Table 1. Precipitation data.

Sample No.	Date	Tritium units* (av. error, ± 8 percent)
	Dhahran	
352	5–6 March 1959	112
	Near Dhahran	
353	7–8 March 1959	96
354	7–8 March 1959	124
	Rub' al Khali area, showers	
420	25 May 1959	63
423	25 May 1959	69
421	26 May 1959	59
422	26 May 1959	54
	Rub' al Khali area	
604	1 January 1960	20
606	3 November 1960	18

* Tritium atoms per 10^{18} hydrogen atoms.

presence of calcium carbonate cement in the upper part of the gravel fill in downstream gorges, and the distances up-wadi to where slopes of stream beds are above grade lead us to believe that there was no man-made tritium in these waters. On the other hand, water from a large open dug well in Wadi Aleysan at Riyadh tested 8.9 tritium units, evidently indicating a mixture of more recent tritium-enriched water with older water seeping out of the gravels in the walls of the well. A year later, rain samples from the Persian Gulf and Rub' al Khali regions gave values up to 124 tritium units, which correspond to the Northern Hemisphere spring tritium peak observed elsewhere. Later rains show the tritium-level decay characteristic of later 1959 and 1960. Tritium values for precipitation are given in Table 1. The value of the large increase in tritium from bomb fallout in infrequent desert rainstorms remains to be evaluated, but certainly age determinations of water in the shallow gravels of the desert will have to be checked by other methods during the next several years.

The C^{14} determinations give hope of widespread use for dating older and deeper desert waters. Six samples consisting of the bicarbonate and CO_2 extracted from deep water samples (Table 2) were analyzed for C^{14} content to determine the time since their precipitation as rainfall. The waters came from aquifers more than 1200 ft below the land surface at the wells. The distances from the outcrop of the aquifers to the wells range from 24 to 250 km.

The method of dating ground waters by their C^{14} content has been applied in the German till plains by Brinkman *et al.* (*1*). The age computations made by Brinkman and his co-workers of the water in this humid carbonate-rich area are based on an initial C^{14} content of 85 percent of modern wood. This subtracts approximately 2000 yr from their dates. In the low-latitude deserts, it is believed that the rainfall, episodic and often violent in nature, adds water directly to the nubian-type sandstones and dunes above the sandstones without uptake of "dead" carbonate. For this reason, the ages of these samples were computed on the basis that the initial C^{14} was the same as that of contemporary wood, or more exactly, 95 percent of the National Bureau of Standards oxalic acid C^{14} standard. The uptake of "dead" carbon by the solution of limestone during transport of the water through the aquifer would tend to be inhibited by the increased temperature (decreased CO_2 solubility) as measured by the geothermal gradient. The ages for the deep artesian waters at Buraida, Riyadh, Khurais, and Abqaiq range from 20,400 to 24,760 yr. This time span is of the same order of magnitude as an estimate of 18,500 yr for the water to move from the outcrop to Abqaiq, as calculated by Whitman Dimock of the Arabian American Oil Company from pumping test data and broad assumptions of aquifer coefficients (*2*). The climax of the Wisconsin glacial stage occurred at about this time, and the high rainfall during this pluvial period must have charged the aquifers. The ages greater than 33,000 yr for the water samples from the western Rub' al Khali may be due to old carbonate taken up from the carbonate rocks in the Yemen highlands and the calcareous loess east of the highlands, or they may be the true age of the water there, which would have fallen as rain during the early Wisconsin glacial stage (*3*).

Table 2. Carbon-14 ages in deep waters of Saudi Arabia. WW, water well.

Sample No.	Water well	Depth of sample (ft)	Age of aquifer	Min. distance to outcrop (km)	Water	
					Temp. (°F)	Age (yr)
W-904	Town well, Buraida	1250	Cambrian and Ordovician	24	100	20,400 ± 500
W-889	Riyadh, WW 180	3647 to 3974	Triassic or Jurassic	60	126	24,630 ± 500
W-897	Khurais, WW 8	1490 to 1693	Cretaceous	70	80	20,760 ± 500
W-894	Abqaiq, WW 32	3003 to 3402	Cretaceous	250	134	22,500 ± 500
W-888	St. WW 7	1617 to 3035	Jurassic and Cretaceous	75	100	> 33,000
W-887	St. WW 13	3435 to 3506	Permian	200	98	> 33,000

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Haptoglobin and Transferrin Gene Frequencies in a Navajo Population: A New Transferrin Variant

Abstract. The distribution of serum haptoglobin, transferrin, and ceruloplasmin has been studied by starch gel electrophoresis for a Navajo Indian population in Arizona. Only the three common haptoglobin phenotypes were observed, but a high percentage of a new faster-moving transferrin variant B_{0-1} was discovered. No unusual ceruloplasmins were found.

The development of starch gel electrophoresis and the subsequent discovery of the genetic basis of human serum haptoglobin types (*1*) have led to an unprecedented proliferation of gene frequency estimates for the two common haptoglobin alleles in numerous population groups. In the comparatively short period of 5 yr, the world haptoglobin map has been rapidly filled. As tabulated by Sutton *et al.* (*2*), the Hp^1 frequency ranges from a low of .09 for Malaya Indians to a high of .87 for Nigerian Negroes and of .93 for Lacandon Indians in Central America. An interesting feature of the haptoglobin map is the progressive increase in Hp^1 frequency from Southeast Asia via Alaska and North America to Central and South America.

A genetic basis has also been established for the inheritance of human

transferrins (*3*), the β_1 iron-binding globulins in serum. Nine different molecular species of transferrin have been distinguished by their starch gel mobilities. In addition to the eight types previously reviewed (*4*), an additional variant D_4, of intermediate mobility between D_0 and D_1, has recently been described by Harris *et al.* (*5*). However, the high frequency of the common transferrin C allele has made population studies more difficult than for the haptoglobins, and only rare examples of homozygotes for the unusual alleles have been reported.

In the present study, haptoglobin and transferrin types were determined for a large group of Navajo Indians in Arizona. Starch gel electrophoresis was carried out in borate buffer at *p*H 8.6 in the vertical system described by Smithies (*6*). A compact apparatus has been designed which permits simultaneous vertical electrophoresis of 96 separate sera in six trays of 16 slots each. Hemoglobin and radioactive iron were added to the samples, and after electrophoresis each gel was sliced into three layers. The top slice was stained for protein with amido black, and the bottom slice was treated with benzidine reagent (0.2 g of benzidine in 100 ml of 50 percent ethanol, 0.2 ml of H_2O_2, and 0.5 ml of acetic acid) for detection of haptoglobin type. Transferrins were identified by autoradiography (*7*), and individual patterns were classified by their mobilities relative to known standard types. The use of autoradiography was of considerable value in the determination of transferrin types. Although transferrin C was readily detected by its characteristic shape and position in the protein stain, the faster moving B types were sometimes obscured by ceruloplasmin and the slower moving D types by haptoglobin. Autoradiographs were made from the middle slice of the gel in order to avoid the slightly blurred patterns caused by trailing at the surfaces of the gel during electrophoresis. The middle slice was subsequently stained for ceruloplasmin with *p*-phenylenediamine (*8*).

Haptoglobin and transferrin types for the Navajo population are given in Tables 1 and 2. No differences in ceruloplasmin mobility were observed in 263 indivduals analyzed. The 0.454 Hp^1 frequency in the Navajo population is significantly different ($P < 0.001$) from the only previously reported data on American Indians, a frequency of 0.59 determined for 98 Apaches (*9*). However, the authors of the Apache survey suggested that their Hp^1 frequency may have been overestimated because of difficulties in differentiating free hemoglobin from the haptoglobin 1–1 band in the horizontal gel system which they used. In the present study the vertical gel system provided clear separation of these two components. Every sample could be placed in one of the three common haptoglobin classes. No sample was observed with the rare phenotype Hp^{2-1} (mod) and no *Hp* 0 types were found. As indicated by the value for *P* of $> .10$, the distribution of observed phenotypes was in reasonable agreement with that expected under Hardy-Weinberg equilibrium.

Table 1. Haptoglobin types in Navajo Indians. The method of estimation of gene frequency is shown below the table.

No. in family* (n)	Total individuals	1–1 (a)	2–1 (b)	2–2 (c)	$2a + b$ (x)	$2(a + b + c)$ (y)	Weight per gene $[w = 2/(n + 1)]$
Unrelated	169	39	80	50	158	338	1.0000
2	54	10	25	19	45	108	.6667
3	21	6	8	7	20	42	.5000
4	4	1	3	0	5	8	.4000
5	15	1	3	11	5	30	.3333
Total	263	57	119	87	233	526	

* Family consists of either parent and children or children alone.

$\Sigma wx = 201.7$ $\Sigma wy = 444.2$ $p^{Hp^1} = \Sigma wx/\Sigma wy = .454$ Std. error S.E. $= (pq/\Sigma wy)^{1/2} = .024$

$\chi^2 = 2.084$ $P > .10$

In addition to the Navajo data, preliminary studies have also been carried out on an Araucanian Indian population near Temuco, Chile (*10*). An Hp^1 frequency of .75 was obtained for 34 individuals, which is in agreement with a value of .73 determined for 173 Peruvian Indians (*11*).

It is difficult in many cases to make accurate comparisons of haptoglobin frequencies in various populations because reports have seldom included the standard error of the observed gene frequency. The standard error is defined as

$$\sigma = (pq/T)^{\frac{1}{2}}$$

where p and q are observed frequencies for the two alleles and T represents the number of *independent* genes analyzed. If gene frequency data from small populations are to be compared, it is necessary that an accurate value of T be obtained in order that a reliable standard error may be calculated. For unrelated individuals, T will equal twice the number of individuals, but where the sample includes related individuals, the value of T must be reduced. Cotterman (*12*) has described a highly efficient system of weighting for determining the number of independent genes in a related sample, and this method has been applied to the Navajo population. Where both parents in a family have been included, all four genes in the family are accounted for, and no further information is gained from the offspring. Where the family consists either of parent and children or of children alone, Cotterman assigns a weight w for the genes in the family which varies with the size of the family and which is calculated as $w = 2/(n + 1)$, where n equals the number of individuals in the family. As the family size increases, the number of independent genes in the family approaches four. The detailed calculation of the haptoglobin gene frequency and the standard error is given in Table 1. A similar calculation was made in the case of transferrin.

Of the 17 unusual transferrin variants found in the population, 16 were of a previously undescribed molecular species of intermediate mobility between transferrins B_0 and B_1 (*13*). In the established transferrin nomenclature, variants which are faster-moving than C are labeled B and slower-moving variants are labeled D, and subscripts in order of decreasing mobility are used to distinguish transferrins within the two classes. According to this system, it is suggested that the new Navajo transferrin be designated B_{0-1}. In addition, one Navajo individual was of transferrin type B_2C, which has an inci-

Table 2. Transferrin types in Navajo Indians.

Total individuals	Total independent genes	CC	$B_{0-1}C$	B_2C	p^{B0-1}	S.E.	χ^2	P
230	393.27	213	16	1	.041	.010	.625	$>.40$

dence of approximately 1 percent in English (*13*) and Canadian (*14*) whites. The 8 percent incidence of phenotype $B_{0-1}C$ is the highest value yet reported for any of the faster-moving transferrin B types, although its incidence is somewhat lower than the average value of 10 percent for type CD_1 in Negro populations and the high of 15.6 percent CD_1 reported for a large population in the New Guinea highlands (*15*).

No factors are known which could maintain the transferrin polymorphism (*16*), although some of the variants may be important for resistance to infectious disease. In this connection it may be possible to relate the wide prevalence of tuberculosis and streptococcal infections in Navajo populations (*17*) to the work of Martin and Jandl on the inhibition by transferrin of viral multiplication and cytopathogenic effects (*18*). If the frequencies of the unusual genes are stable, the similar incidence of $B_{0-1}C$ in Navajos and of CD_1 in Negroes suggests that selective factors of approximately equivalent intensity may be operating in the two populations. The development of a method for the separation and isolation of rare transferrins from the serum of heterozygotes (*19*) has permitted experiments to be undertaken to investigate the nature of the chemical differences among the various transferrin types (*20*).

Note added in proof. Since the submission of this report, we have identified in a Chinese population a transferrin variant of slightly greater electrophoretic mobility than the Negro D_1. The conditions required to demonstrate this difference suggest that the Chinese variant will prove slower-moving than the D_4 of Harris *et al.* (*5*).

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Intrinsic Barriers to Dispersal in Checkerspot Butterfly

Abstract. Capture-recapture studies revealed that the checkerspot butterfly *Euphydryas editha* is extraordinarily sedentary. Since no physical barriers prevent interchange between various portions of the study colony, it is concluded that intrinsic factors play the major role in limiting movement. The few available data on dispersal are discussed.

It is generally accepted (*1*) that most flying organisms display a high degree of vagility, the ability to cross barriers. Nevertheless, as Mayr (*2*) has pointed out, birds are usually quite sedentary and make little use of their dispersal potential. Similarly, the few butterflies which have been studied with any degree of rigor—*Maniola jurtina* L. (*3*), *Polyommatus icarus* Rott. (*4*), *Papilio glaucus* L. (*5*), *Anthocaris sara* Boisduval (*6*), and *Pieris protodice* Boisduval and Leconte (*7*)—have shown a remarkable lack of wanderlust. The present report on *Euphydryas editha* Boisduval (Nymphalidae: Nymphalinae) further underscores the importance of differentiating *potential* and *actual* vagility and emphasizes the dangers of casual assumptions about dispersal patterns, "gene flow," and the like.

In the San Francisco Bay region, *Euphydryas editha* is confined to areas of serpentine outcropping, where its food plant, *Plantago erecta* Morris, is especially abundant. In the spring of 1960 a capture-recapture study was made of the adult population of this butterfly on Stanford University's Jasper Ridge Biological Experimental Area, as part of a long-term investigation of microevolution in this species. There *E. editha* is found only in a hilltop island of grassland, surrounded by dense chaparral and scattered oak woodlands. During the 25-day flight period (31 March to 24 April) 185 individuals were given distinguishing marks and released (*8*). Of these individuals 97 were recaptured at least once, accounting for a total of 224 recaptures. The population size (total number of individuals involved in the flight) was estimated to be between 250 and 400. Sampling was done once a day, so that all recaptures of any given individual were on different days.

Prior to the flight period the region occupied by the colony was arbitrarily divided into eight areas (A to H), and during the flight period a careful record was made of the areas in which the individuals were captured and recaptured. Centers of abundance were found in three areas (C, G, H). Only 12 captures and recaptures were made in areas peripheral to C (A, B, D, E, F), and for analysis areas A to F were lumped as area C. The distribution of individuals taken is shown on the map (Fig. 1). Each dot represents the *first* capture of an individual; placement of the dots within each of the eight areas is approximate. This pattern of distribution, although representing only part of the data, agrees with the impressions of the total distributional picture formed in the field by the investigator and his assistant.

Of the 97 individuals which were marked and subsequently recaptured at least once, only eight were found to have changed areas during the study, and each of these changed areas only once. Therefore 216 of the 224 (96.4 percent) recaptures were in the area of previous capture.

For reasons which will be dealt with in a future paper, the frequency of recaptures varied from area to area. Scoring only those individuals which were recaptured at least once, and ignoring the eight which changed areas, the mean number of recaptures $\pm$ standard error (N) per individual were: area C, 1.79 ± 0.210 (34); area G, 2.96 ± 0.523 (24); and area H, 2.52 ± 0.350 (31). The five individuals with the highest number of recaptures in each area had the following scores: area C,