1.00  R BIOCHEMICAL LOCI  7 .0389 .327 15739 1.65  .000 .609 .609  .066 .709 .467
VAR He N X ENA  3 .0178 .630 15222 2.71  3 .0083 .320 15. 1.633 1.47  7 .0044 .064 15002 1.06  3 .0178 .444 15270 1.79  0 .0171 .320 15165 1.38  3 .0083 .125 15000 1.47  0 .0000 .000 15008 1.14  R BIOCHEMICAL LOCI  R BIOCHEMICAL LOCI  7 .0389 .327 15739 1.65  .524 .000  .609  .709
VAR He N X ENA  3 .0178 .630 15222 2.71  3 .0083 .320 15. 1.633 1.47  7 .0044 .064 15002 1.06  3 .0178 .444 15270 1.79  0 .0171 .320 15165 1.38  3 .0083 .125 15165 1.38  3 .0159 .485 15711 1.95  0 .0171 .602 15. 1.017 2.51  R BIOCHEMICAL LOCI  AV  7 .0389 .327 15739 1.65  .524 .000  .609  .609  .066
VAR He N X ENA  3 .0178 .630 15222 2.71  3 .0083 .320 15. 1.633 1.47  7 .0044 .064 15002 1.06  3 .0178 .444 15270 1.79  0 .0171 .320 15165 1.38  3 .0083 .125 15000 1.47  0 .0000 .000 15000 1.00  3 .0159 .485 15711 1.95  0 .0171 .602 15. 1.017 2.51  R BIOCHEMICAL LOCI  AV  7 .0389 .327 15739 1.65  .524 .000  2.55
HO VAR HE N X ENA  533 .0178 .630 15222 2.71 .133 .0083 .320 15. 1.633 1.47 .067 .0044 .064 15002 1.06 .533 .0178 .444 15270 1.79 .400 .0171 .320 15300 1.47 .333 .0159 .278 15165 1.38 .133 .0083 .125 15000 1.00 .333 .0159 .485 15711 1.95 .400 .0171 .602 15711 1.95 .400 .0171 .602 15739 1.65 .287 .0389 .327 15739 1.65 .524 .000
HO VAR HE N X ENA  533 .0178 .630 15222 2.71  .133 .0083 .320 15. 1.633 1.47  .067 .0044 .064 15002 1.06  .533 .0178 .444 15270 1.79  .400 .0171 .320 15300 1.47  .333 .0159 .278 15165 1.38  .133 .0083 .125 15008 1.14  .000 .0000 .000 15000 1.00  .333 .0159 .485 15711 1.95  .400 .0171 .602 15. 1.017 2.51  FOR BIOCHEMICAL LOCI  AV  .287 .0389 .327 15739 1.65
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VAR He N X ENA 3 .0178 .630 15222 2.71 3 .0083 .320 15. 1.633 1.47 7 .0044 .064 15002 1.06 3 .0178 .444 15270 1.79 0 .0171 .320 15300 1.47 3 .0159 .278 15165 1.38 3 .0083 .125 15008 1.14 0 .0000 .000 15711 1.95
VAR He N X ENA  3 .0178 .630 15222 2.71 3 .0083 .320 15. 1.633 1.47 7 .0044 .064 15002 1.06 3 .0178 .444 15270 1.79 0 .0171 .320 15300 1.47 3 .0159 .278 15165 1.38 3 .0083 .125 15008 1.14 0 .0000 .000 15000 1.00
VAR He N X ENA 3 .0178 .630 15222 2.71 3 .0083 .320 15. 1.633 1.47 7 .0044 .064 15002 1.06 3 .0178 .444 15270 1.79 0 .0171 .320 15300 1.47 3 .0159 .278 15165 1.38 3 .0083 .125 15008 1.14
VAR He N X ENA  3 .0178 .630 15222 2.71 3 .0083 .320 15. 1.633 1.47 7 .0044 .064 15002 1.06 3 .0178 .444 15270 1.79 0 .0171 .320 15300 1.47 3 .0159 .278 15165 1.38
Ho VAR He N X ENA  .533 .0178 .630 15222 2.71  .133 .0083 .320 15. 1.633 1.47  .067 .0044 .064 15002 1.06  .533 .0178 .444 15270 1.79  .400 .0171 .320 15300 1.47
HO VAR HE N X ENA  .533 .0178 .630 15222 2.71  .133 .0083 .320 15. 1.633 1.47  .067 .0044 .064 15002 1.06
HO VAR HE N X ENA .533 .0178 .630 15222 2.71 .133 .0083 .320 15. 1.633 1.47
Ho VAR He N X ENA .533 .0178 .630 15222 2.71
HO VAR HE N X

AVE #	MEAN	MEAN	MEAN	MEAN	pdu	დბე	pdq	Kbg	Dbg	Cbg	Abg	MEAN	MEAN	Ρi	ᄄ	GPI	PGM	PGD	ဝဝ	Αl	단요	AlB	Υf	Locu	
ALLELES	54	VALUES	22	VALUE	2	2	ω	_	80	2	4	32	VALUE	7	2	<u>,</u>	2	8	2	N	បា	ω	δ	S #ALs	
ES ELEC		FOR		S FOR								335	SFOR	N	9	0	Ü	СП	$\vdash$	0	.706	$\vdash$	$\infty$	Но	
= 3.2		ALL LOC		BLOOD G								.0256	BIOCHEM	ហ	œ	0	$\omega$	ယ	9	4	.0130	Ş	5	VAR	
00 A	.349		.300	GROUP LO	0	. 255	4	0	$\vdash$	.058	.218	383	i H i	্ৰ	$^{\circ}$		0				.725	0		He	
AVE # ALI				LOCI								17.	'OCI								17.			Z	
ALLELES BG												.777		$\infty$	$\sim$	0	0	0	$\vdash$	0	.009	ယ		×	
= 3.143	2.046		2.055		1.429	ن	. 21		. 54	.06		2.041		.87	.18	.00	. 67	. 05	. 69	.94	3.634	. 25	.10	ENA	
AVE #												.125	, 121	ထ	9	.000	9	$\sim$	ᆫ	2	.026	.450	176	S	
ALLELES '												14.117		00	σ	0	$\vdash$	$\vdash$	$\vdash$	$\vdash$	.012	4	ບາ	X2	
TOTAL												54		21	1	0	1	1	ᆫ	H	10	ယ	15	d.f	
= 3.1	.382		.365		0	. 262	9	0	u	9	.224	395		.670	.156	.000	.412	.056	.420	.500	.747	.208	.778	Heub	
76												14.619		4	7	0	9	0	$\vdash$	0	.051	9	9	X3	
	.0042		.0054		90	.0068	03	00	03	02	07	.0034	। ਸ	90	05	00	04	02	04	00	.0012	07	01	VAR	
												.150		.209	9		9	0	2	0	.055			Fisub	

AVE	I I I I I	E ME	I ME	ME		Ö	ρ,	K	D	വ	À	I ME	XE	ש	H	ଦ	ַּטִּ	ď	ရ	A	E.	A	H	LO
**		MEAN V	1	MEAN V	Ubg 	рg	рg	Бq	рg	рg	bg	MEAN	12	μį	ם,	ΡI	GM	PGD	O	1	S	AlB	Н	Locus
ALLELES	30	VALUES	12	VALUE	<u> </u>	W	2	1	Ŋ	۲	23	18	VALUES	2	8	Ľ	$\vdash$	2	۲	2	2	2	ယ	#ALS
ES ELEC		FOR	 	S FOR								.300	FOR	.400	.200	.000	.000	.200	.000	.800	.400	.200	.800	HO I
= 1.8		ALL LOCI		BLOOD G								.0316	ВІОСНЕМІ	.0600	.0400	.0000	.0000	.0400	.0000	.0400	.0600	.0400	.0400	VAR
00	265	H	.289	GROUP I	.000	. 584	.465	.000	.480	.000	.495	.248	CAL	.320	.180	.000	.000	.180	.000	.480	œ	.180	.660	He
AVE # AJ	1 1 6 1			TOCI								         51	LOCI		<u></u> ა	<u></u> ნ		<u></u> ნ	<u>ა</u>	ឞ៲	ហ	ហ •	ហ	
ALLELES B			1 1 1 1 1 1	! ! ! ! ! !	 							545		0	$\vdash$	0	.000	.011	0	1.067	.067	$\vdash$	.148	×
BG = 1.714	1.664		1.909	1 	.00	0	.87	1.000	1.923	1.000	1.979	1,492	AVE		. 22	.00	1.000	1.220	.00	. 92	1.923	. 22	2.941	ENA
4 AVE			 	E   								21	F13	lΩ	$\vdash$	0	.00	$\vdash$	0	σ	.16	۲	21	
# ALLELES			 	<b>1</b> 								0 3.0	0					1 .0		2.				
			i I I	 									     	<u>ا</u> ا	$\varphi$	0	0	62	0	2	$\omega$	9	N	X2
TOTAL		[   	i i i i	; [ ] [	i     							9	 	1 1	بر	0	0	۳	0	1	1	1	ω	i df
≈ 1.7e	.311		.361	 	10	4	Ţ	.000	u	0	$\sigma$	.276		.356	.200	.000	.000	.200	.000	. 533	. 533	.200	.733	Heub
65			t t t t	 								1.682		1 7	0	0	0	.000	0	ഗ	Ľ	0	4	X3
	.0075	1 f f l	.0052	 	00	05	05	.0000	03	00	01	:	AVE F	0	0	0	0	.0207	0	W	W	0	0	VAR
	1 1 1 1 1	 	 	 	 							1.089		125	.000	0	0	.000	0	0	SI	0	9	Fisub

SQUARE S WELL AREA

.341 TOTAL = 2.588	.341	OTA	H 1	ALLELES	AVE #	1.917	ALLELES BG	12 AVE # AL	.500	EC = 2	S ELEC	44  ALLELES	MEAN # AVE #
· i i	· i i		1 )			 				ALL L	3 FOR		MEAN
.380	00					2.201		25	<b>.</b> ω			19	MEAN
								LOCI	GROUP	BLOOD	FOR	VALUES	MEAN
4.	4.				         		 	37		     		2	pdu
$\vdash$	$\vdash$					1.991		86	. 4.			N	bqõ
$\sim$	$\sim$					. 45		12	س			w	bad
0	0					1.000		ŏ	. 0			1	Kbg
0	0					. 18		36	. 6			ഗ	Dbq
.060	$\sigma$					1.062		00 6	. OS			N #	Cpd F
O 1	O 1	1	1 1 1	1	1 1 1	ן ו מי	         		ן ן זין	       	! !	       	)   N
.344 26 .313 10.177	44 26 .31	44 2	14	10	029	1.718	.041	04 16.	1 i	.022	.313	25	MEAN
AVE				į	.036	AVE F		LOCI	HEMICAL	BIOCH	FOR	VALUES	MEAN
30 10 .744 .49	30 10 .74	30 1	u		214	. 58	2	1 1	. 7		7	ഗ	Ρį
27 3 .546 .33	27 3 .54	27	2	:_	$\infty$	.12	7	9 1	, UI	.015	$\sim$	ယ	ďН
00 0 .000 .00	00.00	00	0		0	.00	0	0 1	. 0	.000	0	٢	GPI
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28 1 .062 .00	28 1 .06	28	2	. 0	4	.06	0	0 1	. 0	.003	σ	2	PGD
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