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Résumé de l'article

La différenciation de la fertilité au cours des temps de la population athapaskane Kutchin du village d'Old Crow, Territoire du Yukon, a été examinée afin d'établir la part jouée par la sélection naturelle et par la dérive génique dans la formation du patrimoine génétique actuel. Les données de cycles de vie ont été utilisées afin de construire l'indice Crow de Sélection Naturelle pour les périodes de nomadisme et de sédentarité parmi les Kutchins. Les informations démographiques et génétiques ont été combinées afin d'étudier la dérive génique par rapport : 1) au sort d'un allèle neutre, 2) au déclin de l'hétérozygosité et 3) à la durée moyenne de la demi-transformation d'un caractère polymorphe. Une revue de l'histoire culturelle de cette population a permis de constater que la sélection naturelle et la dérive génique n'ont pas contribué de façon déterminante à son réservoir génétique présent. La reconstruction des liens généalogiques au cours de l'histoire souligne, par contre, une contribution importante qui serait attribuable à l'effet aléatoire de « goulot d'étranglement » de l'isolat, portant sur la microdifférentiation génétique, attribuée jadis par les chercheurs à la dérive génique.

Historic Fertility Differentials in a Northern Athapaskan Community

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Historic fertility differentials for the Kutchin Athapaskan population of Old Crow Village, Yukon Territory, were examined to determine the role of natural selection and random genetic drift on the contemporary gene pool. Cohort data were utilized to construct Crow's Index of Natural Selection for nomadic and sedentary Kutchin time periods. Demographic and genetic information was combined to investigate drift with respect to: 1) the fate of a neutral allele, 2) decay of heterozygosity and, 3) the average half-life of a polymorph. Consideration of the population's cultural history indicates that neither selection nor drift is the prime determinant of the present gene pool. Rather, reconstruction of historic genealogical relationships indicates the presence of a strong founder effect responsible for the genetic microdifferentiation attributed by earlier researchers to drift.

La différenciation de la fertilité au cours des temps de la population athapaskane Kutchin du village d'Old Crow, Territoire du Yukon, a été examinée afin d'établir la part jouée par la sélection naturelle et par la dérive génique dans la formation du patrimoine génétique actuel. Les données de cycles de vie ont été utilisées afin de construire l'Indice Crow de Sélection Naturelle pour les périodes de nomadisme et de sédentarité parmi les Kutchins. Les informations démographiques et génétiques ont été combinées afin d'étudier la dérive génique par rapport : 1) au sort d'un allèle neutre, 2) au déclin de l'hétérozygosité et 3) à la durée moyenne de la demi-transformation d'un caractère polymorphe. Une revue de l'histoire culturelle de cette population a permis de constater que la sélection naturelle et la dérive génique n'ont pas contribué de façon déterminante à son réservoir génétique présent. La reconstruction des liens généalogiques au cours de l'histoire souligne, par contre, une contribution importante qui serait attribuable à l'effet aléatoire de « goulot d'étranglement » de l'isolat, portant sur la microdifférentiation génétique, attribuée jadis par les chercheurs à la dérive génique.

Introduction

Physical anthropology has long recognized the importance of fertility differentials in human microevolution (for reviews see Neel and Schull, 1972; Gomila, 1975). However, the recent selectionist-neutralist controversy (Kimura and Ohta, 1971; Salzano, 1975) raises the question of whether these reproductive inequalities are the result of natural selection upon specific genotypes/phenotypes or the stochastic force of random genetic drift. In particular, re-evaluation of the role of drift, or the "Sewall Wright Effect" (Wright, 1948) in evolution has changed dramatically. Originally downplayed (Fisher and Ford, 1950), drift was recently declared the "winner over selection in microevolution" (Cavalli-Sforza, 1973: 84). In large part this shift is due to the formulation of the neutralist paradigm stressing the role of selectively neutral alleles in the evolutionary process.

This paper combines demographic and genetic data to investigate the significance of natural selection and drift for the Northern Athapaskan population of Old Crow Village, Yukon Territory. Today Old Crow is best known for the Pleistocene artifacts and skeletal material recovered from the adjacent Old Crow Flats area (Irving *et al*, 1979). The village itself is relatively recent, with village founding dating to ca. 1912. At this time, Vunta, Chandalar, and Tukkuth Kutchin began to gather around a small trading post at the confluence of the Crow and Porcupine Rivers. For the most part these people were the survivors of a small-pox epidemic in the nearby site of New Ramparts (Figure 1 and 2). Decimated in numbers, the bands intermarried and today constitute the historic ancestors of the present population of roughly 250 Kutchin. The ensuing history of the village featured a gradual transition to sedentism. As recently as 1963 one-third of the population still lived a nomadic hunting-fishing lifestyle for at least part of the year (Balikci, 1963). Today the community represents the northernmost Indian settlement in Canada, and its inhabitants are the only permanent residents of the northern Yukon.

Due to these unique characteristics the village has been the subject of various biological studies. Of particular interest is the blood group genetics study of Lewis *et al.* (1961), whose findings of skewed gene frequencies were attributed to drift. During the 1977 and 1978 field seasons, the present author collected deomographic data for the population, building upon genealogical material collected earlier by Stager (1974) and Lewis *et al* (1961). In addition, a small blood sample was collected and analysed for bio-chemical genetic markers by Dr. N. Simpson, Department of Pediatrics, Queen's University. All of this information will be used in the following sections to delineate the effects of natural selection and drift on the modern Old Crow gene pool. To do so the population will be treated as a "Mendelian population," or closed breeding deme, although the applicability of this general genetic model is discussed in a later section.

Analysis and results

NATURAL SELECTION

The most commonly employed methodology for the detection of natural selection utilizing demographic data is the statistic termed "Crow's Index of Natural Selection" (Crow, 1958). This measure consists of two components. The first is a fertility component (I_f) derived as:

$$(1)\quad I_f = V_f / \bar{x}_S^2$$

where ($\bar{x}_S$) is the mean and (V_f) the variance in

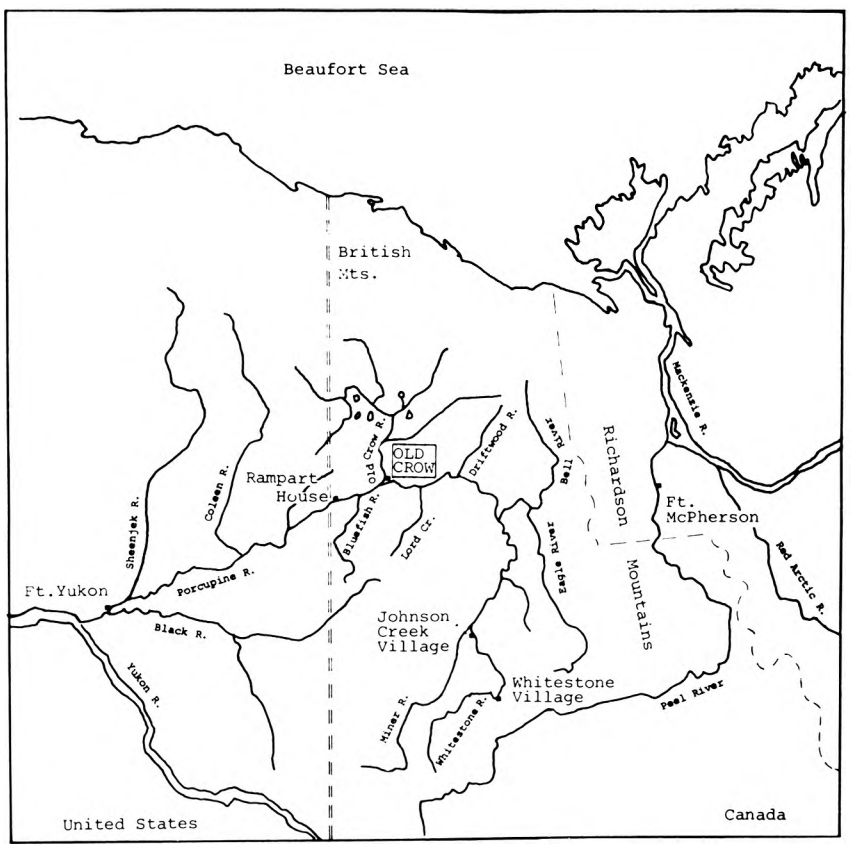

Figure 1. Geographic Locale of Old Crow Village.

Figure 2. Old Crow Village, ca. 1915 (Original photo University of Alaska, Courtesy of Old Crow Museum).

number of total births, restricted to women who have completed the reproductive period of the life-cycle (between the ages of 15-49; Barclay, 1958). The second component is that of mortality (I_m), given as:

(2) $I_m = pd/ps$

where (pd) is the proportion of offspring who die before attaining reproductive age and (ps) the proportion surviving. The index of total selection intensity (I_T) results from the combination of both components as:

(3) $I_T = I_m + I_f/ps$

As Swedlund (1980) notes, this methodology is most useful when observing temporal trends. Therefore, the technique was applied to two historic cohorts of Old Crow women, previously analysed for fertility and mortality trends (Roth, 1981). The first cohort consists of women born before 1900 (n of mothers = 39, n of children = 171), the second of women born after this date (n of mothers = 36, n of children = 231). While both cohorts include only women of completed reproductive age, the pre-1900 cohort consists of women who entered, and in some cases completed, this period during nomadic times. In contrast, the post-1900 cohort is comprised of women who entered this period at a time of incipient sedentism. Thus, the earlier cohort may be considered representative of nomadic demographic parameters, the latter sedentary rates.

Variables in the calculation of the index's components, as well as the total index, are given in Table 1 for both cohorts. Examination of this table shows that elevated fertility rates and lowered infant mortality levels for the sedentary cohort reduce the components and the final index. This pattern reflects demographic changes recorded for Canadian Indians in general (Romaniuk, 1981), while cross-culturally the reduction in values mirrors that recorded for nomadic versus sedentary Lapps (Barrai and Fraccero, 1965).

Although the index does commonly exhibit overall consistent patterns when applied to similar technological or historic periods of human evolution (see Jacquard and Ward, 1976; Spuhler, 1976), the methodology has not gone without criticism. Notable shortcomings of the index include: (1) failure to incorporate maternal mortality within the reproductive period, (2) the assumption that fertility is

TABLE 1
Calculation of Crow's Index

		x_s^2	V_f	p_a	p_d	I_m	I_f	I_T
A)	Pre-1900 Cohort	$(4.38)^2$	11.97	.608	.392	.645	.624	1.670
B)	Post-1900 Cohort	$(6.60)^2$	15.60	.835	.165	.198	.358	0.627

TABLE 2
Parity distributions and allelic loss for a unique neutral allele, a) Pre-1900 female cohort, b) Pre-1900 male cohort

a) Pre-1900 Females

Parity	Frequency	Probability of Loss	Alleles Lost
0	39	1.0	39.0
1	3	.5	1.5
2	8	.25	2.0
3	6	.125	.75
4	5	.0625	.3125
5	4	.03125	.1250
6	5	.015625	.078125
7	3	.0078125	.023440
10	3	.00097656	.0029971
11	1	.00048829	.00048829
16	1	.000015626	.000015626

n of women = 78
n of children = 185
x parity = 2.37
Variance = 10.83

Total Loss = 44.495623

Percentage Loss = 57.04567

b) Pre-1900 Males

Parity	Frequency	Probability of Loss	Alleles Lost
0	45	1.0	45.0
1	3	.5	1.5
2	5	.25	1.25
3	8	.125	1.0
4	6	.0625	.375
5	2	.03125	.0625
6	6	.015625	.09375
7	3	.0078125	.0234375
10	3	.00097657	.00292971
11	1	.00048829	.00048829
16	1	.000015626	.000015626

n of women = 83
n of children = 185
x parity = 2.23
Variance = 10.50

Total Loss = 49.308122

Percentage Loss = 59.40736

inherited and, (3) inclusion of non-genetically related mortality. Despite attempts to correct these obstacles (Kobayashi, 1969; Jacquard, 1970), a major argument against the index remains its inability to detect selection pressures in small human populations, based on demographic materials. For example, Cavalli-Sforza and Bodmer (1971: 317) state that with a selection coefficient of 0.01 a sample size of 320,000 is necessary to verify a deviation from the null hypothesis by a chi-square test with a confidence level of 95% for a single locus genetic trait, using demographic data. Clearly, these are not the sample sizes commonly encountered by anthropologists.

NEUTRALISM AND RANDOM GENETIC DRIFT

Due to the above difficulties it may be profitable to develop models for the delineation of drift in small human populations based on demographic information. Specifically, genetic and demographic data may be combined to (1) determine the fate of a neutral allele and (2) calculate the rate of drift.

The fate of a neutral allele over time is a line of inquiry beginning with Fisher's (1922) deterministic calculations and continuing through the recent simulation studies of Kimura and Ohta (1969a, b), Li and Neel (1974) and Li *et al* (1978). All of these approaches recognize that the fate of any mutant allele is dependent upon demographic parameters. To quote Roberts (1965: 94), "the probability of loss for new mutants in a population depends upon its pattern of fertility, as well as whether the population is numerically stable, expanding, or contracting."

To analyse the fate of a unique neutral allele in the Old Crow population, the previously defined nomadic and sedentary Kutchin female cohorts can be utilized. To these groups can now be added those women who died before completing or entering the reproductive period, the sum of their children, and similarly constructed male cohorts. With this information, the probability of loss for a neutral mutant allele can be ascertained for either or both sexes, based on total parities achieved. Roberts (1965) calculated the probability of loss as 1.0 in cases of zero parities, 0.5 for parity level one, 0.25 for level two, and so on. The rationale behind this approach is the model of a one-locus, two allele polymorphic system, such that there exists a 50% probability of an offspring inheriting a particular allele from one parent. Tables 2 and 3 present parity distributions and allelic loss for the four study cohorts calculated in this manner. Beginning with the pre-1900 female cohort, the cumulative alleles lost is approximately 45, equalling a percentage loss of 57 (45/78), recognizing that only one allele is transmitted to an offspring per parent. Similarly, the male cohort born before 1900 would fail to transmit the neutral mutant allele at a rate of almost 60%.

As noted, the Old Crow population experienced a significant rise in fertility, coupled with a lowering of mortality pressures, with the adoption of sedentism. These factors would lead to an expectation of reduced loss for the post-1900 cohort. However, the female percentage loss of 56% is virtually indistinguishable from the rate of 57% recorded for the earlier female cohort. Roberts (1965) provides the rationale for this surprisingly high level of loss by pointing out that the crucial determinant of a neutral allele's diffusion throughout a population is the shape of the parity distribution. "If the variance is twice the mean, the probability of survival of a mutant is about two-thirds that calculated under a Poisson distribution" (Roberts, 1965: 95). It is only in the post-1900 male cohort that the percentage of loss falls below 50, due to the dramatic decline in zero parities. Overall, the combined probability of loss remains high for all cohorts. The weighted mean probability of loss for the pre-1900 cohort, sexes combined, is .5826, while that of the post-1900 cohort is .5239.

The above calculations may be combined with demographic and genetic data to determine the rate of drift. The speed of drift is determined by the "decay of heterozygosity", i.e. the fixation of one allele at the expense or extinction of other alleles at a specific locus. The speed at which fixation/extinction occurs in a population equals the "half life" of the polymorphism. To calculate these parameters it is necessary to determine the average heterozygosity of a population, plus its generation length.

The blood group sample of Lewis *et al* (1961) (n = 114) and the biochemical sample collected by Roth (n = 40) were employed to determine population heterozygosity. Friedlaender (1975: 129) gives the formula for the degree of heterozygosity represented at each locus in a population as:

$$(4)\quad d = \sum_{k\text{-}1}^{t} p_k^2$$

where t is the number of alleles tested for at a locus, p_k the frequency of the kth allele, and d is locus heterozygosity. The average heterozygosity over n loci is calculated as:

$$(5)\quad \bar{D} = 1/N \sum_{1=1}^{N} d_i$$

where N is the number of loci tested, and d_i is the heterozygosity at loci i.

Applying these formulae to the allele frequencies given in Table 4 reveals a low level of heterozygosity. The blood group heterozygosity (0.1548) is higher

TABLE 3
Parity distributions and allelic loss for an unique neutral allele, a) Post-1900 female cohort, b) Post-1900 male cohort

a) Post-1900 Females

Parity	Frequency	Probability of Loss	Alleles Lost
0	39	1.0	39.0
1	4	.5	3.0
2	1	.25	.25
3	2	.125	.25
4	3	.0625	.1875
5	3	.03125	.09375
6	8	.015625	.12500
7	1	.0078125	.0078125
8	4	.00390625	.015625
9	3	.00195313	.00585939
11	3	.00048829	.0014687
13	3	.000122073	.000366219
16	1	.000015626	.000015626

n of females = 75
n of children = 241
x parity = 3.21
Variance = 18.06

Total Loss = 41.935929

Percentage Loss = 55.914572

b) Post-1900 Males

Parity	Frequency	Probability of Loss	Alleles Lost
0	27	1.0	27.0
1	5	.5	2.5
2	4	.25	1.0
3	3	.125	.375
4	5	.0625	.3125
5	3	.03125	.09375
6	5	.015625	.078125
7	1	.0078125	.0078125
8	2	.00390625	.0078125
9	3	.00195313	.0058539
10	2	.00097657	.00195314
13	2	.000122073	.000244146
15	2	.00003124	.000062480
16	1	.000015626	.000015626

n of males = 65
n of children = 229
x parity = 3.52
Variance = 19.38

Total Loss = 31.3831356

Percentage Loss = 48.281746

than that of the biochemical systems (0.1305), but the total heterozygosity ($\overline{D} = 0.1400$) is far lower than that recorded for Bougainville Island populations (Friedlaender, 1975) ($\overline{D} = 0.338$) or South African groups (Harpending and Chasko, 1976) ($\overline{D} = 0.292$).

To determine the rate at which heterozygosity may be expected to decrease in the future, it is necessary to calculate the mean generation length of the population. In demographic terms, generation length (T) is calculated as the mean age at childbearing (R_1), divided by the Net Reproduction Rate (N.R.R.), with the last representing the eventual sum of daughters born to a cohort of women. Generation length thus constitutes the time it takes for women to "replace" themselves in the population. While the N.R.R. incorporates mortality to women in the reproductive period (Barclay, 1959: 212-222), it does not consider pre-reproductive mortality, an essentiel parameter if allelic loss is to be calculated. Therefore, Howell's (1979: 300-301) methodology of estimating generation length based on overall parity distributions per cohort was followed. Table 5 presents the

TABLE 4
Allele frequencies and heterozygosity levels for blood groups and biochemical polymorphisms

I. BLOOD GROUPS	ALLELES (f)		d
ABO	A	0.0000	0.0008
	B	0.0004	
	O	0.9996	
Kell	k_b^a	0.0000	0.0000
	k	1.0000	
Duffy	Fy(a+)	1.0000	0.0000
	Fy(a-)	0.0000	
Diego	Di(a-)	1.0000	0.0000
	Di(a+)	0.0000	
Cartwright	Yt(a+)	1.0000	0.0000
	Yt(a-)	0.0000	
Lewis	Le(a-)	0.0543	0.0514
	Le(a+)	0.9457	
MNSs	MS	0.2109	0.6399
	Ms	0.5304	
	NS	0.1092	
	Ns	0.1495	
P	P_1	0.1728	0.3157
	P_2	0.8272	
Rhesus	R^1	0.2066	0.3856
	R^2	0.7554	
	R^z	0.0326	
	R^0	0.0054	
	r	0.0000	
	r'	0.0000	
	r''	0.0000	
II. BIOCHEMICAL SYSTEMS			
Adenosine deaminase	ADA^1	1.0000	0.0000
	ADA^2	0.0000	
Malate dehydrogenase	MDH^1	1.0000	0.0000
	MDH^2	0.0000	
Phosphoglycerate kinase	PGK^1	1.0000	0.0000
	PGK^2	0.0000	
Adenylate kinase	AK^1	1.0000	0.0000
	AK^2	0.0000	
Diaphorase	DIA^1	1.0000	0.0000
	DIA^2	0.0000	
Lactase dehydrogenase	LDH^1	1.0000	0.0000
	LDH^2	0.0000	
6-Phosphogluconate dehydrogenase	$6\text{-}PDG^A$	1.0000	0.0000
	$6\text{-}PDG^B$	0.0000	
Nucleoside phosphorylase	NP^1	1.0000	0.0000
	NP^2	0.0000	
Pseudocholinesterase (E_1 locus)	E^u	1.0000	0.0000
	E^a	0.0000	
	E^s	0.0000	
Psuedocholinesterase (E_2 locus)	E	0.0500	0.0950
	E	0.9500	
Esterase D	EsD^1	0.6625	0.4472
	EsD^2	0.3375	
Acid phosphatase	AcP^A	0.4500	0.4950
	AcP^B	0.5500	
Haptoglobin	Hp^1	0.5875	0.4847
	Hp^2	0.4125	
Phosphoglucomutase	PGM_1^1	0.8125	0.3047
	PGM_1^2	0.1875	

$d_{Blood\ Groups} = 0.1548$

$d_{Biochemical} = 0.1305$

$\bar{D} = 0.1400$

steps in these calculations, using information drawn from the female cohorts described earlier.
This methodology reveals that although mean age at childbearing is roughly equivalent for the cohorts, the mean generation length is far shorter for the post-1900 group; a phenomenon arising out of the higher mean parity and N.R.R. of this group. As a result, the post-1900 cohort exhibits a far higher growth rate, as measured by the Intrinsic Rate of Natural Increase.

By combining average heterozygosity with generation length the rate of heterozygotic decay, and hence drift, can be ascertained. This was accomplished by the formula of Nei (1975: 87):

$$(6)\quad H_t = H_O(1-1/2N)^t$$

where H_t is the expected heterozygosity at generation t, H_O is heterozygosity at time of sampling, and N is population size. This formula can be adapted to the Old Crow material by substituting ($\bar{D}$) for (H_O). However, the crucial quantity here is N, population size, which must be adjusted to reflect the breeding structure of a population, or its "effective population size" (Wright, 1931). Effective population size with respect to random extinction of alleles ($N_{e(R)}$) was given by Crow (1954) as:

$$(7)\quad N_{e(R)} = 4N/V_k + 2$$

where N is population size and V_k the variance of offspring produced by the population.

Table 6 gives the variables in the calculation of $N_{e(R)}$ for the study cohorts, sexes combined. The rate of heterozygotic decay is presented for differing time periods in Table 7, based on Formula (6) with both cohorts starting with the previously calculated value of $\bar{D} = 0.1400$ substituted for H_O. While this treatment views each cohort as a discrete generation, ignoring temporal overlap, it does allow for the modelling of changing demographic rates on the speed of decay.

The results of this methodology reveal that the decay of heterozygosity would be increased in the post-1900 cohort. However, in both groups the rate of such loss is surprisingly slow for such small samples. Morris (1971: 303) explains this phenomenon by observing that the decay of heterozygosity is fastest when the degree of heterozygosity is the greatest. In the study population, 43% of the systems studied were polymorphic (10/23), but the average heterozygosity was low ($\bar{D} = .1400$).

That the initial frequency of the alleles comprising the polymorphic systems, plus effective population size, determine the rate of decay can also be shown by calculation of the average half-life of a polymorph in the population. Kimura and Ohta (1969a, b) give the average time until extinction of a neutral mutant allele (disregarding the cases of eventual fixation) as:

TABLE 5
Variables in the estimation of mean generation length and growth rates, Old Crow female cohorts

	Pre-1900	Post-1900
Mean Parity	2.3717	3.2113
Children per 100 Newborns	237.17	321.33
N.R.R.	1.153	1.599
(Daughters per 100 Newborns)	115.3	159.9
R_1	28.18	27.29
T (R_1/N.R.R.)	24.42	17.07
Intrinsic Rate of Natural Increase ($r = N.R.R.-1/R_1$)	.0054	.0351

TABLE 6
Variables in the calculation of random extinction effective population size, Old Crow cohorts

	Pre-1900	Post-1900
N	161	140
V_k	10.648	19.263
$N_{e(R)}$	51	26

Where:

N is population size

V_k is variance of offspring

$N_{e(R)}$ is random extinction effective population size

TABLE 7
Decay of heterozygosity, Old Crow cohorts

Generation	Pre-1900	Post-1900
1	.1400	.1400
10	.1269	.1153
20	.1150	.0950
50	.0856	.0530
100	.0522	.0201
200	.0195	.0029

(8) $\overline{t_{o(p)}} = (-4N_ep/1\text{-}p)\log_e p$

where p is the frequency of the mutant allele, N_e is effective population size (here $N_{e(R)}$) and $\overline{t_{o(p)}}$ is number of generations until extinction. Applying this formula to the polymorphic allele frequencies given in Table 4, the value for the pre-1900 cohorts is $\overline{t_{o(p)}}$ = 112 generations or 2,733 years. For the post-1900 cohort, with half the $N_e(R)$ size, $\overline{t_{o(p)}}$ = 53 generations, or 905 years.

Discussion

The preceding analysis attempted to assess the effect of selection and drift upon a North American Indian population through the examination of historic fertility differentials.

The investigation revealed the same pattern of declining fertility differentials over time for both processes of evolution. In the case of Crow's Index the opportunity for selection is greatest when mean parity levels are low and their variance high. The probability of loss of a mutant neutral allele is greatest when the exact situation is present. These two approaches thus vary only in the explication of fertility differentials, with the former attributing them to selection pressures, while the latter regards them as the stochastic sampling errors which define drift. Unfortunately, the methodological expertise necessary to distinguish deterministic from stochastic processes in small human populations has not yet been developed. However, in the words of Howell (1979: 345):

> ... if our goal is the empirical study of natural selection we should seek the largest and most accurate data base to pursue the problem.

Heeding this advice it is most appropriate to investigate selection via the examination of large empirical (Bajema, 1971) or simulated (MacCluer, 1980) populations, and concentrate on the problem of drift in small human populations.

This paper attempted to explore drift in relation to: (1) the fate of a mutant neutral allele, (2) decay of population heterozygosity and (3) the average half-life of a polymorph. It must be stressed that throughout this analysis the study cohorts were treated as closed populations. Recent computer simulation studies (Dyke and MacCluer, 1976; Wobst, 1976) demonstrate that true populations of this size could not maintain total endogamy for long periods of time without necessitating gene flow in the form of non-consanguineous mating partners. While the mathematics of drift have become increasingly complex, Maruyama (1970) notes that as a rule of thumb only one in-migrant per generation can effectively retard drift. Therefore, estimates of heterozygotic decay and polymorphic half-lives presented here are maximum estimates of the rate of drift, just as Crow's Index provides maximum estimates of selection intensities.

These maximum estimates of the rate of drift in the study population reveal slow decay of heterozygosity and long polymorph half-lives, severely negating the Lewis *et al* (1961) premise that drift is responsible for the observed skewed gene frequencies from Old Crow. Meiklejohn (1977) recently stressed the difference between "long term" and "short term" genetic studies, noting that the former should view population history in millennia, the latter in terms of a few generations. Available demographic material for Old Crow spans only 150 years. Clearly then this is a short range study. Similarly, the historic breeding pool of the present population was only formed shortly before the turn of this century. Certainly it is too recent a population for drift, as delineated here, to have had an appreciable effect on the gene pool.

Rather than drift, it is proposed that the allele distribution reflects the historic sampling accident which resulted in the original founding population. While the stochastic phenomenon of "founder effect" has been recently slighted (Neel, 1978; Thompson and Neel, 1978), it accurately describes the history of the Old Crow population. As originally defined by Roberts (1968), founder effect consists of three unique events: (1) a reduction in population size, (2) rapid growth and, (3) genetic isolation. For Old Crow these events have been noted as (1) the formation of the village population from the survivors of a historic epidemic, (2) rapid population growth due to the already described trends in fertility and mortality and, (3) genetic isolation as revealed in a high degree of consanguineous matings (Lewis *et al*, 1961: 385). As a result of these factors, 134 out of a total 250 people in the 1975 village population (54%) can trace their descent to one of four founding families, as shown in Figure 3.

Summary

This paper, while attempting to delineate random genetic drift in small human populations based on the combination of genetic and demographic materials, has also sought to consider the role of history in the determination of the study population's gene pool. As Lewontin (1975: viii) notes the great virtue of the study of human populations is that it introduces history into evolution. In the present study, reconstruction of the cultural history of the Old Crow population points to neither natural selection nor random genetic drift as the prime determinant of the gene pool. Rather, genealogical examination of

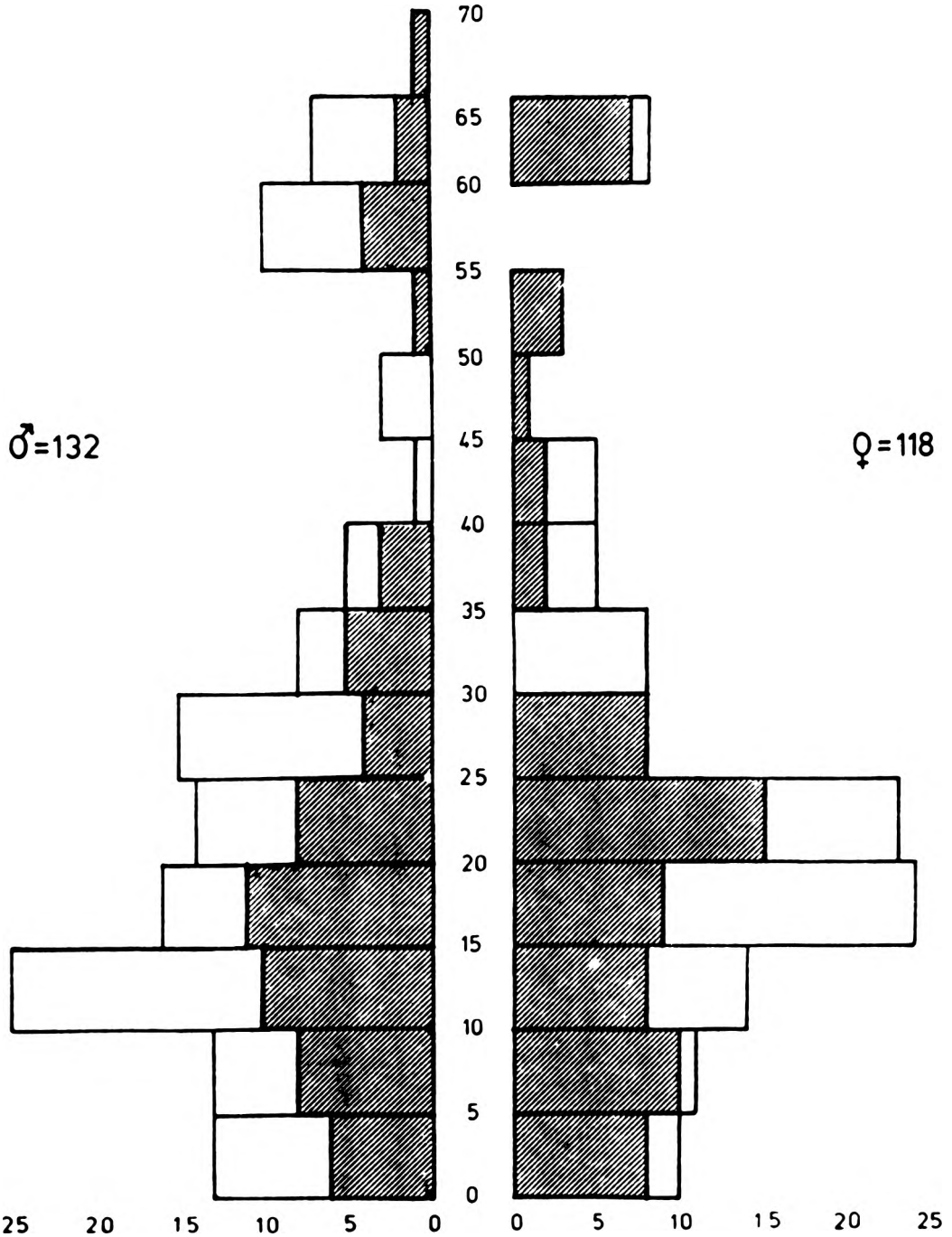

Fig. 3. Members of the 1975 village population who can trace their descent to one of four founding families indicated by darkened areas in the age-sex pyramid.

kin-structured migration and subsequent mating patterns indicates the presence of a pronounced historical founder effect. While founder effect was recently regarded as being "frequently (and glibly) invoked when an unusual allele frequency is encountered" (Neel, 1978: 398), the same may be said for drift and selection. In particular, invocation of drift as a driving force in human population genetics requires a view of the long-term history of populations, not the short-term sampling frame which of necessity is so commonly employed by population geneticists and anthropologists.

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