The goal of the animal breeder is to improve the performance by his favorite species for those traits that in appropriate combination result in maximum productivity of products of importance and value to man. Modern agriculture also requires that the procedures employed be the most efficient possible in terms of the conversion of feed stuffs to animal products and in the economic production of the vast numbers of animals used to produce those products.

The effect of heterosis or hybrid vigor upon productivity has been known for a long time. The plant breeder has made far greater use of this phenomenon than has the animal breeder but in some instances the latter has used it successfully for a relatively long time. The breeders of domestic chickens were the first to violate the tenets of the purebreed associations when they found, more than 50 years ago, that the progeny of a cross of Rhode Island Red $\text{♂}$ and Barred Plymouth Rock $\text{♀}$ were often superior in egg production and, because of sex-linked barring, sex could easily be identified at hatching. Subsequently it was demonstrated that useful levels of hybrid vigor could be obtained by crossing unrelated strains within a single breed of chickens. Around the world today most commercial stocks of chickens, whether they be for egg-production or meat purposes, are produced by crossing breeds or unrelated strains so as to utilize the benefits of heterosis. In their quest for maximum productivity the poultry breeders utilize a variety of procedures. We will discuss here a method of selection and breeding which, in a long-term experiment, met the objectives set forth in the initial paragraph above. It depends on selection for improved performance within closed strains and the utilization of the heterosis realized when the continually improving strains are crossed.

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ORIGIN AND DEVELOPMENT OF THE PARENTAL STRAINS

Four strains of White Leghorns were established in the 1930's for the purpose of subsequently combining them in a 4-way cross, as had been done by the corn breeder. Limitations of space soon made it necessary to eliminate two of those strains. The Cornell C-resistant strain, started in 1935, and the Cornell K-resistant strain, started in 1936 by using C-strain bulls and Kimber-strain hens, with some additional Kimber-strain introductions in 1940, have been maintained as closed-breeding populations ever since.

a) Selection procedures: Each strain was bred for resistance to disease and for other traits of economic importance. Selection of breeders was based upon a progeny test. Outstanding sires and dams were used as long as they reproduced efficiently or until better ones were found. A detailed account of the selection procedures used and of the size of the breeding program has been presented elsewhere (1). Briefly, with the use of multiple shifts of cockerels (2) since 1943, it has been possible to produce 1000 ± daughters and to test 15 or more sires per strain each year. Compared to modern-day practices of the commercial breeders, our program was rather limited by the numbers of breeding animals we could employ, but it was on a scale now feasible for some breeders of large animals.

b) Response to selection: As a result of the selection practised, both the C and K strains responded by demonstrating improvements in several traits, especially those given priority. These included viability, egg production, egg size, and body weight. As shown in Table 1, the over-all productivity (eggs per hen starting the test) nearly doubled. This change resulted from improved ability to live and to lay. They also laid larger eggs.

The remarkable reduction in mortality was due primarily to the genetic improvement in resistance to disease, for the use of other methods of preventing disease such as isolation, drugs, antibiotics, disinfection, or vaccination were not employed. A control strain, selected especially for susceptibility to neoplastic diseases (Marek's and lymphoid leukosis) and continuously intermingled which the others, had in the terminal three-year period a mortality of 59.8 %, which demonstrates that the low levels of 8.0 and 12.7 % for the resistant strains were not a consequence of reduced exposure.

Compared to the K strain, the C strain matures a little earlier, lays more but slightly smaller eggs, has a higher mortality from leukosis and also lower fertility and hatchability. A list of 23 other differences has been reported (1). Because of these differences one might expect these strains to show a good level of heterosis when crossed.

INITIAL TEST FOR HETEROSIS

Reciprocal two-way crosses were made in 1948 and 1949 (3). At that time the C and K strains had been bred as closed flocks for more than a decade. The levels of performance attained by them are shown in Table 1, as averages for four years, 1947-1950. A limited number of proven sires in each strain produced both
pure-strain and strain-cross daughters, hatched at the same time and raised together. The hybrids showed good evidence of heterosis by an increase in egg production, larger egg, larger body size, and earlier maturity.

Clearly these two strains had a good specific combinability. It was planned, therefore, to make appropriate inter-strain crosses at 10-year intervals. Limitations of housing space for the testing of progeny precluded more frequent production and testing of hybrids.

**TABLE 1**

**Effect of selection within the C and K strains upon their performance to an age of 500 days** *

<table>
<thead>
<tr>
<th></th>
<th>1936-38</th>
<th>1947-50</th>
<th>1967-69</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C</td>
<td>K</td>
<td>C</td>
</tr>
<tr>
<td>Egg production, number:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per hen completing test</td>
<td>169</td>
<td>165</td>
<td>186</td>
</tr>
<tr>
<td>Per hen starting test +</td>
<td>116</td>
<td>120</td>
<td>149</td>
</tr>
<tr>
<td>Egg weight, at one year, g</td>
<td>55.1</td>
<td>57.8</td>
<td>59.1</td>
</tr>
<tr>
<td>Body weight, at one year, g</td>
<td>1745</td>
<td>1881</td>
<td>2015</td>
</tr>
<tr>
<td>Mortality, 43-500 days, %:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>From all causes</td>
<td>51.5</td>
<td>44.4</td>
<td>38.7</td>
</tr>
<tr>
<td>From neoplasms</td>
<td>14.2</td>
<td>11.3</td>
<td>10.5</td>
</tr>
</tbody>
</table>

* Averages for all $\varphi \varphi$.
+ At 160 ± days of age.

**SUBSEQUENT TESTS FOR LEVELS OF HETEROSIS**

a) **10 years later:** In 1959 crosses were made between young untested breeders which produced more than 750 purebred daughters and a similar number of hybrids. Management of the flock was similar to that employed 10 years earlier, up until housing time at approximately 22 weeks of age. A major change of facilities for housing ready-to-lay pullets prevented attainment of normal levels of performance. Both lower production and higher mortality were caused by unusual environmental stresses on the birds under test. To compare the performances of that year with those obtained 10 years earlier, egg-production data had to be adjusted. The details of the experiment and the procedure and rationale employed for estimating the effect of the environment for any one year have been described earlier (1).

b) **20 years later:** In 1969 both young breeders and proven sires mated to previously untested yearling hens were used. These produced 1553 pure-strain and 1747 strain-cross daughters, with approximately the same number of each type from each of the two strains of sires.

After an early exposure to disease [first 11 days (4)] the chicks were reared in confinement in one large conventional poultry house until point-of-lay rather than on a grass range as had been done in the previous tests. The effects of three
pathological conditions not seen in previous years made it essential again to correct egg-production data so that the results might be more indicative of productivity under more normal situations.

c) **Data recorded:** Records were obtained of performance by each hen: such as age at first egg, production to 500 days of age, weight of three eggs laid when the birds were approximately one year old, body weight of layers only, and the cause of death as determined by necropsy. All data have been summarized on a basis of sire-family averages.

**Results**

a) **Age at first egg:** Successful selection for production to a given age is usually accompanied by a reduction in age at first egg. As a consequence, the average age at first egg for the K strain was reduced from 186.5 days at the time of the first cross in 1948-49 to 170.3 days in 1969. In the C strain the reduction was from 177.1 to 168.7 days (Table 2).

Heterosis is expressed by an earlier maturity. In these three tests it reduced age at first egg by an average of 5, 5.4, and 6.3 days. The effects of heterosis were greater on the progenies of K-strain sires than on those from C-strain sires.

b) **Egg production:** Between the first and last test for heterosis, the egg production by the pure-strain daughters that survived the 500-day test period, corrected for the year of the cross, rose in the C strain from 190 to 246 and in the K strain from 175 to 226. The actual (uncorrected) production for all $\varnothing\varnothing$ in these two strains, for the years 1967 and 1968 combined, had been 248.5 and 234.5 eggs, hence the correction factor was not excessive. The potential use of these strains as parents of hybrids thus improved considerably (Table 2).

The strain-cross daughters maintained or slightly improved their superiority in egg production which, for the reciprocal crosses, averaged 21.7, 25.0, and 25.4 more eggs in the three tests. The improved capabilities of the parental strains did not modify their combinability. In the first two tests there were, for the reciprocal crosses, similar increases in egg production by the hybrids when compared to their respective purebred half-sisters. However, in 1969 the hybrids from the K-strain sires exceeded their purebred half-sisters by 33 eggs while those from C-strain sires differed by only 18 eggs. The better production, characteristic of the C strain, was also found, in all tests, for the hybrid which received her sex chromosome from that strain. The actual difference in egg production between the reciprocal crosses declined; being 20, 10, and in 1969 only 2 eggs more for hybrid daughters of C-strain sires. Currently there is little or no difference between the reciprocal crosses in egg-production potential.

c) **Egg weight:** The objective of the poultry breeder is to have an egg that weighs 56.7 to 59.0 g or slightly more. The equipment and cartons used in handling and packaging them for market distribution are designed for eggs of that size. Data in Table 2 show that the C and K strains were already producing eggs of that size at the time of the first cross, hence further selection for larger eggs was discontinued.
TABLE 2

EVIDENCE OF HETEROSIS AFFECTING VARIOUS TRAITS *

<table>
<thead>
<tr>
<th>Sires</th>
<th>1948-49</th>
<th>1959</th>
<th>1969</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Purebred</td>
<td>Hybrid</td>
<td>Purebred</td>
</tr>
<tr>
<td>Age at first egg, days</td>
<td>K: 186.5, C: 177.1</td>
<td>K: 171.6, C: 171.6</td>
<td>K: 170.3, C: 168.7</td>
</tr>
<tr>
<td>Egg production, number:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per hen completing test</td>
<td>K: 177.3, C: 197.6</td>
<td>K: 185.0, C: 191.8</td>
<td>K: 217.1, C: 234.3</td>
</tr>
<tr>
<td>Per hen starting test</td>
<td>K: 157.8, C: 158.0</td>
<td>K: 171.5, C: 174.5</td>
<td>K: 199.0, C: 215.8</td>
</tr>
<tr>
<td>Egg weight, at one year, g</td>
<td>K: 59.9, C: 58.8</td>
<td>K: 59.8, C: 59.4</td>
<td>K: 59.1, C: 58.8</td>
</tr>
<tr>
<td>Body weight, at one year, g</td>
<td>K: 2055, C: 1997</td>
<td>K: 1912, C: 1921</td>
<td>K: 1720, C: 1784</td>
</tr>
<tr>
<td>Mortality, 43-500 days, %:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>From all causes</td>
<td>K: 25.5, C: 33.1</td>
<td>K: 16.0, C: 19.7</td>
<td>K: 13.9, C: 14.4</td>
</tr>
<tr>
<td>From neoplasms</td>
<td>K: 8.8, C: 8.3</td>
<td>K: 1.4, C: 3.6</td>
<td>K: 1.1, C: 5.4</td>
</tr>
</tbody>
</table>

* Data are averages for sire-families.
+ Difference from purebreds.
Hybrids usually produce eggs larger in size than the mean for the parental stocks. This relationship was observed in 1948-49 and in 1959, when the hybrids laid eggs averaging more than 61 g, while those from the pure-breds averaged about 59 g. In 1969, egg size was not influenced by heterosis, for both types averaged 59 g.

d) **Body weight:** In this study the hybrids always had slightly higher body weight than either of the two corresponding groups of pure-strain half-sisters. They exceeded the mid-parent values by an average of 3.9% (range 1.9 to 6.8%).

Selection for smaller body size during the last 13 years resulted in a reduction in body weight by 11 and 16% for the pure C- and K-strain daughters. The corresponding reduction in body weight of the hybrids was 15%.

e) **Mortality from 42 to 500 days of age:** There were no special benefits from heterosis upon viability after the early brooding period. The response of the pure strains combined to selection for resistance to disease over the 20-year period resulted in a decrease in mortality from 31.5% in 1948-49 to 13.7% in 1969. When the data are limited to the pure-strain daughters from the sires used to produce the crosses the corresponding figures were 29.3 and 14.1%, respectively. The hybrids had mortalities of 30.0 and 13.4% at the time of the first and last crosses. Because of specific disease conditions present in 1969, mortality was somewhat higher than it had been in the two previous years when it averaged 8.7% for the C and K strains combined.

**TABLE 3**

**Effect of heterosis of the hybrid embryo on hatchability of fertile eggs from hens approximately one year old**

<table>
<thead>
<tr>
<th></th>
<th>K-strain eggs</th>
<th>C-strain eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dams no. +</td>
<td>Purebred %</td>
</tr>
<tr>
<td>1959</td>
<td>100</td>
<td>88.4</td>
</tr>
<tr>
<td>1969</td>
<td>77</td>
<td>90.2</td>
</tr>
</tbody>
</table>

* Unweighted averages for sire-families.
+ Average number of dams having either pure or hybrid embryos within each strain.

f) **Hatchability:** High hatchability is essential for the efficient production of chicks. It is affected by heterosis in two ways: 1) by the viability of the embryo and 2) by the influence of the dam on the quality of the egg. Both are usually used in the production of commercial chicks.

In our crosses hybrid chicks hatched better than purebreds (Table 3). The K strain has about 5% better hatchability than does the C strain. During the last 10 years selection within the pure strains raised hatchability in both. The point to be emphasized is that as hatchability was improved in the pure strains, so was it in the crosses.
DISCUSSION

Several methods have been used by poultry breeders to produce hybrids that excel in productivity. Crosses between existing strains, between three or more inbred lines, and between strains selected specifically for combinability (reciprocal recurrent selection-RRS) have been employed. Except for RRS, success depends upon the fortuitous ability of the strains to nick well, that is, to produce progeny better than either of the pure strains. The development of improved hybrids depends upon testing more and more combinations to identify some better ones. In the case of RRS the breeder is really not concerned with the performance of the pure strains, but rather only with that of the hybrids.

We believe that it is important to improve the performance of the pure strains, to make them more efficient in the production of superior hybrid progeny. The procedure we have discussed does just that. Between 1959 and 1969, the pure strains improved to the extent that they would produce an estimated 22% more hybrid progeny, which, in turn, could lay 20% better than those of 10 years earlier.

That the performance of the hybrids is related to the performance of the non-inbred parental strains is generally accepted. For example, Osawa and Harada (5), who tested 122 crosses between races of silkworms, found that the weight of cocoons of the hybrids excelled the mid-parent weight by a rather consistent value over a range of mid-parent values from 1.40 to 2.15 g.

It seems clear that in searching for the highest level of productivity, crosses of existing superior strains are likely to be most rewarding. Those that yield the largest increment due to heterosis, with due consideration to the actual performance by the hybrids, should, in our opinion, be subjected to further genetic selection by progeny testing within the pure strains. Our results indicate that such selection can be effective, although probably not to the same extent in strains already at high levels of performance, and that as they are improved so will be the performance of the hybrids obtained by crossing them to take advantage of heterosis.

SUMMARY

Progeny-test breeding within two non-inbred but closed strains of White Leghorns resulted in marked improvements in various traits, including resistance to disease, that collectively are essential for high productivity.

Reciprocal crosses between them in the course of their early development revealed excellent combinability for productivity. Over the following 20 years egg production was increased by about 50 eggs per hen and mortality from 42 to 500 days of age was decreased from 32 to 10%.

Reciprocal crosses between the two strains at 10-year intervals, with comparisons between pure-strain daughters and their strain-cross sisters from the same sires, showed that the high level of heterosis initially present was, if anything, slightly improved. The hybrids laid 25 more eggs to an age of 500 days than did their pure-strain half-sisters and survived equally well.
The excellent performance of the pure strains makes them ideal for the efficient and economical production of hybrid progeny. Since the increased productivity resulting from heterosis remained constant over the 20 years, maximum productivity was obviously obtained by continued selection within the parent strains proven to possess specific combinability.

RESUMEN

Una prueba de progenie entre dos líneas de Leghorn blanca, no criadas en consanguinidad, sino en estirpe cerrada, produjo una marcada mejora en varios caracteres, entre ellos la resistencia a las enfermedades, lo cual es colectivamente esencial para obtener una alta producción de huevos.

Los cruces recíprocos entre dichas líneas desarrollaron rápidamente una excelente combinación para la producción. Al cabo de 20 años consecutivos la producción huevera se incrementó en unos 50 huevos por ave; la mortalidad decréció desde el 32 al 10 %.

Los cruces recíprocos entre las dos líneas, a lo largo de 10 años, comparando la línea pura de hijas y la cruzada de hermanas provenientes de los mismos progenitores, demostraron que un alto nivel de heterosis estaba inicialmente presente, siendo ligeramente mejorado. Las híbridas pusieron 25 huevos más a la edad de 500 días que la línea pura de medias hermanas, y sobrevivieron igualmente bien.

El excelente rendimiento de las líneas puras las hace ideales para una producción eficiente y económica de híbridos. Como el incremento de la producción resultante de la heterosis permanece constante durante más de 20 años, la producción máxima fue obtenida sin duda mediante la selección continuada dentro de líneas de antepasados probados que poseen una capacidad específica de combinabilidad.

RESUME

La sélection par l'étude de la progéniture de deux souches non-consanguines mais fermées, conduisit en une amélioration marquée le plusieurs traits, y compris résistance à la maladie, qui dans l'ensemble sont essentiels à une haute productivité.

Des croisements réciproques entre ces souches pendant la période initiale de leur développement révèla une excellente abilité à combiner les traits favorables à la production. Pendant les 20 années suivantes la production des œufs fut augmentée par environ 50 œufs par poule et la mortalité fut diminuée de 32 à 10 % dans l'intervalle d'age de 42 à 500 jours.

Des croisements réciproques entre les deux souches à des intervalles de 10 ans, avec des comparaisons entre les soeurs de la même souche et leurs soeurs provenant de croisement avec les même pères, montrérent que le haut niveau d'hyérosis initialement present fut, même légèrement amélioré. Les hybrides pondirent à l'age de 500 jours 25 œufs de plus que leur demi-soeurs de souche pure et vecurent aussi bien.

L'excellente performance des souches pures en font un moyen efficient et idéal pour la production d'une progéniture hybride. Du moment que l'augmentation
de la productivité resultant de l'hétérosis resta constante pendant les 20 ans, la productivité maximum fût évidemment obtenue par sélection continue parmi les souches possédant des caractères à propriété additive.

REFERENCES
