The Hagedoorn "Nucleus-System" of Breeding - A Critical Evaluation based on an Experiment with Poultry.

By F. SKALLER*

I. INTRODUCTION

THE late Dr. A. L. Hagedoorn was one of the first geneticists who addressed animal breeders in a series of popular articles and books advocating the use of progeny testing and family selection instead of individual (mass) selection, and breeding for economic performance instead of for "showyard ideals". As early as 1927 Hagedoorn recommended the institution of random sample tests instead of the conventional type of egg laying trials. His book on animal breeding, first published in 1939, has been widely read all over the world by practical breeders. His widely advertised "nucleus-system" of breeding appealed on account of its simplicity, particularly to sheep and poultry-breeders in many countries, including Australia. This was especially so after Hagedoorn's visit to this country in 1949 and the publication of a selection of his 80 addresses given during this tour.

However, many breeders who claim to use the Hagedoorn nucleus system of breeding do really nothing but progeny or sib-testing of sires, and it is, therefore, important, in order to avoid further confusion, to re-state clearly Hagedoorn's own definition (1953, p. 50): " . . . selecting the males according to purity (homozygosity) for desirable genes and mating them to females of their own group (inbreeding), comparing the progenies of several of such breeding-groups (nucleus-system)".

This recommended system is based on two main conceptions as explained again and again in Hagedoorn's writings (1950, 1951, 1953), viz.:

1. that it is desirable to create "genetically pure" (homozygous) lines which will make it possible to relax our efforts with no loss of quality (1953, p. 36), and that it is possible to by-pass inbreeding trouble by selection (1953, p. 58), and
2. that the main progress comes from progeny-testing the males (1953, p. 45) with the object of finding animals which are homozygous for many important genes, and hence are prepotent (1953, p. 44, 66).

" With regard to inbreeding, Hagedoorn (1951, p. 33) points out that " . . . however undesirable such unexpected individuals may be, we never witness a general degeneration of inbred progeny", and that on account of inbreeding "culling will be quite unnecessary, i.e., variability be reduced (1953, p. 58). Trouble might arise in the first generation of inbreeding, but will then decrease (1953, p. 58). In poultry hatchability should increase by inbreeding" (1953, p. 59). Clearly, Hagedoorn firmly believes that any bad effects of inbreeding are caused solely by making undesirable recessive genes homozygous. He expresses this also in a different way when he states (1951, p. 27): "I do not really believe in hybrid vigour as such. Certainly I do not believe hybrids are vigorous because they are impure". According to Hagedoorn, they are only better because they may carry an array of favourable dominant genes obtained from the two parent breeds.

Hagedoorn's rejection of mass-selection is based on his belief that monofactorial differences must be very frequent (1953, p. 35); indeed the concept of additive genes is never mentioned by him. "Individual selection will let us down wherever we try to obtain purity for the desirable dominant qualities", he states (1953, p. 35), and distinction between highly and less highly heritable characters is "highly unscientific" to his way of thinking (1953, p. 35).

These references may suffice to indicate the fundamental views on which Hagedoorn has erected his recommended system of animal breeding. These views are understandable as coming from a man who belonged to the classical and early school of Mendelian geneticists and who was originally a plant breeder. Scientific evidence to support his recommendations is not submitted. Sykes, one of his main supporters and co-author (Hagedoorn and Sykes, 1953), does not use consistent half-sib matings to obtain "purity of lines"; the results claimed by him in poultry breeding cannot, therefore, be used in support of the Hagedoorn system. Nor, for the same and other reasons, can the success of

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*C.S.I.R.O., Poultry Research Centre, Werribee, Division of Animal Health and Production, the famous Dutch duck breeder, Jansen, who raised production from 270 to over 340 eggs with "no necessity for culling", be attributed to the application of the nucleus system as claimed by Hagedoorn (1953, p. 65).

Numerous objections can be raised against the Hagedoorn system on theoretical grounds. The most important objections are that Hagedoorn does not allow for variations other than genetic, though such variations may be 90 per cent. of the whole, and does not fully appreciate the consequences of genes having actions which are indistinguishable from one another and from environmental effects. These objections are based on the modern concepts of population genetics, of additive genes, of the different degrees of heritabilities for different traits and their effects on the system of selection (Wright, 1921; Lush, 1937), on over-dominance as a possible explanation of heterosis (Gowen et al., 1952), and on the concept of homeostasis (Lerner, 1953). Inbred lines are no longer considered to exhibit less phenotypic variance than non-inbred strains (Robertson and Reeve, 1952).

There is no scientific evidence that lines with a high degree of homozygosity show the same degree of fitness as non-inbred lines. On the contrary, nearly all workers report a decline of characters connected with the fitness of a species, with increasing homozygosity (Lerner, 1953). Our own data (unpublished) with lines reaching a co-efficient of inbreeding of over 60 per cent., show also the depressing effect of inbreeding. Furthermore, Mather and Hayman (1952) have shown that natural and artificial selection will tend to make the actual increase in homozygosity smaller than the computed one based on relationship.

Morley (1951) and C.S.I.R.O. workers (1955) have shown that mass-selection gives a greater annual rate of genetic gain than progeny-testing for increasing wool production in Merino sheep, as fleece weight is highly heritable. Turner (unpublished paper to the Genetics Society of Australia, 1954) showed that even sib-testing gives no advantage over mass selection for fleece weight in Merinos, though it would be of advantage with characters having a much lower heritability.

There is, therefore, evidence available that family selection is only superior to individual selection where characters are of a low or perhaps medium heritability, and that increased homozygosity depresses characters connected with the fitness of a species. Furthermore, those characters which are depressed by inbreeding (and show heterosis after outbreeding) have usually low heritabilities, whereas characters with high heritabilities, and hence suitable for individual selection, are in many cases not depressed by inbreeding. One would, therefore, assume that if the Hagedoorn system were applied to improve characters with low to medium heritability, such as egg production, then inbreeding depression would reduce its value, and if applied to characters with high heritability, where inbreeding would probably do little harm, then individual selection would be more efficient than progeny-testing. Hence, at least on theoretical grounds, one would not expect the Hagedoorn system to be an efficient breeding system, nor has any evidence been produced to that effect. It should be added that progeny testing and family selection without inbreeding will often be efficient and appropriate methods of breeding.

Therefore, when the C.S.I.R.O. Poultry Research Centre was set up at Werribee, Vic., in 1946 for the purpose of investigating the efficiency of a number of breeding systems, it was decided to include the Hagedoorn nucleus system in the investigation.

II. MATERIAL AND METHODS

The B-generation of White Leghorn fowls hatched at Werribee in 1947 formed the parental flock from which a number of separate and closed flocks was developed according to different breeding systems. The history of these flocks, management and husbandry conditions, have been described elsewhere (Skaller, 1955). Here it should only be noted that all pullets were housed at random in laying cages shortly before onset of sexual maturity, and kept there up to the age of 72 weeks as an unculled population. All environmental conditions which could be controlled were kept as constant as possible during all years of the experiment. However, conditions changed in one respect as, on account of the non-culling policy and hence the non-removal of sick birds, the environment became more contaminated with pathogenic agents, causing an increase in adult mortality from the F-generation onwards (Fig. 3).

The Hagedoorn nucleus system was adopted in two of the breeding flocks developed at the Centre. In one flock (H +), selection was based on a high production index (number of eggs per hen housed) as suggested by Hagedoorn (1953, p. 63), and in the other (H —), on a low production index. Comparisons of progress can be made between these flocks and the control (C), propagated by random selection, as well as another flock (M), in which selection was for absence or short duration of winter-pauses on the survivor basis, and where inbreeding was strictly avoided.

The production record of the control flock should give some indication of the between-years environmental variation. Some inbreeding, rising to a level of 17 per cent., occurred during the years 1949-1953 (generations D to H), due to restrictions on flock size through lack of space, but from 1954 (generation J) onwards, measures have been taken in this flock to avoid inbreeding completely. Differences between the control and the three selection flocks at the beginning and end of the experiment can be taken as demonstrating the effect of the breeding systems, but in 1952 and 1953 (generation G and H) it is estimated from evidence provided by a number of highly inbred lines (Skaller, unpublished data), that inbreeding in the control flock might have lowered production by as much as five eggs.

In the two Hagedoorn flocks (H + and H —), pullets and cockerels were used as breeders in order to have one generation each-year, whilst in the M and C flocks some hens were included in the breeding flocks. Selection was based on part winter records (1st egg to 31st May), checks having shown that ranking on partial records agrees well with ranking on a full year's production. Twelve foundation sires were mated in the (H +) and 13 in the (H —) flocks in 1947, each to 10 pullets. Since then, the general procedure has been to select the cockerel whose daughters give the highest (or lowest) production, and to mate his sons, each to a group of full or half-sibs. The need for finding sufficient sibs places a restriction on such a system, and in two years (1950 and (1954) it was necessary to increase the flock size by mating sons from two or three families instead of one, and to include amongst the females some cousins as well as sibs.*

The expected increase in homozygosity for continued half-sib matings, computed according to Wright (1921), would have risen to 56.2 per cent. by 1955. The use of cousins reduced the rate of increase in inbreeding slightly, and the actual level in 1955 was estimated at approximately 50 per cent. in each of the Hagedoorn flocks. Natural selection, becoming effective through the deleterious effect of inbreeding on hatchability and chick mortality, will have favoured the survival to breeding age of heterozygous animals, thus reducing the actual increase in homozygosity obtained below the theoretical co-efficient of inbreeding computed.

Hagedoorn (1951, p. 20) considered the testing of six families to be adequate. Space restrictions in the early years of the Poultry Research Centre reduced this number to three or four, but from 1951 onwards the flock size has been increased, and has only been limited by the restrictions inherent in a system of sib-matings. This system itself, however, has reduced the number of sire-groups to four in some years, with a maximum of 8 birds tested in 1952. The mean selection differential over seven generations has been + 11.2 eggs for the (H +), and — 11.4 eggs for the (H —) flock.

In the M flock there was no inherent restriction on flock size, and about twice as many sires could be tested yearly as in the Hagedoorn flocks, though more than one family were selected to avoid inbreeding. The mean selection differential for the selected families of this flock will be computed and discussed in a later paper, but it is certainly not higher than in the Hagedoorn flocks, as the percentage of families saved for breeding was higher in the M flock than in the Hagedoorn flocks. However, as in the M flock, the best hens on their own records and best sires on their full-sisters' records were selected within the best families, the total selection pressure applied to this flock was probably higher than in the Hagedoorn flocks.

III. RESULTS AND DISCUSSION

(a) General

The mean egg production for pullets up to 72 weeks of age is shown for each flock in Figs. 1 and 2. Fig. 1 is based on the production index, that is, the mean number of eggs per pullet housed. Fig. 2 shows the mean egg production for pullets which were still surviving at 72 weeks of age. Fig. 3 shows the percentage mortality among pullets in each flock, and Fig. 4 the co-efficient of variability in survivors' egg production in each flock.

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*Two tables giving full details of matings and selection were shown at the Armidale conference, but have not been reproduced here, to save space.

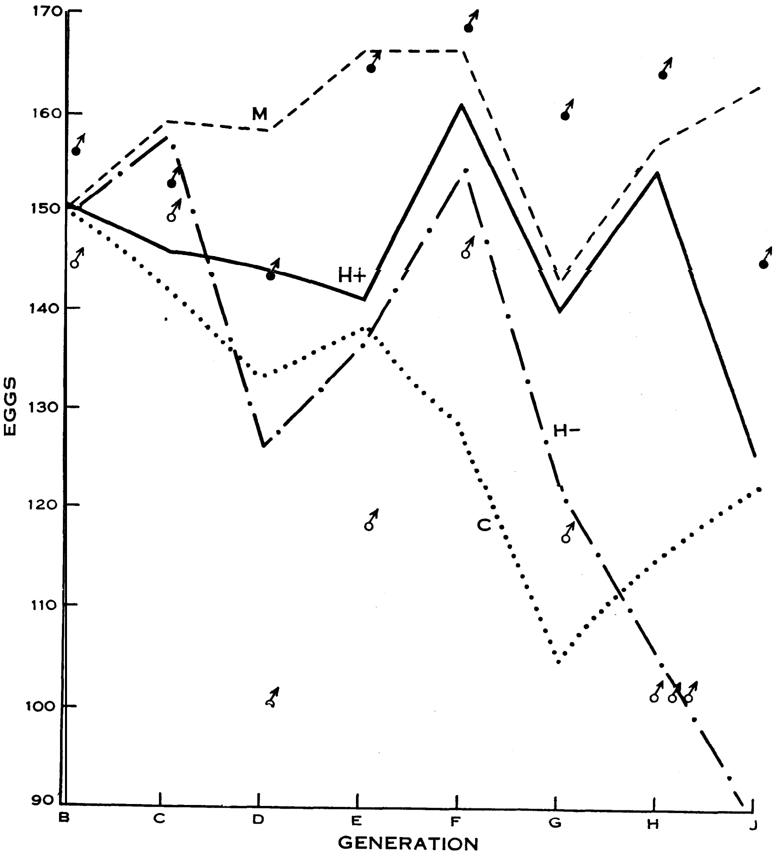

FIGURE 1: Changes of Egg Production Index (hen-housed basis) from 1st egg to 72 weeks of age over 8 generations for 2 Hagedoorn flocks selected in opposite direction (H+ and H—), the control flock (C) and a flock selected for absence of winterpause on the basis of family combined with individual selection and avoiding of inbreeding (M).

The position of the male symbol ( ) indicates the mean performance of the selected (H+) Sire family, hence the distance between this point and the corresponding point on the (H+)-line gives the selection differential. The position of the male symbol ( ) gives the same information in regard to the (H—)-flock.

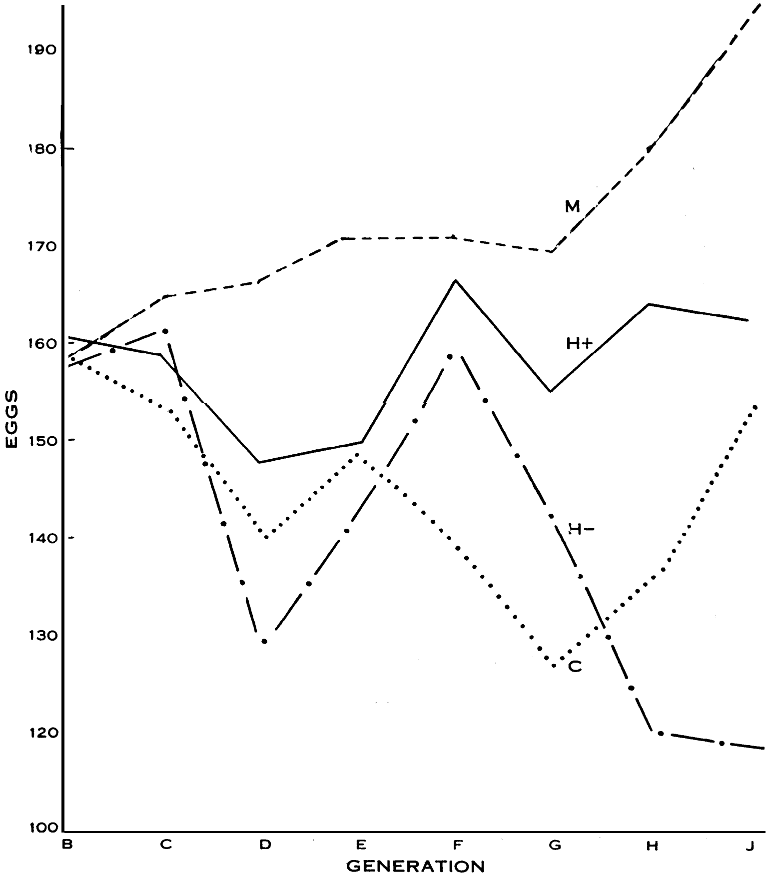

FIGURE 2: Changes of Egg Production on the Basis of Survivors at 72 weeks of age over 8 generations for 2 Hagedoorn flocks selected in opposite direction (H+ and H—), the control flock (C) and a flock selected for absence of winter-pause by family combined with individual selection and avoiding of inbreeding (M).

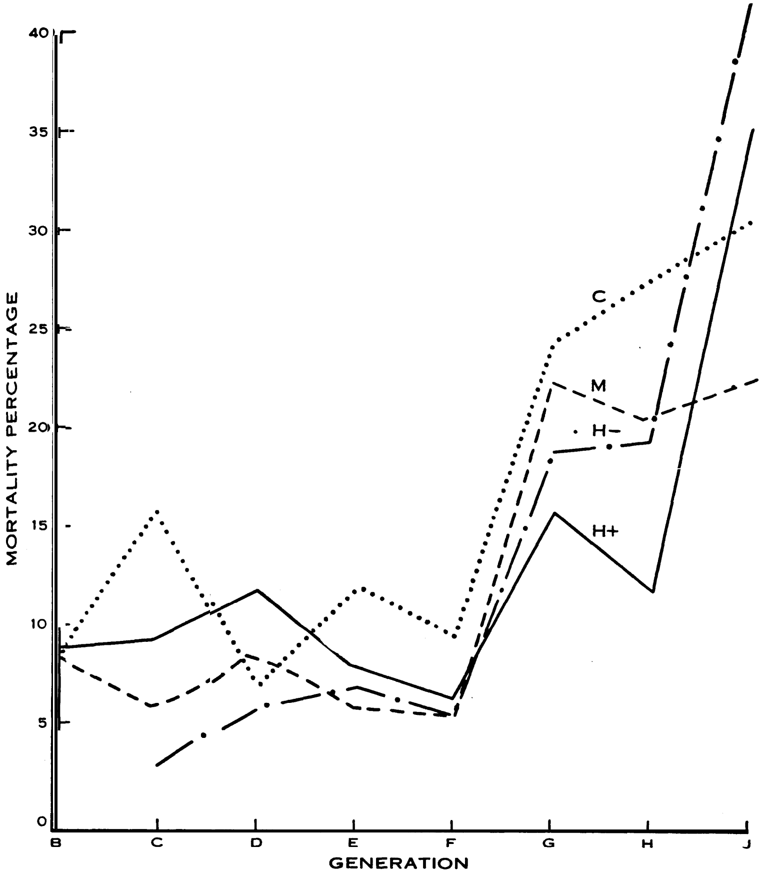

FIGURE 3: Changes in Mortality Rate for 8 generations of pullets from sexual maturity to the age of 72 weeks for 2 Hagedoorn flocks selected in opposite direction (H+ and H—), a control flock (C) and a flock selected for absence of winterpause by family combined with individual selection and avoiding of inbreeding.

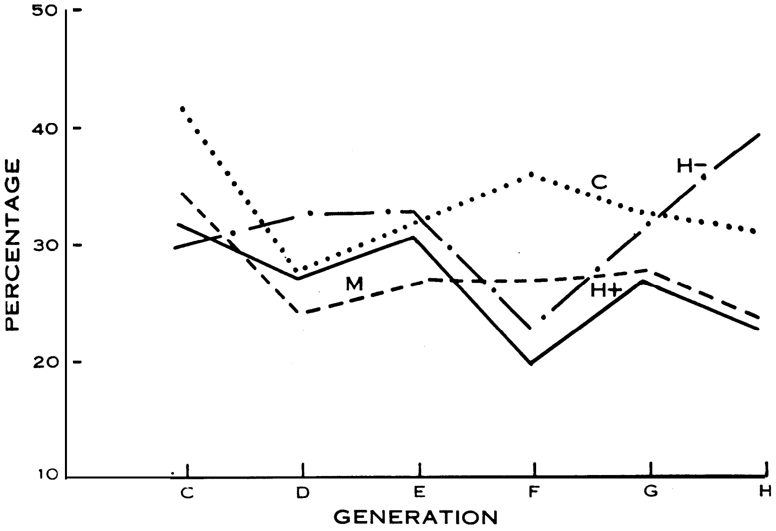

FIGURE 4: Changes in the Coefficient of Variability for egg production of survivors to 72 weeks of age over 6 generations for 2 Hagedoorn flocks selected in opposite direction (H+ and H—), a control flock (C) and a flock selected for absence of winterpause by family combined with individual selection and avoiding of inbreeding.

As mentioned earlier, Fig. 3 shows a continued rise in mortality in the control group after the F-generation, which could be explained by the deterioration in the environment for reasons discussed earlier. There is also a fall in production from the B-generation to the G-generation (Fig. 1 and 2), which could be explained partly by the rise in inbreeding, previously discussed, and partly by the fact that the B-generation was produced by outbreeding two purchased strains. Some heterosis effect was, therefore, possible.

(b) Egg Production

Up to the E-generation, the Control and the two Hagedoorn flocks (H + and H —) did not differ significantly and the H+ flock made no progress, in contrast to the steadily improving M flock. This might have been due to the relatively small number of sires tested. In the F-generation considerable progress was made, but both flocks (H + and H —) moved in the same direction and did not show any significant difference between them, though they now showed a significant difference from the Control flock and nearly reached the level of the M flock. From then onwards production in the (H —) flock declined rapidly and eventually became even lower than the Control flock. The production index of the (H +) flock remained, for the three F-, G-, and H-generations, only slightly below the M flock. This result was mainly caused by the lower mortality of the (H +) flock (Fig. 3), and not by the egg production of the survivors (Fig. 2), which remained significantly below the M flock. Records for the J-generation show large differences between the two Hagedoorn flocks (H + and H —), and between each of them and the M flock. The (H —) flock is now considerably below the Control, whereas the (H +) flock is only very little above it. Considering the whole period of 8 generations under test, very little improvement was made in the (H +) flock as compared with the Control or the M flock.*

On the other hand, selection for a low production index with the superimposed depressing effect of inbreeding eventually succeeded in reducing egg production in the (H —) flock below the unselected Control. Inbreeding probably also counteracted the pull towards improving egg production exerted in the (H +) flock by family selection with a mean positive selection differential of 11.2 eggs.

This is also shown by the calculations presented in Table 1, where the theoretically expected gains in the production index of the (H +) flock are compared with the observed changes, using the production index of the Control flock as basis, thus eliminating between-year variations caused by changes in the environment. The table shows that the observed progress in the production index of the (H +) flock fell behind the expected one from the H-generation onwards, probably under the pressure of increasing homozygosity caused by the accumulative effect of continuous inbreeding.

It must also be considered that constant inbreeding with selection reduces genetic variability (Lerner, 1950, p. 116), and makes the degree of heritability (h^2_{fa}) smaller, thus slowing down the expected genetic changes obtainable per generation. In comparing the (H +) flock with the M flock, one has to consider that in the latter, not only was inbreeding strictly avoided, but also the efficiency of family selection was further improved by superimposed individual selection within the selected families. Finally, selection on a survivor basis in the M flock, although practised for one character only (Tandem method), might be more effective than selection based on the production index with a probably lower degree of heritability.

Furthermore, whereas Hagedoorn recommends a system of keeping all half-sibs in separate pens without trapnesting, the pullets of the (H +) and (H —) flocks at Werribee were randomly distributed over all available laying cages. Consequently, the Werribee system avoided a pitfall of the Hagedoorn system, which tends to increase environmental variation between tested half-sib families and thus reduces family heritability (h^2_{fa} — see Lerner, 1950, p. 211). Therefore, the Hagedoorn system, under the condition of the Werribee flocks, will tend to achieve better genetic progress per generation than would have been obtained with families housed in separate pens, as recommended by Hagedoorn.

(c) Adult mortality

Up to the F-generation selection did not succeed in differentiating the (H +)- and the (H —) flocks. From then onwards mortality increased in the (H —)

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*Part-annual egg production records, referring to the K-generation, which have become available after the reading of this paper at the Armidale Conference, confirm the conclusions drawn from the J-generation.

flock until it eventually surpassed mortality in the control flock. The F- and G-generations of the (H +) flock showed considerably lower mortality than all other flocks, particularly in the group of deaths caused by neoplasms. Autopsy data are available and have been analysed for the F-, G-, H-, and J-generations (Allen and Skaller, 1956), showing mean mortality from neoplasms as 4.8 per cent. for the (H +) flock, compared with 9.3 per cent. and 5.6 per cent. for the Control and M flocks respectively. This favourable picture changed, however, for the J-generation, where the (H +) flock's mortality increased steeply and surpassed the level of the Control and M flocks. A chi-square test showed that differences in mortality rates between the (H +) flock and the pooled Control and M flocks were insignificant for the F-generation, but significant for the G-, H-, and J-generations, with the (H +) flock having lower mortality for the G-, H-generations but higher mortality for the J-generation. Mortality differences were also tested for the (H +) flock against the (H —) flock, revealing a significantly higher mortality for the (H —) flock for the H-generation only.

It seems, therefore, rather doubtful whether selection combined with inbreeding succeeded in reducing mortality in the (H +) flock. This would agree with Hay's (1955) conclusion that "selection for natural immunity is certain to give a slow response when not directed toward one specific disease"; and that . . . "heritability estimates of viability show a very low value".

(d) Chick mortality and hatchability

From the published data of various workers and our own unpublished data it is known that inbreeding reduces hatchability and increases chick mortality. It is, therefore, interesting to note the effect of a slower rate of inbreeding, as practised through half-sib matings in the Hagedoorn system, upon these characters. The relevant data, presented in Table 2, show quite clearly, especially if compared with the outbred M flock, the deleterious effect of inbreeding, and are not in agreement with Hagedoorn's claims (1953, p. 59).

TABLE 2

EFFECT OF INBREEDING ON SOME CHARACTERS OF FITNESS

Generation	Hatchability % Flock				Chick Mort. to 6 Wks. Flock				Reprod. Index* Flock			
Flock	C	M	H+	H—	C	M	H+	H—	C	M	H+	H—
H-1953	63.4	73.9	63.8	60.6	8.6	10.6	6.6	17.6	50.2	61.8	53.2	46.4
J-1954	70.2	79.9	62.5	62.1	18.4	18.1	20.4	33.2	53.3	64.8	43.9	35.8
K-1955	68.5	77.9	66.0	—	16.1	15.6	28.5	—	46.1	59.1	44.1	—
Annual Mean	67.3	77.2	64.1	61.3	14.4	14.8	18.5	25.4	49.9	61.9	47.1	41.1

*Reprod. Index = Fert. % x Hatchability % x Chick Viability % to 6 Wks.

(e) Variability

Hagedoorn (1953, p. 54) states that inbreeding will reduce the phenotypic variability of egg production in a flock. Co-efficients of variability were, therefore, computed and are presented graphically in Fig. 4. Mortality, which, of course, considerably affects the variance of the production index, is not homogeneous in the four flocks (Allen and Skaller, 1956), as selection for or against viability was practised only in the two Hagedoorn flocks. For this reason, the data presented in Fig. 4 refer to survivors at 72 weeks of age. This treatment seems to be justified as we are interested in the effect of inbreeding on the variance. The data presented do not suggest that inbreeding, as practised in the (H +) and (H —) flocks, reduced phenotypic variability.

(f) The number of sires which can be tested

Serious obstacles are encountered in testing a sufficient number of sires by half-sib matings and at the same time maintaining the size of the flock over successive generations; these circumstances are essentially independent from the reduction (if any) of reproductive fitness due to inbreeding. The nature of this self-limitation can be elucidated as follows:

Let a flock, in any given year, contain F mature females; let N be the number of breeding dams chosen from them, and S the number of sires to which these dams are mated. Then in the next generation, the flock is expected to contain $F' = ND$ mature females, where D is the net annual reproduction rate, i.e., the number of daughters, reaching sexual maturity from the average dam, in the average year. Under the Hagedoorn system only the daughters of one sire (namely, the best), are available for further breeding! i.e., if one intends to test sires each year, the expected number of breeding dams now becomes $N' = F'/S$. Repeating the argument for the next generation we get

$$F'' = N'D = F'D/S = ND^2/S.$$

It is seen that if one desires to avoid a gradual decline of flock size, one must have (at least on the average over the generations)

$$N \geq F/D$$

and

$$D \geq S,$$

that is, the number of sires that can be tested annually, cannot on the average exceed D. This circumstance seems to render the Hagedoorn system impracticable for all species of domestic animals with a low reproductive rate, and only applicable to species with a high rate of reproduction such as pigs and poultry. Furthermore, this inherent restriction of the number of families to be tested reduces the expected annual genetic gains from family selection (H. N. Turner, personal communication).

Even in poultry, consideration of efficient management and the need to minimise the effects of date of hatch on part-annual egg production (which must be the basis of selection if breeding from pullets) effectively limit the breeding season, and consequently D. Under normal conditions of fitness and the normal 1 : 1 sex ratio, one daughter per dam per weekly egg production is expected to reach sexual maturity; hence, in a six weeks' hatching season, $D = 6$. Thus, in the long run, not more than six cockerels per year can be tested as sires.

In addition, the reproductive fitness of our Hagedoorn flock appeared to fall below average (see Table 1), and consequently we could test on the average at most 5 sires, as we wanted to keep the flock size constant and did not wish to extend the hatching season beyond the period needed to maintain flock size in the flocks under our other breeding system.

IV. CONCLUSIONS

Results from experimental work with sheep by different workers and our own experiments with poultry confirm the theoretical objections which can be raised against the Hagedoorn nucleus system as a highly efficient breeding system which could be recommended to breeders. Family selection is not superior to mass selection if we wish to improve characters of high or even medium heritability, such as fleece weight. And even where family selection is superior to mass selection — particularly in species where the male does not exhibit the characters for which mass selection is practised, such as egg production in poultry — the efficiency of selection increases with the number of families tested up to an optimal point, which is below the number of families which can be tested under the system of half-sib matings inherent to the Hagedoorn nucleus scheme.

The inbreeding resulting from continuous half-sib matings did not improve hatchability, reduce viability, nor produce stock in which "inbreeding degeneration will cease to occur". (Hagedoorn, 1953, p. 59). On the contrary, the evidence presented suggests that under the impact of continuous inbreeding, as practised under the Hagedoorn system, hatchability was reduced, chick mortality increased, and egg production only slightly increased. This was in spite of family selection, a mean selection differential of 11.2 eggs over 8 generations, and a system of randomly housing all pullets instead of housing families separately and thus reducing heritability.

Furthermore, it was found that the system of half-sib matings limits the number of sire-families which can be tested below its optimum, as no more sires can be tested than the expected number of daughters per dam which will reach sexual maturity each year.

The Hagedoorn system is, therefore, only applicable to poultry and pig breeding, and cannot be recommended as an efficient system of breeding even for these species.

V. ACKNOWLEDGMENTS

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DISCUSSION

Mr. KNIGHT: Eye appraisal should be replaced with measurements. Morley showed that inbreeding with sheep depressed wool production. Continued inbreeding leads to a large increase in homozygosity which is always harmful.

ANS.: Morley has shown that inbreeding of Merinos depressed bodyweight and wool yield, both characters with high heritability, particularly bodyweight do generally not suffer from inbreeding at the same degree as characters with low heritability. This applies also to the bodyweight of our Werribee inbred lines of poultry which were only slightly depressed by inbreeding.

Miss TURNER: If I may comment on Mr. Knight's question, I think it is a matter of balancing the superiority of a sire against the depressing effect of inbreeding. We need more information on the effect of inbreeding before we can answer this question.

Dr. Morley has estimates of inbreeding which are high. As his are the only Australian estimates so far, I think he would agree we need some more before we can draw firm conclusions.

Mr. McDONALD: Following Dr. Hagedoorn's visit several poultry breeders around Sydney began breeding on the lines he recommended. Their results were similar in the early stages to those of Mr. Skaller, namely, 'an increase in production for one or two generations. This can be interpreted merely as due to the elimination of inferior sires and would follow the use of any progeny testing. In subsequent generations either a decline in production or a failure to increase was found, as at Werribee. In practice these breeders have now made the adjustments as Sykes suggests to Hagedoorn's plan and although they claim to follow the plan, they are actually carrying out a progeny test of sons of the superior sires selected in previous generations.

ANS.: In the beginning inbreeding is not harmful. If a good sire is used then progress will result despite one or two generations of inbreeding. But if inbreeding is continued consistently, then characters connected with the fitness of a species will show the depressive effect of inbreeding.

Mr. ROBERTS: Is the harmful influence spoken of as coming from inbreeding equivalent to saying that there are undesirable recessive genes which manifest themselves to an increasing extent as inbreeding progresses?

ANS.: That was Hagedoorn's idea, but there is evidence that apart from this harmful effect, caused by recessive genes becoming homozygous, there is also a depressive effect caused by "homozygosity per se". This makes an animal less adaptive to changes in the environment, just the opposite to what happens in out- or crossbreeding, which results in heterosis.

TABLE 1

THE EFFECT OF INBREEDING ON THE DEVIATION OF THE OBSERVED FROM THE EXPECTED GAINS IN THE PRODUCTION INDEX OF THE (H+) FLOCK

	Selected Family		Mean Prod. Index 72 weeks		(H+) FLOCK							
									Expected			
Generation	No. of Pullets n_{fa}	Selection Differential (i)	(H+) flock	Control flock	Family heritability of Prod. Index h^2_{fa}	Expected gain in Prod. Index in one generation ΔG	Observed gain in one generation	Deviation of observed from expected gain of P.I. in one generation	Cumulative gain ΔG	Prod. Index using Control as Standard	Deviations of observed from expected Prod. Index	Coeff. of Inbreeding (%)†
B	104	+ 6	150	150	0.86					150.0		
C	12	+ 6	146	142	0.44	+ 5.2	+ 4	— 1.2	+ 5.2	147.2	— 1.2	12.5
D	35	— 0.5*	144	133	0.68	+ 2.6	+ 7	+ 4.4	+ 7.8	140.8	+ 3.2	21.8
E	43	+27	141	138	0.72	— 0.3	— 8	— 7.7	+ 7.5	145.5	— 4.5	30.4
F	75	+ 8	161	128	0.81	+19.4	+30	+10.6	+26.9	156.9	+ 4.1	38.0
G	51	+21	140	105	0.75	+ 6.5	+ 2	— 4.5	+33.4	138.4	+ 1.6	44.8
H	21	+11	154	115	0.56	+15.8	+ 4	—11.8	+49.2	164.2	—10.2	51.0
J	61	+ 6	126	123		+ 6.2	—36	—42.2	+55.4	178.4	—52.4	56.2

*The second ranking family out of 3 had to be selected, as the best family was too small.

†Computed for continuous half-sib matings. Actual coefficients are slightly lower on account of matings of cousins in some instances. The value for the H-generation was 46-48 per cent.

Formulae: (1) $\Delta G = h^2_{fa}.i$

(2) $$h^2_{fa} = \frac{}{2\,[1 + (n-1)\,rh^2]}$$

Substitute for:

$r = 0.25$ = coefficient of relationship of half-sibs.

$h^2 = 0.20$ = estimated individual heritability for the Production Index in Werribee Flock. (J. A. Morris, unpublished data)

then—

$$h^2_{fa} = \frac{n\ 0.05 + (n.\ 0.05 + 0.15)}{2\,[1 + (n-1)\ 0.05]} = \frac{n + 1.5}{n + 19.0}$$