GENETIC ALGEBRAS SATISFYING BERNSTEIN'S STATIONARITY PRINCIPLE

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1. *Introduction*

There are several motivating influences behind this paper. Most of the breeding structures studied by algebraists have led to genetic algebras of Schafer's type [**11**]. It seems a worthwhile next step to seek those systems where although the algebra is not necessarily of Schafer's type it contains an important subalgebra which is, or an ideal with respect to which the difference algebra is of Schafer's type. An example of the former possibility arises in sex linkage [**9**].

It will be recalled that genetic algebras are commutative but not associative (see [**4**] for an introductory account) and that among the types of powers of an element x, particular importance attaches to the principal powers x^n and the plenary powers $x^{[n]}$, defined by

$$x^n = x^{n-1}x, \quad x^{[n]} = x^{[n-1]}x^{[n-1]}, \quad x^1 = x^{[1]} = x.$$

If x represents the distribution of genetic types in a first generation, then x^n and $x^{[n]}$ represent the distribution in the n-th generations formed by repeated backcrossing to the original, and by repeated panmictic breeding, respectively. The class of train algebras defined by Etherington [**4**; §4] is specified by a condition on the sequence of principal powers, and the genetic algebras of Schafer are defined by a condition on the associative algebra generated by the multiplication matrices R_x. It would seem more natural to a population geneticist to define classes of algebras in terms of conditions on the sequence of plenary powers.

The opportunity to pursue simultaneously both directions indicated above is presented by a recent revival of interest of some work of Bernstein [**1, 2, 3**] published half a century ago. The classical Hardy–Weinberg law [**7**] for single locus, autosomal, non-selective populations not only specifies the genotype proportions which are stationary under panmictic breeding, but asserts that whatever the proportions may be initially, the stationary distribution is attained after only a single generation of mating. Bernstein sought to determine and classify all quadratic transformations which could represent non-selective systems of inheritance in which a stationary distribution was attained in a single generation. He gave a complete description of the possibilities in three dimensions [**1, 3**] and found some special results in four and more dimensions [**2**]. The problem was taken up by Lyubich [**10**] who obtained a canonical form for evolutionary laws satisfying the " principle of stationarity ", and then investigated the consequences of imposing a further condition, namely that the system should have elementary gene structure.

In this paper I use genetic algebras to study Bernstein's conditions. (Although Lyubich uses these methods in a later part of [**10**] he does not do so in his development of Bernstein's work.) The general theory is developed in §2. In §3, which is not

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essential for §4, Bernstein's own classification of his results is algebraicized, and in the following section an alternative classification based on the results of §2 is introduced.

2. *General properties of Bernstein algebras*

Bernstein studied a quadratic evolutionary operator V, mapping the set of n-dimensional vectors $x = (x_1, \ldots, x_n)$ where $x_i > 0$, $\sum x_i = 1$, into itself, and satisfying his stationarity condition $xV^2 = xV$. If V is extended naturally to all n-dimensional vectors of positive numbers with $\sum x_i = \beta(x)$, then the stationarity condition becomes

$$xV^2 = \beta^2(x)\, xV, \tag{1}$$

while the quadratic nature of the transformation implies

$$\beta(xV) = \beta^2(x). \tag{2}$$

A product of two such vectors can be defined by setting

$$xy = \tfrac{1}{2}\{(x+y)\, V - xV - yV\}, \tag{3}$$

and it can be extended by bilinearity to all vectors x, y of complex numbers. A simple computation using (1) and (3) shows that $\beta(xy) = \beta(x)\, \beta(y)$. Thus $x \to \beta(x)$ is a homomorphism of the algebra defined by (3) into its base field, which characterises it as a baric algebra [**4**; §3]. In the terminology of §1, the operator V maps an element into its square.

Definition 1. A commutative algebra $\mathfrak{B}$ over the complex numbers will be called a *Bernstein algebra* if (i) it is a baric algebra and (ii) if every element x whose baric value $\beta(x)$ is non-zero satisfies the plenary train equation $x^{[3]} - \beta^2(x)\, x^{[2]} = 0$.

Such an algebra must have at least one idempotent, the square of any element of unit baric value. Let e be an idempotent chosen once and for all, and $\mathfrak{E}$ the subalgebra of its scalar multiples. Let $\mathfrak{Z}$ denote the nil ideal of $\mathfrak{B}$, containing all the elements with baric value zero. In general, a lower case letter, possibly with a subscript, will denote an element belonging to a subspace or subalgebra denoted by the corresponding capital. Thus $z \in \mathfrak{Z}$, and by the definition it satisfies

$$(e+\theta z)^{[3]} - (e+\theta z)^{[2]} = 0. \tag{4}$$

If coefficients of powers of θ are equated to zero, the following identities are obtained:

$$z^{[3]} = 0, \tag{5}$$

$$z^2(ze) = 0, \tag{6}$$

$$4(ze)^2 + 2z^2 e - z^2 = 0, \tag{7}$$

$$2(ze)\, e - ze = 0. \tag{8}$$

From (5) it can be seen that elements of baric value zero also satisfy the equation in Definition 1. The fully linearised forms of these, which may be obtained by replacing

z by $\sum \theta_i z_i$ and equating homogeneous terms to zero, are

$$(z_1 z_2)(z_3 z_4)+(z_1 z_3)(z_2 z_4)+(z_1 z_4)(z_2 z_3) = 0, \tag{9}$$

$$(z_1 z_2)(z_3 e)+(z_1 z_3)(z_2 e)+(z_2 z_3)(z_1 e) = 0, \tag{10}$$

$$4(z_1 e)(z_2 e)+2(z_1 z_2) e-z_1 z_2 = 0. \tag{11}$$

Noteworthy intermediate forms are

$$z_1^2 z_2^2 = -2(z_1 z_2)^2 \tag{12}$$

$$z_1^2(z_2 e) = -2(z_1 z_2)(z_1 e). \tag{13}$$

An immediate consequence of these identities is

PROPOSITION 1. *$\mathfrak{Z}^2$ is an ideal in $\mathfrak{B}$.*

Proof. $\mathfrak{Z}^2$ is an ideal in $\mathfrak{Z}$, so it remains to show that $\mathfrak{Z}^2 e \subset \mathfrak{Z}^2$. Now (11) may be written

$$(z_1 z_2) e = \tfrac{1}{2} z_1 z_2 - 2(z_1 e)(z_2 e). \tag{14}$$

Since $\mathfrak{Z}$ is an ideal in $\mathfrak{B}$, the second term on the right as well as the first belongs to $\mathfrak{Z}^2$, which establishes the proposition.

COROLLARY. *A Bernstein algebra in which $\mathfrak{Z}^3 = 0$ is a special train algebra.*

(It will be recalled that a special train algebra is a baric algebra in which the nil ideal is nilpotent, and every power of it is an ideal.)

Let $\mathfrak{U}$ denote the subspace spanned by the elements $u = ze$, $\mathfrak{V}$ the subspace spanned by all products $v = u_i u_j$, and $\mathfrak{W}$ the subspace complementary to the union of $\mathfrak{E}$, $\mathfrak{U}$ and $\mathfrak{V}$.

The result of substituting $u = ze$ in (8) is

$$ue = \tfrac{1}{2} u. \tag{15}$$

The substitution of u_1, u_2 for z_1, z_2 in (14) with $v = u_1 u_2$, taken in conjunction with (15), leads to

$$\begin{aligned} ve &= \tfrac{1}{2} u_1 u_2 - 2(u_1 e)(u_2 e) \\ &= 0. \end{aligned} \tag{16}$$

The contrast between (15) and (16) permits the following conclusion.

PROPOSITION 2. *The subspaces $\mathfrak{U}$ and $\mathfrak{V}$ have no non-zero elements in common.*

The space underlying $\mathfrak{B}$ may therefore, as a vector space, be decomposed into the direct sum $\mathfrak{E} \oplus \mathfrak{U} \oplus \mathfrak{V} \oplus \mathfrak{W}$. Equations (15) and (16) may now be exploited in conjunction with identities (5)–(11). Some results are as follows:

$$
\begin{array}{lcll}
z_1, z_2, z_3 & \textit{Equation} & \textit{Result} & \\
\left.\begin{array}{l} v_1, v_2, u \\ u_1, u_2, v \\ u_1, u_2, u_3 \end{array}\right\} & (10) & \begin{array}{l} (v_1 v_2) u = 0 \\ (vu_1) u_2 + (vu_2) u_1 = 0 \\ (u_1 u_2) u_3 + (u_2 u_3) u_1 + (u_3 u_1) u_2 = 0 \end{array} & \begin{array}{r} (17) \\ (18) \\ (19) \end{array} \\
z_1 z_2 & & & \\
\left.\begin{array}{l} v_1, v_2 \\ u, v \\ w_1, w_2 \\ w, u \\ w, v \end{array}\right\} & (11) & \begin{array}{l} (v_1 v_2) e = \tfrac{1}{2} v_1 v_2 \\ (uv) e = \tfrac{1}{2} uv \\ \left.\begin{array}{l} w_1 w_2 = 2(w_1 w_2) e + 4(w_1 e)(w_2 e) \\ wu = 2(wu) e + 2(we) u \\ wv = 2(wv) e \end{array}\right\} \end{array} & \begin{array}{r} (20) \\ (21) \\ \\ (22) \\ \\ \end{array}
\end{array}
$$

In the usual notation (20) and (21) show that $\mathfrak{V}^2 \subset \mathfrak{U}$ and $\mathfrak{U}\mathfrak{V} \subset \mathfrak{U}$. From (22) it follows that $\mathfrak{W}^2 \subset \mathfrak{U} \oplus \mathfrak{V}$, $\mathfrak{W}\mathfrak{U} \subset \mathfrak{U} \oplus \mathfrak{V}$ and $\mathfrak{W}\mathfrak{V} \subset \mathfrak{U}$. In particular, this establishes

PROPOSITION 3. *$\mathfrak{E} \oplus \mathfrak{U} \oplus \mathfrak{V}$ is an ideal in $\mathfrak{B}$, containing $\mathfrak{B}^2$.*

COROLLARY. *The difference algebra $\mathfrak{B} - (\mathfrak{E} \oplus \mathfrak{U} \oplus \mathfrak{V})$ is a zero algebra.*

Definition 2. The ideal $\mathfrak{E} \oplus \mathfrak{U} \oplus \mathfrak{V}$ will be called the *core* of the Bernstein algebra $\mathfrak{B}$, and will be denoted by $\mathfrak{C}$.

In view of Proposition 3, $\mathfrak{C}$ is independent of the choice of the idempotent e.

In terms of multiplication matrices, (18) may be written

$$v(R_{u_1} R_{u_2} + R_{u_2} R_{u_1}) = 0.$$

Of the characteristic features of a Lie algebra therefore, the right transformations corresponding to elements of $\mathfrak{U}$ are anticommutative in their action on $\mathfrak{V}$, while (19) shows that the elements themselves satisfy Jacobi's identity, even though multiplication appears to take them outside $\mathfrak{U}$.

It is clear that $\mathfrak{C}$ is a baric algebra, with $\mathfrak{U} \oplus \mathfrak{V}$ as its nil ideal. Let d_u and d_v be the dimensions of $\mathfrak{U}$ and $\mathfrak{V}$, and let $R_u{}^*$ denote the $(d_u+d_v) \times (d_u+d_v)$ matrix of the right multiplication by u, restricted to $\mathfrak{U} \oplus \mathfrak{V}$. Since by definition of $\mathfrak{V}$ and the consequence of (20), $R_u{}^*$ maps $\mathfrak{U}$ into $\mathfrak{V}$ and $\mathfrak{V}$ into $\mathfrak{U}$, it can be put into the form

$$R_u{}^* = \begin{bmatrix} 0 & R_u{}^{*(1)} \\ R_u{}^{*(2)} & 0 \end{bmatrix}$$

where $R_u{}^{*(1)}$ is $d_u \times d_v$ and $R_u{}^{*(2)}$ is $d_v \times d_u$. Then

$$R_u{}^{*2} = \begin{bmatrix} R_u{}^{*(1)} R_u{}^{*(2)} & 0 \\ 0 & R_u{}^{*(2)} R_u{}^{*(1)} \end{bmatrix}.$$

But the special case $u_1 = u_2$ of (18) shows that $0 = (vu)u = vR_u{}^{*2}$. This implies that $R_u{}^{*(2)}R_u{}^{*(1)} = 0$. If, further, $R_u{}^{*(1)}R_u{}^{*(2)} = 0$ and hence $R_u{}^{*2} = 0$, the Bernstein algebra will be called *orthogonal*. If u_3 is then set equal to u_2 in (19) it takes the form

$$0 = (u_1 u_2)u_2 + 2u_1 u_2{}^2$$
$$= u_1(R_{u_2}^{*2} + 2R_{u_2^2}^{*}).$$

But since the first term on the right has just been proved to be zero, so must be the second. Thus $u_1 u_2{}^2 = 0$, and since any $v = u_2 u_3 = \frac{1}{2}\{(u_2+u_3)^2 - u_2{}^2 - u_3{}^2\}$, it follows that $uv = 0$. This is a strengthening of (21) and also implies that the left-hand sides of (18) and (19) are zero term by term in the orthogonal case.

Equation (17) shows that $\mathfrak{V}^2$ annihilates $\mathfrak{U}$, and since $\mathfrak{V}^2 \subset \mathfrak{U}$ the result just proved shows that it annihilates $\mathfrak{V}$.

PROPOSITION 4. *In an orthogonal Bernstein algebra the ideal* $\mathfrak{U} \oplus \mathfrak{V}$ *is nilpotent of degree* 4.

Proof. The powers of $\mathfrak{U} \oplus \mathfrak{V}$ may be calculated using the above results.

$$(\mathfrak{U} \oplus \mathfrak{V})^2 \subset \mathfrak{V} \oplus \mathfrak{V}^2$$
$$(\mathfrak{U} \oplus \mathfrak{V})^3 \subset \mathfrak{V}^2$$
$$(\mathfrak{U} \oplus \mathfrak{V})^4 = 0.$$

This makes it possible to formulate the main result of this section.

THEOREM 1. *The core of an orthogonal Bernstein algebra is a special train algebra, in which every element of unit baric value satisfies the train equation*

$$2x^4 - 3x^3 + x^2 = 0.$$

It is clear that multiplication by e maps every subspace of $\mathfrak{U} \oplus \mathfrak{V}$ into itself, which establishes the first proposition. The last assertion may be verified by elementary computation.

The idempotent elements play an important role, and they are described in

THEOREM 2. *In a Bernstein algebra, the idempotent elements are precisely those of the form* $e+u+u^2$.

Proof. Clearly an idempotent can have no component in $\mathfrak{W}$. The elements specified in the theorem are clearly idempotents. If $e+u+v$ is idempotent, squaring and equating the components in $\mathfrak{V}$ gives $v = u^2$. This establishes the result, which does not involve the orthogonality condition.

Now that $\mathfrak{C}$ and $\mathfrak{B} - \mathfrak{C}$ have been studied it remains to consider the products of elements of $\mathfrak{W}$ with those of $\mathfrak{C}$. It is convenient to denote by $\mathfrak{U}^*$ the subspace of $\mathfrak{U}$ consisting of elements which annihilate $\mathfrak{U} \oplus \mathfrak{V}$.

Equation (17) shows that $\mathfrak{V}^2 \subset \mathfrak{U}^*$. Now $(e+\theta w)^2 = e + 2\theta we + \theta^2 w^2$. By definition, $we \in \mathfrak{U}$. Taking Theorem 2 into account, and noting the powers of θ which multiply the terms, it can be seen that if $we \neq 0$, then $w^2 \in \mathfrak{V}$ and $w^2 = 4(we)^2$.

(This may be zero.) Alternatively if $we = 0$ it is possible that $w^2 \in \mathfrak{U}$. Again, on examining $(e+\phi u+\theta w)^2 = e+\phi u+\theta^2 w^2+2\theta\phi uw+\phi^2 u^2$ it is clear that $uw^2 = 0$, or $\mathfrak{W}\mathfrak{B}^2 \subset \mathfrak{U}^*$, and $\mathfrak{U}\mathfrak{W}\mathfrak{B} \subset \mathfrak{U}^*$. Finally, a similar exercise with the square of $e+\phi u+\psi v+\theta w$ shows that $\mathfrak{B}\mathfrak{W}\mathfrak{B} \subset \mathfrak{U}^*$.

In examining particular Bernstein algebras a large number of cases were found where $\mathfrak{B}^2 = 0$, compared with the assertion just before Proposition 4 that in general $\mathfrak{B}^3 = 0$. A consequence of this, obtained by reworking the computation in the proof of Proposition 4, is

PROPOSITION 5. *If in an orthogonal Bernstein algebra* $\mathfrak{B}^2 = 0$, *then* $\mathfrak{U} \oplus \mathfrak{B}$ *is nilpotent of degree* 3.

In view of that, it is of interest to establish conditions under which $\mathfrak{B}^2 = 0$.

PROPOSITION 6. *If every element in* $\mathfrak{B}$ *is the square of some element in* $\mathfrak{U}$, *then* $\mathfrak{B}^2 = 0$.

Proof. If $v = u^2$, $v^2 = u^{[3]} = 0$, and $v_1 v_2 = \frac{1}{2}\{(v_1-v_2)^2 - {v_1}^2 - {v_2}^2\} = 0$.

COROLLARY. *If* $\mathfrak{B}$ *is one-dimensional, then* $\mathfrak{B}^2 = 0$.

Proof. There must be some element in $\mathfrak{U}$ whose square is v.

An example showing that the case $\mathfrak{B}^2 \neq 0$ can arise is as follows. Consider the algebra with basis e, u_1, u_2, u_3, v_1, v_2, v_3 and multiplication table

$$\begin{aligned} &e^2 = e, \quad eu_i = \tfrac{1}{2}u_i, \quad ev_i = 0 \qquad (i = 1, 2, 3) \\ &{u_1}^2 = \theta v_1, \quad {u_2}^2 = \phi v_2, \quad u_1 u_2 = \psi v_3 \\ &v_1 v_2 = \delta u_3, \quad {v_3}^2 = \gamma u_3, \qquad \text{other products zero.} \end{aligned}$$

A typical element of weight one, $x = e+\sum \alpha_i u_i+\sum \beta_i v_i$ has a square

$$x^2 = e+\alpha_1 u_1+\alpha_2 u_2+(\alpha_3+{\beta_3}^2\gamma+2\beta_1\beta_2\delta)u_3+{\alpha_1}^2\theta v_1+{\alpha_2}^2\phi v_2+2\alpha_1\alpha_2\psi v_3.$$

The square of this is

$$x^{[3]} = x^2+2{\alpha_1}^2{\alpha_2}^2(\theta\phi\delta+2\psi^2\gamma)u_3.$$

If therefore the constants in the multiplication table are chosen so that $\theta\phi\delta+2\psi^2\gamma = 0$ the algebra is of Bernstein's type. Moreover, it satisfies the orthogonality conditions.

3. *Bernstein's classification of* 3- *and* 4-*dimensional populations*

In contrast to the approach adopted by Lyubich **[10]** and here, Bernstein made essential use of the fact that his evolutionary operators mapped the set of vectors of proportions into itself, and he based his classification on the number of "pure types" that would exist subject to this. If e_i denotes the basis vector with 1 in the i-th position and 0 elsewhere, the i-th type is said to be pure if $e_i V = e_i$. In three dimensions the laws of inheritance satisfying the stationarity principle are of five types. The corresponding families of algebras are denoted here by $\mathfrak{B}_0$, in which there are no pure types, $\mathfrak{B}_2$ and $\mathfrak{B}_3$ in which there are two and three pure types, and $\mathfrak{B}_{11}$ and $\mathfrak{B}_{12}$ the two different laws admitting one pure type.

For each of these situations the quadratic transformation will be quoted from [3], in a notation more appropriate to the present purpose. The genetic types will be denoted by F, G, H, their coefficient in the initial generation by x, y, z, and those in the next by x', y', z'.

In all cases except $\mathfrak{B}_{12}$ it is possible to find a linear transformation of the algebra, depending on the parameters of the family, which reduces it to a single canonical form. In the case of $\mathfrak{B}_{12}$ one of the parameters is accounted for by the transformation, leaving a canonical form involving the other. This is a less "linear" situation. The parameter values are assumed to be "general". There will be subfamilies determined by relationships between the initial multiplication constants for which the structures simplify, and this aspect is not investigated here.

The transformation and the new multiplication table are given in each case.

$\mathfrak{B}_0$. From equation (30) of [3],

$$x' = \alpha(x+y+z)^2, \quad y' = \beta(x+y+z)^2, \quad z' = \gamma(x+y+z)^2$$

with $\alpha+\beta+\gamma = 1$

Multiplication table:

$$F^2 = G^2 = H^2 = FG = FH = GH = \alpha F+\beta G+\gamma H.$$

New basis:

$$b_0 = \alpha F+\beta G+\gamma H, \quad b_1 = F-G, \quad b_2 = F-H.$$

Canonical multiplication table:

$$b_0^2 = b_0, \quad b_i b_j = 0 \text{ unless } i = j = 0.$$

$\mathfrak{B}_{11}$. From equations (31) of [3],

$$x' = (x+z)\{\tfrac{1}{2}(1+\alpha)(x+z)+(1-\beta)y\}$$

$$y' = y(x+y+z)$$

$$z' = (x+z)\{\tfrac{1}{2}(1-\alpha)(x+z)+\beta y\}.$$

Multiplication table:

$$F^2 = H^2 = FH = \tfrac{1}{2}(1+\alpha)F+\tfrac{1}{2}(1-\alpha)H$$

$$G^2 = G$$

$$FG = GH = \tfrac{1}{2}(1-\beta)F+\tfrac{1}{2}G+\tfrac{1}{2}\beta H.$$

New basis:

$$b_0 = G, \quad b_1 = (1-\beta)F-2G+2\beta H, \quad b_2 = \tfrac{1}{2}(\alpha+2\beta-1)(F-H).$$

Canonical multiplication table:

$$b_0^2 = b_0, \quad b_0 b_1 = \tfrac{1}{2}b_1, \quad b_1^2 = b_2,$$

other products zero.

$\mathfrak{B}_{12}$. From equations (32) of [3],

$x' = x(x+y+z)+\alpha x(-\beta z+y)$

$\beta z' = y'$.

Multiplication table:

$F^2 = F$

$G^2 = H^2 = GH = (\beta G+H)/(1+\beta)$

$FG = \tfrac{1}{2}(1+\alpha)\, F+\tfrac{1}{2}(1-\alpha)(\beta G+H)/(1+\beta)$

$FH = \tfrac{1}{2}(1-\alpha\beta)\, F+\tfrac{1}{2}(1+\alpha\beta)(\beta G+H)/(1+\beta)$.

New basis:

$b_0 = F,\quad b_1 = F-G,\quad b_2 = F-\{\beta/(1+\beta)\}\, G-\{1/(1+\beta)\}H.$

Canonical multiplication table:

$b_0{}^2 = b_0,\quad b_0\, b_1 = \tfrac{1}{2}(1-\alpha)\, b_2,\quad b_0\, b_2 = \tfrac{1}{2}b_2$

$b_1{}^2 = -\alpha b_2,\quad b_1\, b_2 = -\tfrac{1}{2}\alpha b_2,\quad b_2{}^2 = 0.$

$\mathfrak{B}_2$. From equations (28) of [3],

$$x' = \left(x+\frac{\alpha}{\alpha+\beta}\, y\right)\left\{x+\left(1-\frac{\alpha\beta}{\alpha+\beta}\right)y\right\}$$

$$y' = (\alpha+\beta)\left(x+\frac{\alpha}{\alpha+\beta}\, y\right)\left(z+\frac{\beta}{\alpha+\beta}\, y\right)$$

$$z' = \left(z+\frac{\beta}{\alpha+\beta}\, y\right)\left\{(1-\beta)\, x+z+\left(1-\frac{\alpha\beta}{\alpha+\beta}\right)y\right\}.$$

Multiplication table:

$F^2 = F,\quad H^2 = H$

$$G^2 = \frac{\alpha}{\alpha+\beta}\left(1-\frac{\alpha\beta}{\alpha+\beta}\right)F+\frac{\alpha\beta}{\alpha+\beta}\, G+\frac{\beta}{\alpha+\beta}\left(1-\frac{\alpha\beta}{\alpha+\beta}\right)H$$

$$FG = \frac{1}{2}\left\{1+\frac{\alpha(1-\beta)}{\alpha+\beta}\right\}F+\tfrac{1}{2}\beta G+\frac{1}{2}\left\{\frac{\beta(1-\beta)}{\alpha+\beta}\right\}H$$

$FH = \tfrac{1}{2}(1-\alpha)\, F+\tfrac{1}{2}(\alpha+\beta)\, G+\tfrac{1}{2}(1-\beta)\, H$

$$GH = \frac{1}{2}\left\{\frac{\alpha(1-\alpha)}{\alpha+\beta}\right\}F+\tfrac{1}{2}\alpha G+\frac{1}{2}\left\{1+\frac{(1-\alpha)\beta}{\alpha+\beta}\right\}H.$$

New basis:

$b_0 = F,\quad b_1 = F-H,\quad b_2 = \alpha F-(\alpha+\beta)\, G+\beta H.$

Canonical multiplication table:

$b_0^2 = b_0, \quad b_0 b_1 = \tfrac{1}{2}b_1 + \tfrac{1}{2}b_2, \quad b_0 b_2 = 0,$

$b_1^2 = b_2, \quad b_1 b_2 = b_2^2 = 0.$

$\mathfrak{B}_3$. From equations (29) of [3],

$x' = x(x+y+z), \quad y' = y(x+y+z), \quad z' = z(x+y+z).$

Multiplication table:

$F^2 = F, \quad G^2 = G, \quad H^2 = H$

$FG = \tfrac{1}{2}F + \tfrac{1}{2}G, \quad FH = \tfrac{1}{2}F + \tfrac{1}{2}H, \quad GH = \tfrac{1}{2}G + \tfrac{1}{2}H.$

New basis:

$b_0 = F, \quad b_1 = F - G, \quad b_2 = 2G + H.$

Canonical multiplication table:

$b_0^2 = b_0, \quad b_0 b_1 = \tfrac{1}{2}b_1, \quad b_0 b_2 = \tfrac{1}{2}b_2,$

$b_1^2 = b_1 b_2 = b_2^2 = 0.$

The nil ideal $\mathfrak{Z}$ is nilpotent of degree 2 in $\mathfrak{B}_0$ and $\mathfrak{B}_3$, and is nilpotent of degree 3 in $\mathfrak{B}_{11}$ and $\mathfrak{B}_2$. In the former cases the train equation relating principal powers of elements of weight one is $x^2 - x = 0$, and in the latter it is $x^3 - x^2 = 0$. From inspection of the canonical multiplication tables it can be seen that in $\mathfrak{B}_{11}$, $\mathfrak{B}_2$ and $\mathfrak{B}_3$, the value $\tfrac{1}{2}$ is a train root in Gonshor's sense [6; §2] but not a principal train root. The algbera $\mathfrak{B}_{12}$ is most interesting in that it is not a special train algebra. In fact $\mathfrak{Z}^k = \{b_2\}$ for $k > 2$. The rank equation satisfied by x, x^2 and x^3 depends on x other than through $\beta(x)$. The case $\mathfrak{B}_3$ is of course the elementary algebra of [**8**; §2].

Bernstein's work on the four-dimensional case is a continuation of his concern to find minimal conditions which, when added to his principle of stationarity, ensure that a population is Mendelian. He showed that the only two systems involving four pure types are the Mendelian (whose genetic algebra is the elementary special train algebra of [**8**; §2], and the "quadrille law", which has been identified biologically by Lyubich [**10**; §4]. If $G_1, \ldots, G_4$ are the genetic types the multiplication table of the algebra is

$$G_i^2 = G \qquad (i = 1, 2, 3, 4)$$

$$G_1 G_2 = \tfrac{1}{2}G_3 + \tfrac{1}{2}G_4, \quad G_3 G_4 = \tfrac{1}{2}G_1 + \tfrac{1}{2}G_2$$

$$G_i G_j = \tfrac{1}{2}G_i + \tfrac{1}{2}G_j \quad \text{when} \quad i = 1, 2;\ j = 3, 4.$$

An appropriate canonical basis is

$$e = \tfrac{1}{4}(G_1 + G_2 + G_3 + G_4)$$

$$c_1 = G_1 - G_3, \quad c_2 = G_1 - G_4$$

$$d = G_1 + G_2 - G_3 - G_4.$$

Then

$$e^2 = e, \quad ec_1 = \tfrac{1}{2}c_1, \quad ec_2 = \tfrac{1}{2}c_2, \quad c_1 c_2 = \tfrac{1}{2}d$$

other products zero.

$$\mathfrak{Z} = \{c_1, c_2, d\}, \quad \mathfrak{Z}^2 = \{d\}, \quad \mathfrak{Z}^3 = 0.$$

The algebra is special train.

4. *A new classification of Bernstein algebras of low dimension.*

It is possible to classify types of Bernstein algebras on the basis of the theory developed in §2, in terms of the dimensions of the subspaces $\mathfrak{U}$, $\mathfrak{V}$, $\mathfrak{W}$. Let these be denoted by d with appropriate subscripts. The subspace of $\mathfrak{U}$ consisting of annihilators of $\mathfrak{U}$ (and $\mathfrak{V}$) has been called $\mathfrak{U}^*$. Let its complement in $\mathfrak{U}$ be called $\mathfrak{U}\dagger$. Then

$$d_v < \tfrac{1}{2}d_u(d_u+1),$$

$$d_v > 0 \text{ implies } d_u > 0.$$

The types of three-dimensional Bernstein algebras are obtained by distributing the two dimensions of $\mathfrak{Z}$ among $\mathfrak{U}\dagger$, $\mathfrak{U}^*$, $\mathfrak{V}$, $\mathfrak{W}$. Denoting the results by vectors, there are four which satisfy the above inequalities.

(i) (0, 0, 0, 2). The only possible multiplication table is $e^2 = e$, remaining products zero. This may be called the equipotent algebra since the square of every element is e.

(ii) (0, 2, 0, 0). This is the elementary algebra of [4; §2], with $e^2 = e$, $eu_i = \frac{1}{2}u_i$ $(i = 1, 2)$, the remaining products being zero.

(iii) (0, 1, 0, 1). This is the interesting case where the algebra is not special train. The multiplication table contains 3 parameters, and is $e^2 = e$, $eu = \frac{1}{2}u$, $ew = \theta u$, $u^2 = 0$, $uw = \phi u$, $w^2 = \psi u$.

(iv) (1, 0, 1, 0). This is the one-parameter family $e^2 = e$, $eu = \frac{1}{2}u$, $u^2 = \theta v$, the remaining products being zero.

In view of the different principles of classification adopted, the classes described here do not correspond to those of the previous section.

In four dimensions, the three dimensions of $\mathfrak{Z}$ have to be allocated to $\mathfrak{U}\dagger$, $\mathfrak{U}^*$, $\mathfrak{V}$ and $\mathfrak{W}$. There are seven admissible cases. Where $\mathfrak{W}$ is absent, $\mathfrak{B}$ is a special train algebra by Theorem 1. This occurs where the dimensions are (i) (0, 3, 0, 0) (the elementary algebra), (ii) (2, 0, 1, 0) and (iii) (1, 1, 1, 0). The equipotent algebra (iv) (0, 0, 0, 3) is also special train. There then remain three cases that are not special train algebras (except possibly for certain sub-families defined by relationships between the multiplication constants). The families (0, 2, 0, 1) and (1, 1, 1, 0) have three-dimensional cores, and (0, 1, 0, 2) has a two-dimensional core.

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