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ON DOMINANCE RELATIONS AND THE STRUCTURE OF ANIMAL SOCIETIES: I. EFFECT OF INHERENT CHARACTERISTICS

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Societies are considered in which a non-transitive dominance relation exists between every pair of members, such as the peck-right in a flock of hens. A one-dimensional measure of the structure of such a society, h, is defined, with $h = 0$ for equality and $h = 1$ for the hierarchy. It is assumed that each member of the society is characterized by an ability vector whose components depend on individual characteristics such as size, concentration of sex hormone, etc., but not on social factors such as social rank. The distribution of abilities among members of the society is assumed to be given by a distribution function which is the same for all members, and the probability that one member dominates another is given by a function of the ability vectors of the two.

On these assumptions formulas for the expected (mean) value and variance of h are determined in terms of the distribution and dominance probability functions. Some special cases are calculated, especially that for normally distributed abilities and dominance probability given by the normal probability integral.

Several conclusions are derived. If all members are of equal ability, so that dominance probability is 1/2, then any sizable society is much more likely to be near the equality than the hierarchy; and, as the size of the society increases, the probability that it will be near the hierarchy becomes vanishingly small. If the dominance probability is a weighted sum of several independent components, which make up the ability vector, then the society is less likely to be close to the hierarchy as the number of these components increases. The hierarchy is the prevalent structure only if unreasonably small differences in ability are decisive for dominance. From this it appears that the social factors, or psychological factors such as the previous history of dominance, which are not included in the present treatment, may be of great importance in explaining the observed prevalence of structures very close to the hierarchy in flocks of domestic hens.

1. INTRODUCTION. It was observed by T. Schjelderup-Ebbe (1922) that between every two hens in a flock there exists a relation known as the "peck right" which establishes the dominance of one hen over the other. Similar dominance relations have been observed in social groups of many other vertebrates, although not always as clearly defined as in domestic hens and not always holding between every pair of members of the group. These relations have been intensively studied by W. C. Allee (1938, 1949) and his students

(Potter, 1949; Collias, 1943; Guhl and Allee, 1944) using mainly domestic hens.

The mathematical theory of such dominance relations has been investigated by A. Rapoport (1949a, 1949b, 1950), and in the following we make use of some of the concepts introduced by him. Some suggestions toward a theory were also given by C. C. Lienau (1947).

We shall be concerned with societies containing a finite number, n, of members with a dominance relation holding between the two members of every pair. A dominance relation is a binary, asymmetric, non-transitive relation, j dominates k being written $j > k$.

Although the motivation and most of the applications of this study are from animal societies it should be remarked that there are other examples of dominance relations. Any tournament—chess, tennis, etc.—consisting of a single round robin with no games ending in draws is an example. If the tournament is a multiple round robin (each contestant plays more than one game with every other one), the member of each pair who wins the majority of the games between them can be said to dominate the other. The baseball leagues are examples. Dominance relations also occur in the von Neumann-Morgenstern theory of games (von Neumann and Morgenstern, 1947) where they are needed to define a solution. These writers also point out that the same idea, i.e., a pairwise ordering without transitivity, occurs in the "paper-form" in sports and races, comparisons of the strength of chess players in a tournament, etc.

A complete description of the structure of a society with a dominance relation requires, of course, the statement of the $n(n-1)/2 = \binom{n}{2}$ dominance relations between all the pairs of members of the society. This statement is most conveniently formulated as a matrix (a_{jk}) where

$$\begin{aligned} a_{jk} &= +1 && \text{if } j > k, \\ a_{jk} &= -1 && \text{if } k > j, \\ a_{jj} &= 0, && j = 1, 2, \cdots, n \end{aligned}$$

(Lienau, 1947). However, this matrix is not unique because renaming the members, that is, permuting rows and corresponding columns of the matrix, does not change the structure of the society. Thus the structure is given by the set of matrices which can be obtained from a given one by any permutation of rows and the same permutation of columns.

A geometric (topological) description of the structure can also be given by n points with lines connecting every pair of these points and a direction assigned to every line.

Let us call the structure, when thus completely defined, the "dominance structure" to distinguish it from another definition of structure introduced below. It is easily possible to find a lower bound for the number of possible dominance structures. There are $2^{\binom{n}{2}}$ different matrices which can be obtained by assigning either $+1$ or -1 to the $\binom{n}{2}$ elements a_{jk} which are above the principal diagonal, $j < k$; the a_{jk} below the principal diagonal are then determined. When the $n!$ permutations of n objects are applied to the rows and columns of any one matrix it will go into at most $n!-1$ of the other matrices. Hence there must be at least $2^{\binom{n}{2}}/n!$ different dominance structures. This number becomes very large even for moderate n. For $n = 8$ there are over 6,000 possible dominance structures, and for $n = 12$ there are more than 10^{11}.

2. SCORE STRUCTURE AND HIERARCHY INDEX. Our aim is to characterize the structure of the society under certain assumptions about the properties of the members. For this purpose we do not use the dominance structure, but a simpler definition of structure, the score structure, and from it derive a one-dimensional measure of the structure, the hierarchy index, with which we shall be mainly concerned.

The score structure, V, of a society is a set of n integers $V = (v_1, v_2, \cdots, v_n)$, where v_j means that the jth member dominates v_j of the others. Any permutation of the v_j does not, of course, alter the score structure. This definition of structure was introduced by Rapoport (1949a) but without the name used here.

The score structure can be obtained from a dominance structure matrix by adding the +1's in each row. A little consideration shows that more than one dominance structure can give the same score structure. The simplest example occurs for $n = 5$. The following two matrices

$$\begin{bmatrix} 0 & 1 & 1 & 1 & -1 \\ -1 & 0 & -1 & 1 & 1 \\ -1 & 1 & 0 & -1 & 1 \\ -1 & -1 & 1 & 0 & 1 \\ 1 & -1 & -1 & -1 & 0 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 0 & 1 & 1 & -1 & 1 \\ -1 & 0 & 1 & 1 & -1 \\ -1 & -1 & 0 & 1 & 1 \\ 1 & -1 & -1 & 0 & 1 \\ -1 & 1 & -1 & -1 & 0 \end{bmatrix}$$

both have $V = (3, 2, 2, 2, 1)$, but they cannot be equivalent under row and column permutation because in the first matrix $5 \succ 1$ with $v_5 = 1$ and 1 dominates all the others, whereas in the second $4 \succ 1$

with $v_4 = 2$, and again 1 dominates all the others. Thus V is a less complete definition of the structure derived from the dominance structure. It will not suffice for all purposes, as will be discussed in a later paper, but can be used for our present purpose which is to show the conditions under which the structure approaches the hierarchy.

The hierarchy is the structure with $V = (n-1, n-2, \cdots, 0)$ so that the members of the society can be ordered

$$1 > 2 > 3 > \cdots > n$$

with each dominating all the members below it and being dominated by all those above. At the opposite extreme is what we call the "equality" with

$$v_1 = v_2 = \cdots = v_n = \frac{n-1}{2}, \qquad (1)$$

which can occur exactly only for n odd.

As a one-dimensional measure of the position of any society with respect to the extremes of equality and hierarchy we introduce the "hierarchy index,"

$$h = \frac{12}{n^3 - n} \sum_{j=1}^{n} \left(v_j - \frac{n-1}{2} \right)^2 . \qquad (2)$$

The hierarchy index has the range 0 to 1, the factor $12/(n^3 - n)$ being chosen to make $h = 1$ when V is the hierarchy and, of course, $h = 0$ for equality. The quantity, h, is simply a multiple of the variance of the v_j since $(n-1)/2$ is the mean of the v_j.

The remainder of this paper is concerned with the investigation of h. We shall find that it gives a great deal of information about how the structure of the society depends on the properties of its members. Lienau (1947) thought that it would not be possible to define a useful one-dimensional measure of structure, but we hope to show that h does fulfill this function.

3. PROPERTIES DETERMINING DOMINANCE. The actual structure of the society will depend on what assumptions are made about the properties of the members. The model used here is a generalization of that introduced by Rapoport (1950) and would appear to be sufficiently broad to include most of the factors making for dominance in animal societies, except social factors. Some excluded factors which limit its applicability are pointed out below.

It is assumed that each member is characterized by an "ability vector," $x_j = (x_{j1}, x_{j2}, \cdots, x_{jm})$. These x_{ja} measure the individual characteristics which make for dominance such as size, concentration of male sex hormone, etc. (Collias, 1943). However, they do not depend on the social characteristics such as v_j.

We now introduce probability concepts. For the definitions and statements of the methods and theorems used we refer to H. Cramér (1946). It is assumed that the abilities are distributed among the members of the society according to the multivariate distribution function $F(x) = F(x_j)$, $j = 1, 2, \cdots, n$. Assuming that the distribution is the same for all members of the society means assuming that it is homogeneous, all members being of the same breed. The modification needed to take into account societies of mixed breeds, as were used in the experiments of J. H. Potter (1949), would not be difficult, although the statement of the results would be more complicated.

For given values of x_j and x_k it is assumed that the probability that j dominates k is given by a function of the two vectors $p(x_j, x_k) = p_{jk}$, i.e.,

$$Pr\,[j > k] = p(x_j, x_k) = p_{jk}, \quad j, k = 1, 2, \cdots, n. \tag{3}$$

Since p_{jk} is a probability we must, of course, have

$$0 \leq p_{jk} \leq 1, \tag{4}$$

and since either $j > k$ or $k > j$, we have

$$p_{jk} + p_{kj} = 1. \tag{5}$$

We do not attempt to discuss here the problem, or even the possibility, of determining the functions $F(x)$ and p_{jk} from observations on societies. The latter is the identification problem which is discussed by T. C. Koopmans and O. Reiersøl (1950). It appears from the results below that under certain assumptions on the form of $F(x)$ and p_{jk}, these functions may not be completely identifiable on the basis of observations on the structure of societies, that is, not completely determined from such observations. However, the indeterminism appears to be of not a very essential nature; and more important, planned experiments like the paired combats carried out by Collias (1943) should permit direct determination of these functions.

4. Expected Value of h. We denote the mean, or expected, value of a random variable, y, by $E(y)$. Now

$$E(h) = \frac{12}{n^3 - n} \sum_{j=1}^{n} E\,[(v_j - \bar{v})^2], \tag{6}$$

where $\bar{v} = (n-1)/2$ is the mean of each v_j. Since $F(x_j)$ is the same for all j, and p_{jk} is the same function of x_j and x_k for all j and k, the n terms in the summation in (6) will be the same, so that

$$E(h) = \frac{12}{n^2 - 1} E\,[(v_1 - \bar{v})^2]. \tag{7}$$

If $x_1, x_2, \cdots, x_n$ are fixed, then the probability that $v_1 = v$ is given by

$$Pr\,[v_1 = v] = \sum p_{1j_1} p_{1j_2} \cdots p_{1j_v} p_{j_{v+1}1} p_{j_{v+2}1} \cdots p_{j_n 1}, \tag{8}$$

where j_1 to j_v are any v of the $n-1$ integers $2, \cdots, n$ and j_{v+1} to j_n are the remaining $n-1-v$, and the summation is over all terms of this type. This is the same as the sum of the terms in the expansion of

$$\prod_{j=2}^{n} (p_{1j} + p_{j1}) \tag{9}$$

which contain v factors p_{1j} and $n-1-v$ factors p_{j1}. The characteristic function of v_1, i.e., $E(e^{itv_1})$ is then

$$E(e^{itv_1}) = \prod_{j=2}^{n} (p_{1j}e^{it} + p_{j1}), \tag{10}$$

the characteristic function of $v_1 - \bar{v}$ is

$$\begin{aligned} E(e^{it(v_1-\bar{v})}) &= e^{-it\left(\frac{n-1}{2}\right)} \prod_{j=2}^{n} (p_{1j}e^{it} + p_{j1}) \\ &= \prod_{j=2}^{n} \left(p_{1j}\, e^{\frac{it}{2}} + p_{j1}\, e^{-\frac{it}{2}}\right), \end{aligned} \tag{11}$$

and $E\,[(v_1 - \bar{v})^2]$ is the coefficient of $(it)^2/2!$ in the expansion of (11) in powers of t. Now

$$\begin{aligned} \prod_{j=2}^{n} \left(p_{1j}\, e^{\frac{it}{2}} + p_{j1}\, e^{-\frac{it}{2}}\right) &= \prod_{j=2}^{n} \left[\sum_{k=0}^{\infty} (p_{1j} + (-1)^k p_{j1}) \frac{(it)^k}{2^k k!}\right] \\ &= \prod_{j=2}^{n} \left[1 + (p_{1j} - p_{j1}) \frac{it}{2 \cdot 1!} + \frac{(it)^2}{2^2 \cdot 2!} + \cdots\right]. \end{aligned} \tag{12}$$

Let

$$g_{jk} = g(x_j, x_k) = p_{jk} - p_{kj} . \tag{13}$$

Multiplying out the product in (12) we obtain

$$\begin{aligned} E(e^{it(v_1-\bar{v})}) &= 1 + \frac{it}{2 \cdot 1!} \sum_{j=2}^{n} g_{1j} \\ &\quad + \frac{(it)^2}{2^2 \cdot 2!} [n - 1 + \textstyle\sum' g_{1j} g_{1k}] + \cdots, \end{aligned} \tag{14}$$

where $\sum'$ indicates summation over the $(n-1)(n-2)$ terms with $j, k = 2, 3, \cdots, n$ and $j \neq k$. Then for fixed x_j,

$$E(v_1 - \bar{v})^2 = \tfrac{1}{4} [n - 1 + \textstyle\sum' g_{1j} g_{1k}] . \tag{15}$$

Since the x_j are actually distributed according to the distribution function $F(x_j)$, we have

$$\begin{aligned} &E(e^{it(v_1-\bar{v})}) \\ &= \int \left[\prod_{j=2}^{n} \left(p_{1j} e^{\frac{it}{2}} + p_{j1} e^{-\frac{it}{2}} \right) \right] dF(x_1) dF(x_2) \cdots dF(x_n) \end{aligned} \tag{16}$$

where the integral is the Lebesque-Stieltjes integral and the integration is over the range of the x_j. Then, as in (15),

$$\begin{aligned} E[(v_1 - \bar{v})^2] &= \tfrac{1}{4} \int [n - 1 + \textstyle\sum' g_{1j} g_{1k}] \, dF(x_1) dF(x_2) \cdots dF(x_n) \\ &= \frac{(n-1)}{4} \left\{ 1 + (n-2) \int \left[\int g_{1j} \, dF(x_j) \right]^2 dF(x_1) \right\} . \end{aligned} \tag{17}$$

Finally using (7) and putting

$$A(x) = \int g(x, y) dF(y), \tag{18}$$

$$E(h) = \frac{3}{n+1} \left[1 + (n-2) \int A^2(x) dF(x) \right] . \tag{19}$$

Some applications of this formula and some of the conclusions which can be drawn from it are discussed in Sections 6 and 7 below.

5. VARIANCE OF h. The variance of h, $\sigma^2(h)$, may be similarly obtained by use of the characteristic function. The calculation is more involved and the general result is rather complicated. We shall only outline the steps and state the final formula as follows:

$$\sigma^2(h) = E(h^2) - E^2(h) = \left(\frac{12}{n^3 - n}\right)^2 E\left[\left(\sum_{j=1}^{n} (v_j - \bar{v})^2\right)^2\right] - E^2(h)$$

$$= \left(\frac{12}{n^3 - n}\right)^2 \left\{ \sum_{j=1}^{n} E\left[(v_j - \bar{v})^4\right] + \sum_{\substack{j,k=1 \\ j \neq k}}^{n} E\left[(v_j - \bar{v})^2 (v_k - \bar{v})^2\right]\right\} \tag{20}$$

$$- E^2(h) =$$

$$\left(\frac{12}{n^3 - n}\right)^2 \left\{ n\left[E(v_1 - \bar{v})^4\right] + n(n-1)E\left[(v_1 - \bar{v})^2 (v_2 - \bar{v})^2\right]\right\}$$

$$- E^2(h).$$

The quantity $E[(v_1 - v)^4]$ is given by the coefficient of $(it)^4/4!$ in the expansion of $E(e^{it(v_1 - \bar{v})})$ in (16). This gives

$$E[(v_1 - \bar{v})^4] = \frac{n-1}{16}\Big[3n - 5 + 2(3n-7)(n-2)\int A^2(x)\,dF(x)$$
$$+ (n-2)_{(3)} \int A^4(x)\,dF(x)\Big], \tag{21}$$

where

$$n_{(r)} = n(n-1)\cdots(n-r+1). \tag{22}$$

Similarly $E\ [(v_1 - \bar{v})^2 (v_2 - \bar{v})^2]$ is obtained from the expansion of the characteristic function of $v_1 - \bar{v}$ and $v_2 - \bar{v}$:

$$E(e^{it_1(v_1 - \bar{v}) + it_2(v_2 - \bar{v})}) = \int \left[\prod_{j=2}^{n} \left(p_{1j}\, e^{\frac{it_1}{2}} + p_{j1}\, e^{-\frac{it_1}{2}}\right)\right]$$
$$\cdot \left[\prod_{k=3}^{n} \left(p_{2k}\, e^{\frac{it_2}{2}} + p_{k2}\, e^{-\frac{it_2}{2}}\right)\right] dF(x_1)\,dF(x_2)\cdots dF(x_n), \tag{23}$$

which gives

$$E[(v_1 - \bar{v})^2 (v_2 - \bar{v})^2]$$
$$= \tfrac{1}{16}\Big\{(n-1)^2 + 2(n-2)(n^2 - 2n - 1)$$
$$\cdot \int A^2(x)\,dF(x) + 2(n-2)_{(2)} \int\int \Big\{4g(x,y)A(y) \tag{24}$$
$$+ 2(n-4)A(x)[A(x) + A(y)] + B(x,y)\Big\}$$
$$\cdot B(x,y)\,dF(x)\,dF(y) + (n-2)_{(4)}\left[\int A^2(x)\,dF(x)\right]^2\Big\},$$

where we have put

$$B(x, y) = \int g(x, z) g(y, z) dF(z). \tag{25}$$

Then from (20) we finally have

$$\sigma^2(h) = \frac{18(n-2)}{(n+1)(n+1)_{(3)}} \Bigg\{ 1 + 2(n-4) \int A^2(x) dF(x) - \frac{3}{2}(3n^2 - 15n + 20) \left[\int A^2(x) dF(x) \right]^2 + \frac{(n-3)_{(2)}}{2} \cdot \int A^4(x) dF(x) + (n-3) \int \int \Big\{ 4g(x, y) A(y) + 2(n-4) A(x) [A(x) + A(y)] + B(x, y) \Big\} \cdot B(x, y) dF(x) dF(y) \Bigg\}. \tag{26}$$

This formula is too complicated to be very useful but we can point out two simple cases.

If $p_{jk} = 1/2$ for all j and k, that is, for any pair of members the probability of the dominance relation going in either direction is the same; then $g_{jk} = 0$ and all the integrals in (26) vanish so that

$$\sigma^2(h) = \frac{18(n-2)}{(n+1)(n+1)_{(3)}} \sim 18/n^3. \tag{27}$$

In general, when the integrals do not vanish we have

$$\sigma^2(h) = O(1/n), \tag{28}$$

that is, $n\sigma^2(h) \to$ constant, as $n \to \infty$.

6. APPLICATIONS. *No Dominance Bias.* This case, with equal probability of dominance in either direction for every pair, $p_{jk} = \frac{1}{2}$ for all j and k, occurs if the x_j are all equal, that is, when every member of the society has the same ability. We then have $g_{jk} = 0$ and

$$E(h) = \frac{3}{n+1}. \tag{29}$$

As soon as n becomes moderately large, $E(h)$ becomes small and $E(h) \to 0$ as $n \to \infty$. Remembering that $0 \leq h \leq 1$, it follows, using the generalized Chebychev inequality (Cramér, 1946, p. 182), that the probability that h will differ very much from zero becomes very small as n increases. Among these societies equality rather than hierarchy would be the rule.

This then gives for general n the behavior of societies without bias toward dominance, which was given in detail for $n = 3, 4, 5$ by Rapoport (1949a). We also give a table of the distribution of V for $n = 6$. This was computed by induction from Rapoport's Table 2

DISTRIBUTION OF V FOR $n = 6$, $p_{jk} = \frac{1}{2}$

V	2^{15} . Probability of V	$35h$
(5, 4, 3, 2, 1, 0)	720	35
(5, 4, 3, 1, 1, 1)	240	31
(5, 4, 2, 2, 2, 0)	240	31
(5, 3, 3, 3, 1, 0)	240	31
(4, 4, 4, 2, 1, 0)	240	31
(5, 4, 2, 2, 1, 1)	720	27
(5, 3, 3, 2, 2, 0)	720	27
(4, 4, 4, 1, 1, 1)	80	27
(4, 4, 3, 3, 1, 0)	720	27
(5, 3, 3, 2, 1, 1)	1440	23
(4, 4, 3, 2, 2, 0)	1440	23
(5, 3, 2, 2, 2, 1)	1680	19
(4, 4, 3, 2, 1, 1)	2880	19
(4, 3, 3, 3, 2, 0)	1680	19
(5, 2, 2, 2, 2, 2)	144	15
(4, 4, 2, 2, 2, 1)	1680	15
(4, 3, 3, 3, 1, 1)	1680	15
(3, 3, 3, 3, 3, 0)	144	15
(4, 3, 3, 2, 2, 1)	8640	11
(4, 3, 2, 2, 2, 2)	2400	7
(3, 3, 3, 3, 2, 1)	2400	7
(3, 3, 3, 2, 2, 2)	2640	3
$E(h) = 3/7$		
$\sigma^2(h) = 12/245$		

(*loc. cit.*), using the fact that the probability of $V = (v_1, v_2, \cdots v_n)$ is the sum of the coefficients of terms of the form $t_{j_1}^{v_1} t_{j_2}^{v_2} \cdots t_{j_n}^{v_n}$ in the expansion of

$$\prod_{\substack{j,k=1 \\ j \neq k}}^{n} (t_j + t_k).$$

Suppose $p_{jk} \neq 1/2$ for some j and k, that is, there are differences in ability making for biases toward dominance. Then it can be seen from equation (19) that $E(h)$ will be increased over its value in the unbiased case; a society tends to move from equality toward hierarchy when any bias is introduced. This was suggested by Rapoport, based on $n = 3$. We now determine $E(h)$ for some assumed forms of p_{jk} and $F(x)$.

Dominance Strictly Determined. At the opposite extreme from absence of any bias toward dominance, we might consider the case in which dominance is completely determined by any difference in ability, that is, we assume that the ability vector has a single component and that

$$\begin{aligned} p_{jk} &= 1 \quad \text{for } x_j > x_k, \\ &= 0 \quad \text{for } x_j < x_k, \end{aligned} \tag{30}$$

and we also assume that $F(x)$ is continuous, so that $Pr(x_j = x_k) = 0$. It is clear that in this case the only possible structure for the society is the hierarchy, but it is interesting to see how this follows from the formula for $E(h)$.

We have

$$\begin{aligned} g_{jk} &= 1 \quad \text{for } x_j > x_k, \\ &= -1 \quad \text{for } x_j < x_k; \end{aligned}$$

then

$$\begin{aligned} A(x_j) &= \int_{-\infty}^{x_j} dF(x_k) - \int_{x_j}^{\infty} dF(x_k) \\ &= F(x_j) - [1 - F(x_j)] = 2F(x_j) - 1, \end{aligned}$$

and

$$\int_{-\infty}^{\infty} A^2(x)\, dF(x) = \int_{-\infty}^{\infty} [4F^2(x) - 4F(x) + 1]\, dF(x) = \tfrac{1}{3};$$

so from (19)

$$E(h) = 1; \tag{31}$$

and since $h \leq 1$, then $h = 1$, or the hierarchy, is the only possible structure. From (26) we can also obtain $\sigma^2(h) = 0$ for this case.

Linear Dominance Probability. Suppose the probability of dominance depends linearly on the ability vector. This requires that the range of values of the ability factors be bounded. Let

$$x_j = (x_{ja}) = (x_{j1}, x_{j2}, \cdots, x_{jm}),$$

with $0 \leq x_{ja} \leq b_a$. Using the notation

$$\begin{aligned} S(x) &= 0, \quad x < 0 \\ &= x, \quad 0 \leq x \leq 1 \\ &= 1, \quad x > 1, \end{aligned} \tag{32}$$

we put

$$p_{jk} = \sum_{a=1}^{m} w_a S\left(\frac{x_{ja} - x_{ka} + b_a}{2b_a}\right), \quad \text{with } w_a \geq 0, \sum w_a = 1, \tag{33}$$

so that p_{jk} is a weighted sum of linear functions of $x_{ja} - x_{ka}$ with w_a as weights.

Then

$$g_{jk} = \sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - x_{ka}), \quad \text{for } 0 \leq x_{ja}, x_{ka} \leq b_a,$$

and

$$\begin{aligned} A(x_j) &= \int_0^{b_m} \cdots \int_0^{b_1} \sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - x_{ka})\, dF(x_{k1}, \cdots, x_{km}) \\ &= \sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - \xi_a), \end{aligned}$$

where ξ_a is the mean of x_{ka}.

$$\begin{aligned} \int A^2(x_j)\, dF(x_j) &= \int_0^{b_m} \cdots \int_0^{b_1} \left[\sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - \xi_a)\right]^2 \\ &\quad \cdot dF(x_{j1}, \cdots, x_{jm}) \\ &= \sum_{a=1}^{m} \left(\frac{w_a}{b_a}\sigma_a\right)^2 + \sum_{\substack{a,\beta=1 \\ a \neq \beta}}^{m} \frac{w_a w_\beta \sigma_a \sigma_\beta}{b_a b_\beta}\rho_{a\beta}. \end{aligned} \tag{34}$$

where σ_a^2 = variance of x_{ja}, and $\rho_{a\beta}$ = correlation coefficient of x_{ja} and $x_{j\beta}$.

We could have chosen the x_{ja} to be uncorrelated, or transformed to uncorrelated variables. Assuming then $\rho_{a\beta} = 0$ we have

$$E(h) = \frac{3}{n+1}\left[1 + (n-2)\sum_{a=1}^{m}\left(\frac{w_a\,\sigma_a}{b_a}\right)^2\right] \sim 3\sum_{a=1}^{m}\left(\frac{w_a\,\sigma_a}{b_a}\right)^2. \quad (35)$$

In this case $E(h)$ has an upper bound which is less than one. Since $0 \leq x_{ja} \leq b_a$, we have $\sigma_a^2 \leq b_a^2/4$, so that, using (33),

$$E(h) \leq \frac{3}{n+1}\left[1 + \frac{n-2}{4}\sum_{a=1}^{m} w_a^2\right] \leq \tfrac{3}{4}\left(\frac{n+2}{n+1}\right). \quad (36)$$

This result indicates that in this case also the hierarchy will not be the usual structure, but structures far from equality may frequently occur. For rectangular distributions of the x_{ja}, we have

$$E(h) \leq \tfrac{1}{4}\left(\frac{n+2}{n+1}\right),$$

which is not far from equality.

If the number of factors, m, becomes large, while none of the weights, w_a, approaches zero, then $E(h)$ will become small. Thus for equal weights

$$w_1 = w_2 = \cdots = w_m = \frac{1}{m},$$

$$E(h) \leq \frac{3}{4m}\left(\frac{n+4m}{n+1}\right) \to 0, \quad \text{as } m \to \infty, \quad n \to \infty,$$

so that if there are a large number of significant factors in the ability vector the structure approaches the equality.

Normal Distribution. We now suppose that the factors of the ability vector are each normally distributed and uncorrelated, and that the probability of dominance is a weighted sum of normal probability integrals of the differences of the factors. Using the notation

$$G(x) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{x} e^{-\frac{t^2}{2}}\,dt$$

for the normal probability integral, we put

$$p_{jk} = \sum_{a=1}^{m} w_a\, G\left(\frac{x_{ja} - x_{ka}}{s_a}\right), \quad \text{with } w_a \geq 0, \sum_{a=1}^{m} w_a = 1, \quad (37)$$

and

$$F(x_j) = \prod_{a=1}^{m} G\left(\frac{x_{ja}}{\sigma_a}\right). \quad (38)$$

Then

$$g_{jk} = \sum_{a=1}^{\infty} w_a \left[2G\left(\frac{x_{ja} - x_{ka}}{s_a} \right) - 1 \right] = -1 + 2 \sum_{a=1}^{m} w_a \, G\left(\frac{x_{ja} - x_{ka}}{s_a} \right)$$

and

$$A(x_j) = \int_{-\infty}^{\infty} \cdots \int_{-\infty}^{\infty} \left[-1 + 2 \sum_{a=1}^{m} w_a \, G\left(\frac{x_{ja} - x_{ka}}{s_a} \right) \right] \prod_{a=1}^{m} dG\left(\frac{x_{ka}}{\sigma_a} \right)$$

$$= -1 + 2 \sum_{a=1}^{m} w_a \, G\left(\frac{x_{ja}}{\sqrt{s_a^2 + \sigma_a^2}} \right),$$

using

$$\int_{-\infty}^{\infty} G(ax + b) \, dG(x) = G\left(\frac{b}{\sqrt{1 + a^2}} \right), \text{ (Landau, 1950).}$$

Then

$$\int A^2(x_j) \, dF(x_j) = \int_{-\infty}^{\infty} \cdots \int_{-\infty}^{\infty} \left[1 - 4 \sum_{a=1}^{m} w_a \, G\left(\frac{x_{ja}}{\sqrt{s_a^2 + \sigma_a^2}} \right) \right.$$

$$+ 4 \sum_{a=1}^{m} w_a^2 \, G^2\left(\frac{x_{ja}}{\sqrt{s_a^2 + \sigma_a^2}} \right) + 4 \sum_{\substack{a,\beta=1 \\ a \neq \beta}}^{m} w_a \, w_\beta \, G\left(\frac{x_{ja}}{\sqrt{s_a^2 + \sigma_a^2}} \right) \tag{39}$$

$$\left. \cdot \, G\left(\frac{x_{j\beta}}{\sqrt{s_\beta^2 + \sigma_\beta^2}} \right) \right] \prod_{a=1}^{m} dG\left(\frac{x_{ja}}{\sigma_a} \right).$$

Using a method similar to that for $\int_{-\infty}^{\infty} G(ax + b) \, dG(x)$, it can be shown that

$$\int_{-\infty}^{\infty} G^2(ax) \, dG(x) = \frac{1}{4} + \frac{1}{2\pi} \arcsin\left(\frac{a^2}{1 + a^2} \right).$$

Then (39) becomes

$$
\begin{aligned}
&\int A^2(x_j)\,dF(x_j) \\
&= 1 - 2\sum_{\alpha=1}^{m} w_\alpha + 4\sum_{\alpha=1}^{m} w_\alpha^2\left[\frac{1}{4} + \frac{1}{2\pi}\arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2}\right)\right] \\
&+ 4\sum{}' w_\alpha w_\beta = 1 - 2\sum_{\alpha=1}^{m} w_\alpha \\
&+ \left(\sum_{\alpha=1}^{m} w_\alpha\right)^2 + \frac{2}{\pi}\sum_{\alpha=1}^{m} w_\alpha^2 \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2}\right) \\
&= \frac{2}{\pi}\sum_{\alpha=1}^{m} w_\alpha^2 \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2}\right), \quad \text{using } \sum_{\alpha=1}^{m} w_\alpha = 1,
\end{aligned}
\tag{40}
$$

and

$$
E(h) = \frac{3}{n+1}\left[1 + \frac{2(n-2)}{\pi}\sum_{\alpha=1}^{m} w_\alpha^2 \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2}\right)\right]. \tag{41}
$$

The unbiased and strictly determined cases (29) and (31) can be obtained as limits from (41). For the unbiased case let $s_\alpha \to \infty$, then $p_{jk} \to \frac{1}{2}$, and

$$
\arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2}\right) \to 0,
$$

so

$$
E(h) \to \frac{3}{n+1}.
$$

For the strictly determined case take $m = 1$ and let $s_\alpha \to 0$, then $p_{jk} \to$ equation (30) and

$$
\arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2}\right) \to \frac{\pi}{6},
$$

so $E(h) \to 1$.

Here, as in the previous case, it can be seen from (41) that increasing the number of factors in the ability vector tends to reduce $E(h)$. When the number of significant factors determining dominance becomes large, the structure of the society moves toward equality.

7. SIGNIFICANCE FOR FLOCKS OF HENS. The observations and experiments on flocks of hens by Schjelderup-Ebbe and by Allee and

coworkers all show that stable flocks of hens almost always have a structure that departs very little from the hierarchy. A flock of ten to twenty hens will normally have not more than two or three cycles, i.e., $j \succ k$, $k \succ l$ and $l \succ j$. This means that h is normally very close to unity in such a flock. A typical example quoted by Schjelderup-Ebbe is the following score structure for a flock of ten hens: $V = (8, 8, 8, 6, 5, 4, 3, 2, 1, 0)$. This gives $h = .975$.

We wish to show that if the probability of dominance depended only on inherent individual characteristics as assumed in the present treatment (and not on social factors), then the occurrence of societies with h near one would be unusual rather than the rule.

We use the results for the normal distribution (Sec. 6) as being probably closest to reality. As noted in Section 6, if the ability vector contains several uncorrelated factors this will tend to reduce the expected value of h, so that we can consider the case of a single factor. Then

$$E(h) = \frac{3}{n+1} + \frac{n-2}{n+1} h_a,$$

where

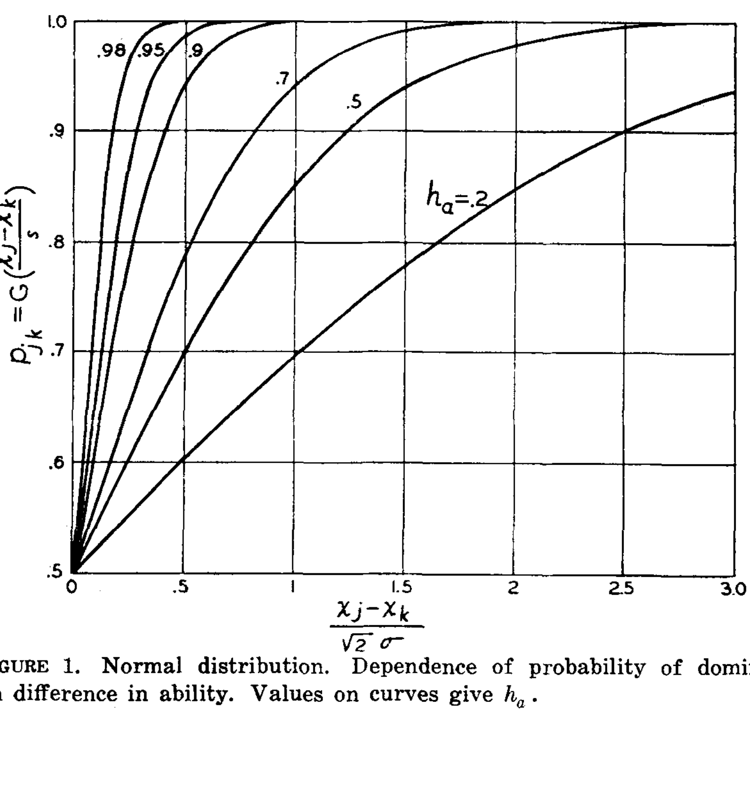

FIGURE 1. Normal distribution. Dependence of probability of dominance, p_{jk}, on difference in ability. Values on curves give h_a.

$$h_a = \frac{6}{\pi} \arcsin \frac{\sigma^2}{s^2 + 2\,\sigma^2}. \tag{42}$$

For even moderate n, $E(h)$ is close to h_a, its asymptotic value, and in any case

$$E(h) - h_a = \frac{3}{n-2}\,(1 - E(h)),$$

so we consider how h_a depends on s/σ.

In Figure 1 we have drawn the probability of dominance,

$$p_{jk} = G\left(\frac{x_j - x_k}{s}\right),$$

as a function of the difference in ability for various values of s/σ with the corresponding values of h_a noted on each curve. The abscissa is

$$\frac{x_j - x_k}{\sqrt{2}\,\sigma},$$

since the variance of $x_j - x_k$ is $2\,\sigma^2$. It can be seen that for h_a to be very close to one, very small differences in ability would have to be quite decisive as to dominance.

This very close dependence of dominance on ability hardly seems reasonable, but there is also some experimental evidence on this point. Collias (1943) staged 200 combats between hens in which he measured degree of moult, comb size, weight and rank in own flock, and obtained for the correlation with success the values: .580, .593, .474, and .262. The correlation measure used was Pearson's coefficient of biserial correlation, r, (Pearson, 1909) except for degree of moult which was not measured on a continuous scale. In the present case

$$r = \sqrt{\frac{\pi}{2}}\,\frac{\overline{x_1 - x_2}}{\sigma_{x_1 - x_2}}, \tag{43}$$

where $\overline{x_1 - x_2}$ is the mean of $x_1 - x_2$ when $x_1 > x_2$, and $\sigma_{x_1 - x_2}$ is the standard deviation of $x_1 - x_2$. It is not difficult to determine the value of r in terms of s/σ for our assumed normal distribution. The result is

$$r = \left(1 + \frac{s^2}{2\,\sigma^2}\right)^{-1/2}, \tag{44}$$

and this gives

$$h_a = \frac{6}{\pi} \arcsin \frac{r^2}{2}. \qquad (45)$$

Hence the largest value of r obtained by Collias, .593, gives only $h_a = .34$. Figure 2 shows the dependence of h_a on r. It is apparent that h_a close to one requires r to be unreasonably large.

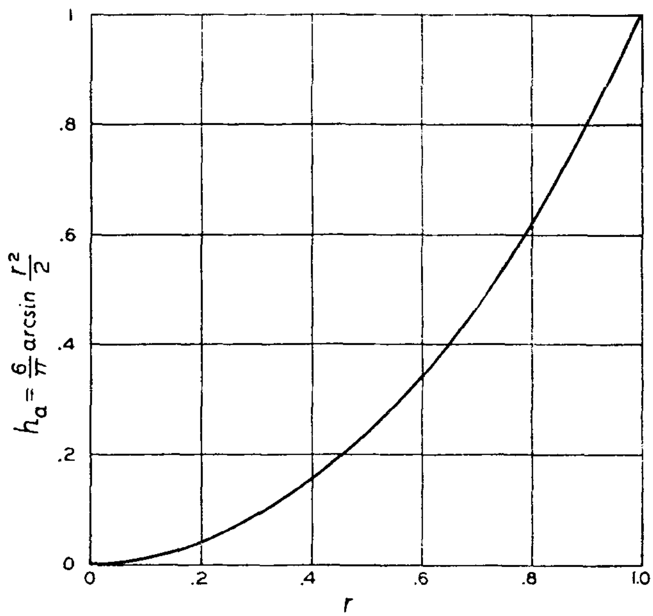

FIGURE 2. Dependence of h_a on biserial correlation coefficent, r.

We must conclude that factors omitted from the present treatment must be included to account for the observed frequency of structures near the hierarchy in flocks of hens. The most obvious omissions are the social factors, such as social lag, or the effect of existing differences in social rank on the probability of continued dominance. All observers agree that such social factors are of great importance. An attempt will be made to treat them mathematically in a later communication.

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