

# LINKAGE-1 : a PASCAL computer program for the detection and analysis of genetic linkage

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**ABSTRACT:** LINKAGE-1 is a PASCAL computer program designed to aid the geneticist in the detection and estimation of linkage in segregating progenies. Loci segregating for both dominant and codominant genes can be simultaneously analyzed. Goodness-of-fit to expected ratios for single-factor segregations are tested by chi-square analyses. Contingency chi-square analyses are used to test for independent assortment between all pairs of jointly segregating loci. If significant deviation is detected, recombination percentages and their standard errors are calculated. The program and instructions for its use are available from the authors.

**IN GENE SEGREGATION** studies the estimation of recombination intensities between linked loci is most accurately provided by the method of maximum likelihood as discussed by Allard<sup>1</sup> and Mather<sup>3</sup>. In progenies where numerous loci are simultaneously segregating, the number of locus pairs to be sorted and tested for linkage can be quite large. The required data manipulations resulting from such progenies are tedious and time consuming.

In order to facilitate segregation and linkage analyses, we have developed LINKAGE-1, a computer program that performs many of the steps routinely employed in the detection of linkage and the calculation of its intensity.

### Description of Program

LINKAGE-1 is capable of analyzing in a single run an unlimited number of progenies generated from a variety of genetic situations. These families can represent F<sub>2</sub> and backcross types as well as all other combinations of the allowable single-factor segregation ratios (e.g., where one locus is in testcross mode and the other has a 1:2:1 expected ratio). The program accepts both dominant (3:1 and 1:1 expected ratios) and codominant (1:1, 1:2:1, and 1:1:1:1 expected ratios) genes as segregating loci. Input for each family consists of single-individual genotype data for each segregating locus.

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### Single-factor segregation

Goodness-of-fit to expected segregation ratios at each locus are tested by chi-square analyses. The output for each locus consists of the observed segregation, and the chi-square and associated *P* value for deviation from expected frequencies (Figure 1).

### Two-factor segregation

Contingency chi-square tests are employed to analyze for independent assortment between jointly segregating loci. If significance is detected (significance threshold: *P* = 0.10), the recombination fraction (*r*) and its standard error (SE) are calculated using maximum likelihood for-

Locus	Offspring Genotype	Exp. Ratio	Chi-square	Df	P
PGM3	BB:13 BC:17 CC:10	1:2:1	1.35000E+00	2	0.75-0.50
Locus	Offspring Genotype	Exp. Ratio	Chi-square	Df	P
PGM2	AB:17 BB:23	1:1	9.00000E-01	1	0.50-0.25
Locus	Offspring Genotype	Exp. Ratio	Chi-square	Df	P
DOM1	A-:29 aa:11	3:1	1.33333E-01	1	0.75-0.50
Locus	Offspring Genotype	Exp. Ratio	Chi-square	Df	P
PG11	AA:20 AB:20	1:1	0.00000E+00	1	>0.95

FIGURE 1 Sample output for single-locus goodness-of-fit tests.

**A** Total number of individuals compared = 40 out of 40  
The two loci being compared are PGM3 and DOM1

PGM3		DOM1		
	BB	BC	CC	
A-	2	17	10	
aa	11	0	0	
Chi-square	Df	P	r +/- SE	
3.15119E+01	2	<0.01	5.0000E-02 +/- 3.5811E-02	

**B** Total number of individuals compared = 40 out of 40  
The two loci being compared are PGM3 and PG11

PGM3		PG11		
	BB	BC	CC	
AA	12	8	0	
AB	1	9	10	
Chi-square	Df	P	r +/- SE	
1.93665E+01	2	<0.01	4.0000E-02 +/- 4.3818E-02	

**C** Total number of individuals compared = 40 out of 40  
The two loci being compared are PGM2 and PG11

PGM2		PG11		
	AB	BB		
AA	10	10		
AB	7	13		
Chi-square	Df	P	r +/- SE	
9.20716E-01	1	0.50-0.25	none	

This value is not significant

FIGURE 2 Sample output for two-factor linkage analysis. Three different family types (A, B, C) are shown. The expected ratios for each gene are the same as in Figure 1.

mulae<sup>1,3</sup>. For some family types (i.e., those where at least one gene has an expected segregation ratio of 1:1:1:1) linkage intensities may not be calculated, particularly if the progeny size is small or the linkage is weak. In these cases, the possibility of multiple parental linkage arrangements precludes the estimation of linkage without prior knowledge of correct phase. For each pair-wise comparison, the two-locus genotype table, chi-square value and *P* value, and the recombination fraction and its standard error (if calculated) are printed (Figure 2).

LINKAGE-1 is written in the Waterloo version of the PASCAL language (Jensen and Wirth<sup>2</sup>) and is compatible with the PASCALW compiler. It is currently operating on the 3081 IBM computer at the Triangle Universities Computation Center. The program is presently dimensioned for a maximum of 15 loci and 300 individuals per progeny and, as such, requires approximately 400K bytes of core memory. The program is easily redimensioned to suit the requirements of the user.

The program listing and instructions for its use

and implementation can be obtained from the authors.

### References

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The Journal of Heredity 74:204-206. 1983.

## Desired family size and sex of children in Nigeria

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for both sexes and for more males may influence family size in the same population<sup>5</sup>. Several studies<sup>1,6,8,16</sup> have failed to detect any influence of sexual composition of children on family size.

The Nigerian population was selected for ex-

tension of the human sex ratio and family characteristics studies because of its magnitude (variously estimated at 77 to 107 million) and its growth rate (estimated at 3.2-3.7 percent annually)<sup>2,3,13</sup>. Also, approximately 47.4 percent of the population is 14 years of age or younger.

**ABSTRACT:** During 1981, sex ratio data and preferences for family size and for combinations and permutations of children were provided by 333 Nigerian students at the University of Ilorin, Ilorin, Nigeria. For the present and parental generations combined, the secondary sex ratio was estimated to be 95.8 males:100 females. In the projected families, preferences for family sizes resulted in an average of 4.88 children per family. The most preferred family consisted of four children—a 2m2f combination in a mfmf order, whereas the second most preferred family consisted of five children—a 3m2f combination in a mfmfm order. Also expressed was a strong preference for permutations of sexes, resulting in a male child as first-born followed by an alternation of sexes. A greater preference for male children was indicated by the combined sex ratio of 167 males:100 females for the preferred families.

**MOTIVATION** for smaller families is prerequisite to stabilization of world population. Family size is the critical variable in population growth. Reductions in average family size have been responsible for slower growth rates of human populations in technologically developed countries. Further reductions in family sizes will be needed to ease mounting pressures on global resources.

Of the several factors that influence family size, some are biological, including sexual composition of the children. In some populations<sup>4,5,10,15</sup>, parents are less likely to have additional children after both sexes are represented. In other populations<sup>11</sup>, parents are less likely to have additional children when existing children include a high proportion of males. Preferences

Table I. Desired family size, combination, and permutation of sexes of children

No. children	Combination of sexes	Respondents' preferences %	Permutation of sexes	Respondents' preferences %
0		0.0		
1	1m	0.6		
	1f	0.0		
	Total	0.6		
2	2m	0.0		
	1m 1f	2.4	mf	1.8
			fm	0.6
	2f	0.6		
	Total	3.0		
3	3m	0.0		
	2m 1f	6.7	mmf	1.8
			mfm	4.3
			fmm	0.6
	1m 2f	0.6	mff	0.6
			fmf	0.0
			ffm	0.0
Total	7.3			
4	4m	2.5		
	3m 1f	10.4	mmm	3.7
			mmfm	4.3
			mfmm	1.2
			fmmm	1.2
	2m 2f	21.5	mmff	2.5
			ffmm	0.0
			mffm	1.2
			fmmf	1.8
			mfmf	11.7
		fmfm	4.3	
1m 3f		0.0	mfff	0.0
			fmff	0.0
			ffmf	0.0
			fffm	0.0
			ffff	0.0
4f	0.0			
Total	34.4			

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