

Kinship and Inbreeding on Namu Atoll (Marshall Islands)¹

By Nancy Pollock², J. M. Lalouel and N. E. Morton

ABSTRACT

Genealogical, migration, and clan data have been collected in Namu atoll, Marshall Islands. Endogamy, where both parents come from the atoll population, is high (.89). Ascertained inbreeding in 4-6 generation pedigrees is low (.0076), as is kinship estimated from pedigrees (.0130), in comparison to asymptotic predictions from migration and clan data (.044 to .045), and island model reduction applied to genealogical data (.025 with chains of inbreeding, .047 with chains of kinship). The discrepancy between observation and expectation appears largely due to incompleteness of genealogies. Clans and geographical subdivision of the atoll population do not seem to have important effects on kinship. After 30 generations the random kinship on Namu is predicted to be .022, and random kinship in the Marshalls to be .003. Because of internal migration, the Marshalls appear to have differentiated by genetic drift as a group: there seems to be less divergence among Marshallese atolls, compared with the more isolated atolls of the Eastern Carolines. These predictions should be tested by bioassay of kinship as more data on polymorphisms become available.

Few studies of kinship and inbreeding have been carried out in the Pacific. Investigations in the Eastern Carolines (Morton et al., 1971a, c) have revealed considerable isolation of Pingelap and Mokil atolls. In contrast, the Marshall Islands appear to be characterized by greater contact between atolls, which in prehistoric times led to close political contacts between the Ratak and Ralik chains (Krämer and Neverman, 1938).

During the course of field work on the economic anthropology of Namu (Pollock, 1970), pedigrees were collected for all inhabitants, extending 4-6 generations. Data on parentage, places of birth and residence, and clan affiliation of each identified couple were reduced

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² Present address: Department of Anthropology, Victoria University, Wellington, New Zealand.

to standard form for computation of inbreeding and kinship (Harada, 1969) and for tabulation of migration between islets and clans (Harris, 1969). The material has a shorter time depth than data on Pingelap and Mokil atolls, where a prehistoric typhoon greatly reduced the number of founders. Genetic polymorphisms have not been studied on Namu, nor to any great extent in the Marshalls. In other respects the material is comparable to studies on Pingelap and Mokil, permitting quantification of the difference in gene flow within the Marshalls and Eastern Carolines.

INBREEDING AND KINSHIP FROM PEDIGREES

The probability that a pair of alleles drawn at random from two individuals be identical by descent from a common ancestor is called *kinship*; if the individuals are mates, this probability is called *inbreeding*. Close inbreeding can be detected for generations 4-6, and only matings where progeny belong to these generations have been tabulated. Kinship has been computed for a number of pairs of sibships equal to those utilized in calculating inbreeding. These pairs were drawn at random from generations 4-6 by circular permutation, omitting pairs with both sets of parents unknown (Hussels, 1969). The computer programs COEF and KIN (Harada, 1969), using an algorithm of MacLean (1969), calculate inbreeding and kinship. They also permit a tabulation of the number of chains of length c contributing $(1/2)^c$ to inbreeding or kinship, where the corresponding generation number is $t = (c - 1)/2$. The results of such an analysis are given in Table 1. For each value of c are given the corresponding value of t , the number of chains n_c , the partial inbreeding $F_p^{(t)}$ and the cumulative inbreeding $F^{(t)}$ defined by:

$$F_p^{(t)} = n_c(1/2)^c/N$$

$$F^{(t)} = \sum_{i=1.5}^t F_p^{(i)}$$
(1)

A similar calculation can be made for kinship, where N is the number of pairs. For this atoll population cumulative inbreeding (.0076) is lower than kinship (.0130), reflecting avoidance of consanguineous mating. By inclusion of generation 4, the genealogies are incomplete for $c > 8$, and so these estimates are undoubtedly too low. They can

Table 1
Chains of Length *c* in generations 4 to 6: Mates and Random Pairs

<i>c</i>	<i>t</i>	Inbreeding			Kinship		
		No. of chains	partial F	cumulative inbreeding	No. of chains	partial Φ	cumulative kinship
3	1.0	0	0	0	0	0	0
4	1.5	0	0	0	12	.004573	.004573
5	2.0	24	.004491	.004491	22	.004192	.008765
6	2.5	11	.001039	.005530	20	.001905	.010670
7	3.0	27	.001263	.006793	26	.001238	.011908
8	3.5	22	.000515	.007308	21	.000500	.012408
9	4.0	16	.000187	.007495	33	.000393	.012801
10	4.5	18	.000105	.007600	24	.000143	.012944
11	5.0	14	.000041	.007641	21	.000063	.013007
12	5.5	6	.000009	.007650	10	.000015	.013022
13	6.0	1	$< 10^{-6}$.007650	5	.000004	.013026
14	6.5	1	$< 10^{-6}$.007650	0	0	.013026
Number of chains		140			194		
Number of pairs		167			164		

be extrapolated to a stationary state by the formula for cumulative kinship in generation *t* under an island model:

$$\Phi^{(t)} = \Phi [1 - e^{-t/2N_e\Phi}] \quad (2)$$

where the stationary kinship is

$$\Phi = 1/(4N_e m_e + 1) \quad (\text{Morton et al., 1971a})$$

To estimate Φ a computer program, DEMOGEN, makes the least squares fit to the parameters N_e , the evolutionary size, and m_e , the effective migration rate. Using values of *c* from 4-8 for kinship and 5-8 for inbreeding, we obtained the results of Table 2. The standard errors are large, but the estimates suggest that after an indefinitely large number of generations inbreeding and kinship would amount to several per cent, largely due to multiple chains of remote consanguinity.

PREDICTED KINSHIP WITH MIGRATION DATA

The above conclusion can be tested by examining the consequences of the migration pattern. Data on place of residence and birthplace of

both parents were collected for each sibship. Tabulation showed that the endogamy of Namu atoll is high: both parents are from Namu atoll with a frequency of .89, and from the same islet with a frequency of .53.

Kinship $\phi_{ij}^{(t)}$ between gametes drawn from populations i and j in generation t can be predicted as a function of three factors: a migration matrix P , a vector of population sizes N and a systematic pressure m

Table 2

Estimation of Equilibrium Kinship, Evolutionary Size, and Effective Systematic Pressure from Pedigrees

	Φ	N_e	m_e
Inbreeding	.0252 \pm .0160	198.2 \pm 20.7	.0488 \pm .0368
Kinship	.0468 \pm .0813	113.6 \pm 29.4	.0448 \pm .0930

(Malécot, 1950; Morton, 1969). These are obtained by using the program NUMIX (Harris, 1969) to compute the recurrence:

$$\phi_{ij}^{(t)} = (1 - m)^2 \left\{ \sum_{h,k} p_{ki} p_{hj} \phi_{kh}^{(t-1)} + \sum_{k=1}^n p_{ki} p_{kj} (1 - \phi_{kk}^{(t-1)}) / 2N_k \right\} \quad (3)$$

The migration matrix (Table 4) is constructed using a tabulation of children's residence according to birthplace of father and mother (Morton et al., 1971a). The n_{ij} elements are defined in the following way: for $i, j \leq 4$, i.e. for migration between islets of Namu, n_{ii} is the number of children resident in i and having one parent born in i , with a mating counted twice if both parents were born in i ; n_{ij} ($i \neq j$) is a mean of the corresponding numbers n_{ij}^* and n_{ji}^* . The n_{ij} elements for $j \leq 4$ are obtained as numbers of children in j of parents born in i , and the n_{ji} symmetrical elements have been taken equal to n_{ij} . The systematic pressure, approximated by the long range immigration of Caucasians, is $2/1473 = .0014$ (Table 3). The effective sizes are taken as one third of the census sizes.

No data are available on migration between atolls which send migrants to Namu. The assumption of symmetry of migration leaves the problem of estimating the number of migrants between each pair of atolls (i, j) for $i, j > 4$. To approximate these numbers, we suppose that

Table 3
Immigration into Namu

Population of birth	Namu Namu residents				Majkin residents			
	fathers	mothers	children of fathers	children of mothers	fathers	mothers	children of fathers	children of mothers
Namu Namu	49	42	187	131	11	12	38	51
Majkin	13	12	19	47	53	45	154	153
Mae	4	9	19	57	11	14	47	55
Leuen	4	5	11	9	1	4	1	22
Ailinglapalap	1	1	9	9	4	5	20	13
Ebeye	2	0	6	0	4	0	9	0
Lae	5	1	18	7	1	0	7	0
Ebon	0	0	0	0	0	0	0	0
Majuro	1	1	6	3	0	3	0	4
Arno	0	3	0	13	1	0	4	0
Namorik	1	0	1	0	0	0	0	0
Rongelap	1	0	1	0	0	0	0	0
Wotje	0	0	0	0	0	0	0	0
Jaluit	0	2	0	3	0	0	0	0
Totals			277	279			280	298
Caucasians	2	0	2	0	0	0	0	0

Table 4
Migration Factors for Namu Islets with other Atolls Pooled

	Observed migration				Symmetrical migration				Census size N_0	Effective size $N_0/3$	Asymptotic kinship					
	NN	Mj	Me	L	NN	Mj	Me	L			NN	Mj	Me	L	O	
Namu Namu (NN)	318	89	39	6	318	[77]	[57]	[13]	(76)	210	71	.0439	.0427	.0431	.0442	.0353
Majkin (Mj)	66	307	78	0	[77]	307	[90]	[11]	(57)	230	77	.0427	.0447	.0443	.0447	.0352
Mae (Me)	76	102	153	0	[57]	[90]	153	[10]	(32)	120	40	.0431	.0443	.0455	.0453	.0352
Leuen (L)	20	23	21	8	[13]	[11]	[10]	8	(0)	97	32	.0442	.0447	.0453	.0463	.0352
Outside (O)	76	57	32	0	76	57	32	0	(27582)	13791	4600	.0353	.0352	.0352	.0352	.0355
Total	556	578	323	14	541	542	342	42	27747							

$$m = 2/(1473) = .0014.$$

Extrapolated numbers in parentheses.

Interpolated numbers in brackets.

migration between atolls has a Pareto distribution, so that the expected number of migrants from atoll i to atoll j is given by:

$$n_{ij} = CN_i N_j / d_{ij}^r, \quad i \neq j$$

$$n_{ii} = N_i - \sum_{j \neq i} n_{ij}$$

where N_i and N_j are sample sizes and d_{ij} the distance between i and j . Estimates of c and r can be obtained by least squares: using the data on migration between Namu and other atolls as observed values whose expectations are given by the above formula, we estimate C and r by least squares fit of the linear regression:

$$\ln (n_{ij}/N_i N_j) = \ln(C) - r \ln(d_{ij})$$

As sample sizes of Namu summed over generations are larger than census sizes, it is necessary to take sizes of atolls proportional to their census sizes, the proportionality constant taken as the ratio of the sample size of Namu to the census size.

We have obtained $r = .93$, with a standard error of 1.19, the intercept being -7.43 . Considering the large error in r , we have used two different values of r , $r = 1$ and $r = 2$, and computed C from the relation on expectations:

$$\ln C \Big|_{r=a} = \overline{\ln (n_{ij}/N_i N_j)} - a \overline{\ln (d_{ij})}$$

The horizontal bars indicate means. This gives for C the values .00087 and .238 respectively. The kinship coefficients for these two different migration patterns are very similar; the predictions of random kinship obtained for $r = 1$ are given in Table 8. At the stationary state the random kinship is .035, the mean kinship within populations .040, and the mean kinship within islets .046. Fitting the $\phi_{ij}^{(\infty)}$ to the values predicted by

$$\phi(d) = ae^{-bd}$$

by using the program DISTAN gives in both cases $a = .043$ and $b = .0005$. This small value of b suggests that the Marshalls have differentiated as a group, with little drift among atolls.

Two other migration matrices have been constructed: in one of them, the four islets of Namu atoll are pooled (Table 5); the mean kinship within populations at the stationary state is just slightly lower than in the preceding case; the mean kinship within Namu atoll (.044) is

Table 5
 Migration Matrix Constructed from the Pareto Distribution for $r = 1$

Parent/Child	Na	Ai	Ebe	La	Ebo	Ma	Ar	Na	Ro	Wo	Ja	Census size N_0	Effective size $N_0/3$
Namu atoll	1302	58	15	32	14	20	17	1	1	4	3	657	220
Ailinglapalap		2284	71	2	14	83	18	11	2	7	32	1158	386
Ebeye			8283	14	25	152	36	18	18	22	42	3900	1300
Lae				211	1	4	1	1	0	0	1	120	40
Ebon					1724	41	10	14	1	3	23	838	279
Majuro						9004	354	24	6	26	98	4400	1467
Arno							2124	5	2	6	21	1163	388
Namorik								967	1	2	13	474	158
Rongelap									467	1	2	225	75
Wotje										785	5	386	129
Jaluit											2273	1127	376

also lower than the corresponding values estimated for islets (.046). The other matrix considered deals with the four islets and the pool of all the other atolls. Mean kinship within populations is slightly lower in that case, but random kinship remains unaltered. Thus our conclusions do not critically depend on distinguishing islets within atolls or assuming a Pareto pattern of migration among atolls.

CLAN ANALYSIS

So far we have neglected division of the population into clans, which now must be taken into account. Subjects have been classified according to father's clan and mother's clan if known (Table 6). No subject is found on the diagonal elements, confirming that exogamy is complete. As when dealing with migration data, we have assumed that reciprocal exchanges (i,j and j,i) were equally frequent, in order to keep constant the clan sizes, and a migration matrix has been constructed in the following way: if n_{ij} is the number of sibships having i and j as father's and mother's clans, then we take:

$$p_{ii} = 1/2$$

$$p_{ij} = (n_{ij} + n_{ji})/2 \left(\sum_{i \neq j} (n_{ij} + n_{ji}) \right), i \neq j$$

assuming complete exogamy; if m_i and f_i are respectively the numbers of mothers and fathers in clan i , the effective size of clan i has been taken as:

$$N_i = (m_i + f_i) N_e / (\sum_i m_i + \sum_i f_i)$$

where N_e is the evolutionary size of Namu atoll.

Kinship predictions with this exchange matrix can be made according to a similar recurrence relation as Equation 3, using the program NUMIX. In order to assure good comparability of the results with the predictions obtained from migration, the evolutionary size N_e and effective migration m_e have been estimated simultaneously with the program DEMOGEN, using as input the kinship for Namu atoll predicted from the matrix of Table 5, which gave $N_e = 473$ and $m_e = .01152$. The large effective size reflects migration from other atolls. The effective systematic pressure is dominated by the contribution of short-range migration, rather than the much smaller value for long-range migration. With these values taken as total size of clans and systematic pressure,

Table 6
Clans of Mates

Mother/Father	1	2	3	4	5	6	7	8	9	10	11	12	Others	Blanks	Total
1	0	0	7	1	0	1	0	1	2	1	0	2	1	13	29
2	1	0	3	0	0	2	0	1	1	1	0	1	4	8	22
3	5	4	0	1	2	2	1	3	0	2	0	0	2	15	37
4	0	1	1	0	1	0	2	2	1	1	0	1	0	11	21
5	0	1	4	2	0	2	0	0	1	0	0	0	1	4	15
6	1	2	2	5	0	0	0	5	2	0	0	0	1	11	29
7	0	1	0	1	2	1	0	1	1	0	0	0	0	3	10
8	2	3	3	1	0	8	0	0	0	0	0	0	0	20	37
9	1	1	4	0	0	1	0	0	0	0	0	0	0	9	16
10	1	0	1	0	0	0	0	0	0	0	0	0	0	3	5
11	1	0	1	0	1	0	0	0	0	0	0	0	0	6	9
12	1	0	0	1	0	0	1	0	0	0	0	0	0	9	12
Others	0	0	0	0	2	0	1	2	1	1	0	1	1	3	12
Blanks	8	15	13	9	0	11	1	7	2	3	1	6	3	6	85
Total	21	28	39	21	8	28	6	22	11	9	1	11	13	121	339

Table 7
Exchange Matrix of Clans from Table 6

	1	2	3	4	5	6	7	8	9	10-12	Others	Total	Effective size
1	29	1	12	1	0	2	0	3	3	6	1	58	50
2	1	27	7	1	1	4	1	4	2	2	4	54	46
3	12	7	48	2	6	4	1	6	4	4	2	96	82
4	1	1	2	22	3	5	3	3	1	3	0	44	38
5	0	1	6	3	19	2	2	0	1	1	3	38	33
6	2	4	4	5	2	35	1	13	3	0	1	70	60
7	0	1	1	3	2	1	12	1	1	1	1	24	20
8	3	4	6	3	0	13	1	32	0	0	2	64	55
9	3	2	4	1	1	3	1	0	16	0	1	32	27
10-12	6	2	4	3	1	0	1	0	0	19	2	38	33
Others	1	4	2	0	3	1	1	2	1	2	17	34	29
												552	473

Table 8
Random Kinship Predicted from Migration

Matrix	Marshalls			Namu		
	t = 10	t = 30	t = ∞	t = 10	t = 30	t = ∞
4 islets, 10 other atolls	.0010	.0029	.0354	.0098	.0133	.0453
4 islets, outside pooled	.0010	.0030	.0355	.0090	.0117	.0440
Islets pooled, 10 other atolls	.0010	.0030	.0352	.0087	.0119	.0439
Clans, observed exchanges	—	—	—	.0093	.0222	.0430
Clans, reference population assuming clans of equal size and random exogamy	—	—	—	.0093	.0222	.0430
Namu, clans pooled	—	—	—	.0093	.0223	.0432

Random kinship: $\phi_R = \sum N_i N_j \phi_{ij} / \sum N_i N_j$

we have obtained the results of Table 8. The mean kinship and the random kinship of Namu are very close to the values obtained neglecting clans, which increase only slightly the mean kinship and decrease also slightly the random kinship, as seen when these values are compared to the kinship expected of a random mating population of same effective size and submitted to the same systematic pressure.

To test the possible effect of non-random exogamy and different sizes of the clans, we have compared these results to the values expected of a population with n_c effective clans of equal sizes under random exogamy. If q_i is the frequency of the i^{th} clan, $1/\sum q_i^2$ is an estimate of the 'effective number of clans', found here to be $n_c = 9$. Assuming equal size and random exogamy, a comparable population of effective size 473 as precedingly has the exchange matrix composed of the elements:

$$m_{ii} = 1/2$$

$$m_{ij} = 1/2 (n_c - 1), i \neq j$$

(Morton et al. 1971b)

and the predicted kinship in that case is given in Table 8. Deviations from this ideal model are insignificant. This result is in agreement with the conclusion of Morton et al. (1971b) that intermarrying clans represent negligible genetic barriers.

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