HETEROZYGOSITY IN PIN-THRUM PLANTS OR WITH PARTIAL SEX LINKAGE

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ABSTRACT

A two locus model is constructed for selection of a gene closely linked to the S locus in pin-thrum plants or to the sex determining part of the Y chromosome. Using this model, conditions for stability at the equilibrium point which is predicted by one-locus theory when there is heterozygotic superiority are derived. If the recombination value is small, it is found that this equilibrium point is unstable and that the gene frequencies go to a new stable equilibrium point at which the population has a higher average fitness. A few simple cases of selection and the implication of these to the theory of the evolution of the Y chromosome are discussed.

HETEROSTYLY was recognized by DARWIN (1877) as a mechanism to enforce outcrossing in plants. Since then the genetics and physiology of this mechanism have been elucidated. For recent reviews of this work see VULLEU-MIER (1967) or LEWIS (1954).

Heterostyly has been shown to be controlled by two alleles designated by s and S. Pin plants (ss) have long styles and short stamens while thrum plants (sS) have short styles and long stamens. This dimorphism is accompanied by pollen incompatibility causing the pollen of one form to be fertile on the other form, but almost completely infertile on plants of the same form. Therefore, this type of genetic system indeed dictates that outcrossing shall occur.

The effect that close linkage to the S locus has on the equilibrium properties of an adjacent heterotic locus is discussed in this paper. It is shown that if the recombination value is sufficiently small then the equilibrium point, which is determined by the fitness values at the heterotic locus and the assumption of no linkage disequilibrium, becomes unstable. This results in the population moving to a new equilibrium at which the average fitness of the population is greater.

The S gene is essentially a sex gene with pins as females and thrums as males. Thus, the results presented here apply to those plants and animals which have a Y chromosome with a sex determining part, in which no crossing-over occurs, and a part homologous to the X chromosome, in which crossing-over is allowed.

THEORY

The model presented here is the deterministic theory with discrete generations.

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TABLE 1

Frequency of gametes produced

Genotype	Frequency	Gametes produced			
		A s	a s	A S	a S
PINS					
A A s s	px	px			
A a s s	p(1—x) + x(1—p)	½p(1—x) + ½x(1—p)	½p(1—x) + ½x(1—p)		
a a s s	(1—p)(1—x)		(1—p)(1—x)		
THRUMS					
A A S s	py	½py		½py	
A S / a s	y(1—p)	½ry(1—p)	½(1—r)y(1—p)	½(1—r)y(1—p)	½ry(1—p)
a S / A s	p(1—y)	½(1—r)p(1—y)	½rp(1—y)	½rp(1—y)	½(1—r)p(1—y)
a a S s	(1—p)(1—y)		½(1—p)(1—y)		½(1—p)(1—y)

It will be assumed throughout this paper that one form only mates with the other form, that is pin × pin and thrum × thrum matings are illegitimate. For a discussion of the selections process when pin × pin matings are allowed, see BODMER (1960) or CROSBY (1949). Two loci are considered each with two alleles, the S locus, which controls heterostyly or sex, and the A locus, on which selection occurs. The selection values on the genotypes $A\,A\,\_\,\_$, $A\,a\,\_\,\_$, and $a\,a\,\_\,\_$ are W_1, 1, and W_2, respectively. The recombination value between the two loci will be denoted by r.

Let p be the frequency of the As gametes in pins (females). In the thrums (males), let x be the conditional frequency of the As gametes given $\_s$, i.e., $\dfrac{f_{As}}{f_{As} + f_{as}}$; and y, the conditional frequency of the AS gametes given $\_S$, i.e. $\dfrac{f_{AS}}{f_{AS} + f_{aS}}$. Using the selection values given above and the frequency of gametes produced from Table 1, the recurrence relationships for p, x, and y in the next generation are found to be

$$p' = \frac{apx + \frac{1}{2}p + \frac{1}{2}x}{1 + apx + b(1-p)(1-x)} \tag{1}$$

$$x' = \frac{apy + p - r(p-y)}{1 + apy + b(1-p)(1-y)} \tag{2}$$

$$y' = \frac{apy + y + r(p-y)}{1 + apy + b(1-p)(1-y)} \tag{3}$$

where $a = W_1 - 1$ and $b = W_2 - 1$.

From these equations the equations for Δp, Δx, and Δy, are derived and are

$$\Delta p = p' - p = \frac{y(1-y)[ap - b(1-p)] + r(p-y)}{1 + apx + b(1-p)(1-x)} \tag{4}$$

$$\Delta x = x - x' = \frac{apy(1-x) - b(1-p)(1-y)x + p - x - r(p-y)}{1 + apy + b(1-p)(1-y)} \tag{5}$$

$$\Delta y = y' - y = \frac{p(1-p)[ax - b(1-x)] + .5(x-p)}{1 + apy + b(1-p)(1-y)} \tag{6}$$

The equilibrium values must satisfy the equations obtained by setting $\Delta p = \Delta x = \Delta y = 0$ in equations (4), (5), and (6). After multiplication by the denominators, the equations that the equilibrium values must satisfy are

$$0 = p(1-p)[ax - b(1-x)] + .5(x-p) \tag{7}$$
$$0 = apy(1-x) - b(1-p)(1-y)x + p - x - r(p-y) \tag{8}$$
$$0 = y(1-y)[ap - b(1-p)] + r(p-y) \tag{9}$$

It can be seen by substitution that the point $(\hat{p}, \hat{x}, \hat{y}) = \left(\dfrac{b}{a+b}, \dfrac{b}{a+b}, \dfrac{b}{a+b}\right)$ satisfies equations (7), (8) and (9) and therefore it must be an equilibrium

point. This point is the equilibrium point that would be obtained in one-locus theory using the selection values W_1, 1, W_2 for the genotypes $A\,A$, $A\,a$, and $a\,a$, respectively.

The stability of this equilibrium point may be studied by considering an expansion about this point and then making the equations linear by neglecting quadratic or higher order terms. Toward this end, let $p = \hat{p} + \varepsilon_1$, $x = \hat{x} + \varepsilon_2$, and $y = \hat{y} + \varepsilon_3$. Substituting these values for p, x, and y in equations (1), (2), and (3); rearranging the resulting equations; and neglecting quadratic and higher order terms in ε_1, ε_2, and ε_3; the following recurrence relationships for ε_1, ε_2, and ε_3 are obtained.

$$\varepsilon_{1'} = \frac{\left(\dfrac{a\,b}{a+b} + \tfrac{1}{2}\right)\varepsilon_1 + \left(\dfrac{a\,b}{a+b} + \tfrac{1}{2}\right)\varepsilon_2}{1 + \left(\dfrac{a\,b}{a+b}\right)} \tag{10}$$

$$\varepsilon_{2'} = \frac{\left(\dfrac{a\,b}{a+b} + 1 - r\right)\varepsilon_1 + \left(\dfrac{a\,b}{a+b} + r\right)\varepsilon_3}{1 + \left(\dfrac{a\,b}{a+b}\right)} \tag{11}$$

$$\varepsilon_{3'} = \frac{\left(\dfrac{a\,b}{a+b} + r\right)\varepsilon_1 + \left(\dfrac{a\,b}{a+b} + 1 - r\right)\varepsilon_3}{1 + \left(\dfrac{a\,b}{a+b}\right)} \tag{12}$$

These can be written in the matrix form

$$\begin{bmatrix} \varepsilon_{1'} \\ \varepsilon_{2'} \\ \varepsilon_{3'} \end{bmatrix} = \frac{\begin{bmatrix} c + \tfrac{1}{2} & c + \tfrac{1}{2} & 0 \\ c + 1 - r & 0 & c + r \\ c + r & 0 & c + 1 - r \end{bmatrix}}{1 + c} \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \end{bmatrix}$$

where $c = \dfrac{a\,b}{a+b}$.

The system of equations (1), (2), and (3) will be stable at the equilibrium point $(\hat{p}, \hat{x}, \hat{y})$ if and only if the eigenvalues of the above matrix, $\dfrac{A}{1+c}$, are all less than one in absolute value.

The eigenvalues of $\dfrac{A}{1+c}$ are found to be

$$\lambda_1 = \frac{1 + 2c}{1 + c}$$

$$\lambda_2 = \frac{1 - 2r + \sqrt{(1 - 2r)^2 + 8(1 - 2r)(1 + 2c)}}{4(1 + c)}$$

$$\lambda_3 = \frac{1 - 2r - \sqrt{(1 - 2r)^2 + 8(1 - 2r)(1 + 2c)}}{4(1 + c)}$$

If W_1 and W_2 are greater than one, then c is greater than zero. This implies λ_1 is greater than one and therefore the equilibrium point with heterozygotic inferiority remains unstable regardless of any degree of linkage to the S locus.

If W_1 and W_2 are less than one, the only values allowing a stable heterozygosity to exist in the one locus model, then

$$-1 \leq a, b < 0$$

and

$$-\tfrac{1}{2} \leq c < 0.$$

The inequality on c shows that λ_1 is restricted between zero and one. Since $r \leq .5$, it is seen that λ_2 is positive and if λ_2 is positive and if λ_2 is less than one, then λ_3 is less than one in absolute value. Therefore $(\hat{p}, \hat{x}, \hat{y})$ will be stable if and only if

$$\lambda_2 = \frac{1 - 2r + \sqrt{(1 - 2r)^2 + 8(1 - 2r)(1 + 2c)}}{4(1 + c)} < 1 . \tag{13}$$

Upon rearranging equation (13), it becomes

$$r > \frac{-c(1 + 2c)}{2(2 + 3c)} = f(c) \tag{14}$$

Insight into the process of selection on a gene which is closely linked to the S locus can be gained by using equation (14) to investigate a few simple cases.

CASE 1: The maximum value of r at which the point $(\hat{p}, \hat{x}, \hat{y})$ is not stable:

Taking the derivative of $f(c)$ with respect to c and setting it equal to zero, equation (15) is obtained.

$$0 = \frac{d f(c)}{d c} = \frac{-(1 + 4c)(4 + 6c) + (c + 2c^2)6}{4(2 + 3c)^2} = \frac{-(3c + 1)(c + 1)}{(2 + 3c)^2}$$

The solutions to this equation are $c = -1$ and $c = \frac{-1}{3}$. Since c must lie between 0 and $-\tfrac{1}{2}$, the solution of interest is $c = -\frac{1}{3}$. At this value $f(c) = \frac{1}{18}$, and therefore the maximum value of r that is allowed for the point $(\hat{p}, \hat{x}, \hat{y})$ to be unstable is $r = .0555$.

CASE 2: Recessive lethal selection model:

Let the selection values W_1 and W_2 have the values $1 - s$ and 0, respectively. The value of c is therefore $c = -\frac{s}{1 + s}$ and equation (14) becomes

$$r > \frac{s(1 - s)}{2(1 + s)(2 - s)}$$

The regions of stability and instability on the r-s plane are shown in Figure 1a.

CASE 3: Symmetric selection model:

Let the selection values W_1 and W_2 have the values $W_1 = W_2 = 1 - s$. Then
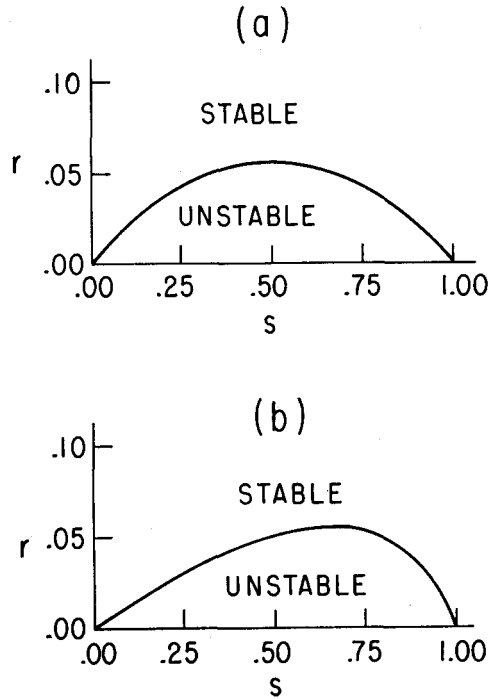
FIGURE 1.—Stability of $(\hat{p}, \hat{x}, \hat{y})$ for (a) recessive lethal selection and (b) symmetric selection.

$(\hat{p}, \hat{x}, \hat{y}) = (.5, .5, .5)$ and c has the value $c = -\frac{1}{2}s$. Substituting this value of c into equation (14), one obtains

$$r > \frac{s(1-s)}{2(4-3s)}$$

The regions of stability and instability for this selection model on the r-s plane are shown in Figure 1b.

Thus far only the stability properties of the point $(\hat{p}, \hat{x}, \hat{y})$ have been examined and nothing has been said about what happens if this point is unstable. The complete solution of the system of simultaneous equations (7), (8) and (9) for all the equilibrium values is in the realm of possibility. By solving equation (9) for p and (8) for x in terms only involving y, then substituting these values into equation (7); a seventh degree equation in y is obtained. Since three of the roots are known; $y = 0$, $y = 1$, and $y = \dfrac{b}{a+b}$, it can be factored. This results in a fourth degree equation, which is solvable. However, the solution of a fourth degree equation is a complicated process and results in roots which have no neat form.

Therefore, the procedure outlined above was not used to obtain the other equilibrium points. Instead, the selection process defined by equations (1), (2), and (3), with initial gene frequencies slightly off the equilibrium point $(\hat{p}, \hat{x}, \hat{y})$, was reiterated until an equilibrium was attained. The set of equilibrium values

TABLE 2

Equilibrium values when $(\hat{p}, \hat{x}, \hat{y})$ is unstable for the symmetric selection model

s	p	x	y	$\overline{WF}$	$\overline{WM}$	$\overline{W}$
			$r = .00$			
.1	.263	.243	1.00	.9378	.9737	.9558
.2	.278	.235	1.00	.8765	.9444	.9105
.3	.294	.226	1.00	.8161	.9118	.8639
.4	.313	.214	1.00	.7571	.8750	.8161
.5	.333	.200	1.00	.7000	.8333	.7667
.6	.357	.182	1.00	.6455	.7857	.7156
.7	.385	.158	1.00	.5947	.7308	.6628
.8	.417	.125	1.00	.5500	.6667	.6083
.9	.455	.077	1.00	.5154	.5909	.5531
			$r = .01$			
.1	.420	.412	.733	.9486	.9537	.9512
.2	.350	.317	.898	.8891	.9238	.9064
.3	.340	.282	.938	.8291	.8915	.8603
.4	.345	.257	.949	.7699	.8556	.8128
.5	.357	.236	.956	.7124	.8151	.7637
.6	.375	.215	.959	.6573	.7688	.7130
.7	.398	.191	.959	.6060	.7153	.6607
.8	.427	.164	.953	.5607	.6529	.6068
.9	.462	.141	.926	.5256	.5790	.5523
			$r = .02$			
.1	—	—	—	—	—	—
.2	.431	.414	.714	.8976	.9059	.9018
.3	.386	.341	.841	.8392	.8733	.8562
.4	.377	.303	.883	.7807	.8376	.8092
.5	.381	.275	.903	.7233	.7978	.7606
.6	.394	.251	.911	.6682	.7525	.7103
.7	.413	.228	.911	.6166	.7003	.6585
.8	.438	.208	.897	.5710	.6394	.6052
.9	.471	.221	.832	.5356	.5671	.5514
			$r = .03$			
.1	—	—	—	—	—	—
.2	—	—	—	—	—	—
.3	.444	.420	.686	.8473	.8563	.8518
.4	.412	.357	.795	.7899	.8207	.8053
.5	.407	.320	.835	.7332	.7813	.7572
.6	.413	.292	.852	.6783	.7368	.7075
.7	.428	.270	.852	.6267	.6857	.6562
.8	.450	.261	.828	.5810	.6261	.6035
.9	.484	.343	.689	.5455	.5554	.5504

thus obtained for the symmetric selection model with different values of r and s is shown in Table 2 and for the recessive lethal model, in Table 3. Also included in these tables are the average fitness values for pins (females) $\overline{WF}$, for thrums (males $\overline{WM}$), and for the population $\overline{W} = \frac{1}{2} \overline{WF} + \frac{1}{2} \overline{WM}$.

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TABLE 3

Equilibrium values when ($\hat{p}$ $\hat{x}$, $\hat{y}$) is unstable for the recessive lethal selection model

s	p	x	γ	$\overline{WF}$	$\overline{WM}$	$\overline{W}$
			$r = .00$			
	1.000	1.000	.000	.9000	1.0000	.9500
.1	.872	.859	1.000	.9070	.9128	.9099
	1.000	1.000	.000	.8000	1.0000	.9000
.2	.776	.735	1.000	.8265	.8448	.8357
	1.000	1.000	.000	.7000	1.0000	.8500
.3	.703	.623	1.000	.7565	.7893	.7729
	1.000	1.000	.000	.6000	1.0000	.8000
.4	.645	.522	1.000	.6957	.7414	.7188
	1.000	1.000	.000	.5000	1.0000	.7500
.5	.600	.429	1.000	.6429	.7000	.6714
	.833	1.000	.000	.5000	.8333	.6667
.6	.565	.342	1.000	.5976	.6613	.6294
	.714	1.000	.000	.5000	.7143	.6071
.7	.537	.258	1.000	.5596	.6240	.5918
	.625	1.000	.000	.5000	.6250	.5625
.8	.517	.177	1.000	.5294	.5862	.5578
	.556	1.000	.000	.5000	.5556	.5278
.9	.505	.092	1.000	.5084	.5459	.5271
			$r = .01$			
	.987	.990	.115	.9022	.9775	.9398
.1	.888	.882	.966	.9085	.9104	.9094
	.983	.990	.055	.8052	.9736	.8894
.2	.789	.760	.966	.8295	.8403	.8349
	.976	.989	.036	.7101	.9662	.8381
.3	.714	.651	.964	.7607	.7833	.7720
	.958	.989	.028	.6206	.9485	.7845
.4	.655	.553	.962	.7008	.7348	.7178
	.904	.988	.025	.5526	.8947	.7237
.5	.609	.463	.958	.6489	.6921	.6705
	.799	.983	.029	.5253	.7912	.6582
.6	.572	.381	.953	.6044	.6527	.6286
	.697	.974	.037	.5168	.6903	.6035
.7	.544	.307	.944	.5672	.6148	.5910
	.614	.955	.056	.5132	.6085	.5608
.8	.524	.244	.924	.5377	.5767	.5572
	.548	.893	.119	.5113	.5430	.5271
.9	.511	.221	.861	.5174	.5361	.5267

TABLE 3—(Continued)

s	p	x	γ	$\overline{WF}$	$\overline{WM}$	$\overline{W}$
			$r = .02$			
	.974	.978	.270	.9042	.9548	.9295
.1	.906	.905	.919	.9091	.9091	.9091
	.967	.978	.120	.8102	.9475	.8789
.2	.804	.786	.926	.8317	.8366	.8341
	.953	.977	.079	.7195	.9342	.8268
.3	.726	.680	.924	.7642	.7779	.7711
	.925	.976	.062	.6371	.9066	.7719
.4	.665	.585	.919	.7054	.7283	.7169
	.865	.972	.058	.5761	.8475	.7118
.5	.618	.500	.912	.6545	.6846	.6695
	.773	.962	.064	.5455	.7573	.6514
.6	.581	.424	.900	.6108	.6445	.6276
	.681	.942	.083	.5326	.6676	.6001
.7	.552	.361	.879	.5743	.6061	.5902
	.603	.898	.128	.5264	.5920	.5592
.8	.532	.323	.833	.5455	.5676	.5565
	.536	.697	.337	.5233	.5297	.5265
.9	.522	.438	.624	.5255	.5272	.5264
			$r = .03$			
	—	—	—	—	—	—
.1	—	—	—	—	—	—
	.950	.965	.202	.8150	.9214	.8682
.2	.820	.813	.877	.8330	.8340	.8335
	.931	.963	.131	.7284	.9033	.8159
.3	.740	.710	.878	.7669	.7734	.7702
	.896	.960	.104	.6517	.8696	.7606
.4	.677	.619	.871	.7093	.7224	.7159
	.834	.953	.098	.5950	.8092	.7021
.5	.629	.539	.859	.6594	.6777	.6685
	.749	.936	.109	.5634	.7273	.6453
.6	.590	.472	.839	.6165	.6369	.6267
	.664	.902	.142	.5478	.6457	.5968
.7	.561	.424	.802	.5807	.5980	.5894
	.589	.816	.232	.5399	.5750	.5575
.8	.542	.428	.710	.5524	.5593	.5559
	—	—	—	—	—	—
.9	—	—	—	—	—	—

For each value of r and s there are two equilibrium points. Only one of these equilibrium points is given for the symmetric selection model, the other being $(\bar{p}, \bar{x}, \bar{y})$, where $\bar{p} = 1 - p$, $\bar{x} = 1 - x$, and $\bar{y} = 1 - y$, which has the same values for $\overline{WF}$, $\overline{WM}$, and $\overline{W}$. Both equilibrium points are given for the recessive lethal model.

There are two inferences that can be drawn from the data given in Tables 2 and 3. For a given value of s, the average fitness of the population is seen to increase as r decreases. These differences in the average fitness of the population could result in the selection for reduced recombination between the A locus and the S locus. Secondly, the average fitness of pins (females) is always less than the average fitness in thrums (males). If the fitness values are relative viabilities, this would result in a ratio of pins to thrums less than one. This second inference was noted by HALDANE and MOSCHINSKY (1939) when discussing partial sex linkage in human inbreeding populations.

There is one other inference that can be drawn in the case of the recessive lethal model, Table 3. It will be noticed that if a, the recessive allele, is coupled to the S allele, a greater difference between $\overline{WM}$ and $\overline{WF}$ and a higher average fitness $\overline{W}$ results compared to having A coupled to S.

If the point $(\hat{p}, \hat{x}, \hat{y})$ is stable this does not rule out the possibility that there are other equilibrium points which are also stable. An example of this using the recessive lethal selection model is given in Table 4. The possibility of other stable equilibrium points existing does not seem to extend greatly the range of r over which an effect due to linkage to the S locus is observed. For in the example presented in Table 4, $(\hat{p}, \hat{x}, \hat{y})$ becomes the only stable equilibrium value at an r value equal to $r = .07$.

CASE 4: Complete linkage to the S locus:

Since $-\frac{1}{2} < c < 0$ if $0 < W_1, W_2 < 1$, the right hand side of equation (14) is always greater than zero. Therefore with $r = 0$, equation (14) is never satisfied and the point $(\hat{p}, \hat{x}, \hat{y})$ is always unstable.

Substituting $r = 0$ into equations (7), (8), and (9), one obtains

$$\Delta p = 0 = p(1 - p)\,[ax - b(1 - x)] + .5(x - p) \tag{15}$$
$$\Delta x = 0 = apy(1 - x) - b(1 - p)(1 - y)x + p - x \tag{16}$$
$$\Delta y = 0 = y(1 - y)\,[ap - b(1 - p)] \tag{17}$$

From equation (17) it can be seen that $\Delta y = 0$ if and only if $y = 0$, $y = 1$, or

TABLE 4

Stable equilibria ($W_1 = .5$, $W_2 = 0$ and $r = .06$)

p	x	y	$\overline{WF}$	$\overline{WM}$	$\overline{W}$
.667	.667	.667	.6667	.6667	.6667
.745	.849	.319	.6453	.7075	.6764

$p = \dfrac{b}{a+b}$. It can also be shown using equations (15) and (16) that if $p = \dfrac{b}{a+b}$ and $\Delta p = \Delta x = \Delta y = 0$, then x and y must also be equal to $\dfrac{b}{a+b}$.

However, the point $(\hat{p}, \hat{x}, \hat{y}) = \left(\dfrac{b}{a+b}, \dfrac{b}{a+b} \ \dfrac{b}{a+b} \right)$ has been shown above always to be unstable when $r = 0$. Therefore, the only stable equilibrium values that are allowed if $r = 0$ must have $y = 0$ or $y = 1$.

This transforms the model presented here into the normal model of sex linked selection. The selection values of $A\,A$, $A\,a$, and $a\,a$ in the females become equal to W_1, 1, and W_2, respectively. The selection values in the male for the genotypes A and a become W_1 and 1 if $y = 1$ or 1 and W_2 if $y = 0$. The equilibrium values under sex linked selection can be found in WRIGHT (1970) and are not given here.

DISCUSSION

DARLINGTON (1958) considers the evolution of the Y chromosome to have three phases: (1) the mutation of the sex gene or gene complex, (2) the reduction of recombination between the sex gene and other genes in the heterogametic sex, and (3) the erosion of the genes on the thus formed chromosome. The theory presented here has bearing on the second phase of this evolution.

It has been shown, by the data in Table 2, and Table 3, that a decrease in r increases the average fitness of the population. Since the pins (females) are homozygous for $s\,s$, the value of r does not enter directly into the equations for p' or Δp. Therefore in the equations given in this paper, r only refers to the recombination value in the thrums (males). The increase in average fitness due to a reduction of r could result in the selection for low recombination in a similar manner as NEI (1969 and 1967) has shown selection for reduced recombination in the normal two locus models.

If the recombination was reduced so that no crossing-over with the X chromosome occurs, then by case four, all the genes on the Y chromosome must be fixed. This could be the preliminary step of phase three.

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