by that lethal factor - on the average, I calculate that you lose about 3⅛ per cent. That is an extreme programme. In practice, you would not be likely to use a bull every other generation that was a carrier. Sometimes, you might do worse than that, and show an epidemic of the killing of calves by lethal factors, but it would happen very rarely. From the point of view of national production, lethal factors matter very little, as Dr. McMeekan pointed out five years ago. I do not say that they should be neglected entirely. A breeder should tell, and occasionally drastic steps might be justifiable, but, in general, the tendency is for geneticists as well as other people, to overrate them.

MR. RANSTEAD: We have no Dexter Kerry cattle, but they have at Home - one calf in every four is a bull-dog calf. When they get one dose of the lethal, they have the short legs, and when they get two doses they are the bull-dog calf.(x) So those farmers are very much affected by the lethal character.

MR. HANCOCK: I would like to confirm Dr. Dry's statement that that importance of lethals is not very great, providing it is a random breeding population. In random breeding populations, there will always be some inbreeding, but only to a certain extent, and in those cases you will have lethals creeping in. If you start with a population that contains 25 per cent. lethals, all lethals die, and in the next generation only 11 per cent. of lethals will be born, and in the tenth generation there will be only 1 per cent. left. But that is when you are working with a random breeding population. If A.I. is used extensively, however, it is quite possible that the genes of some bulls will be spread to a much higher degree than with a random population, and in such cases lethals may be of some great economic importance. I know of breeds in Northern Europe which have been altogether spoiled, not by a straight-out lethal but recessive factors that affect their fertility. There is also a lethal factor that gained great spread in Europe, because the bull which introduced the factor in the breed was one of three imported bulls, and, being an imported bull, he gained great prominence, and several hundreds of his sons were sold. It is calculated now that a great proportion of the Ayrshire breed in Finland is attended by this factor.

(x) These calves are not viable; they die and are aborted usually at about the seventh month.

THE INFLUENCE OF HETEROSIS IN THE PROGENY TESTS

From records of 32 years' breeding experience in seventeen herds of the Government of India's Dairy Farms.

by

J. MATSON, OPARAU.

The value of the progeny test as a means of raising the yield of milk cattle to the highest possible level, so far as it can depend on inherited characters, has won popular acceptance. It is not my purpose to decry it but to suggest that there is a danger of erroneous interpretation of the phenomena, through the influence of heterosis in certain cases.

These suggestions are based on a continuing detailed study of the crossing of European cattle, chiefly Ayrshires and Friesians, with the native cattle of India, commonly called Zebu by Europeans, during a period of 32 years. I am speaking only of cattle which came under my personal observation and as to which I was able to satisfy myself that the records kept were reliable and complete.

In order that you may judge of the degree of credibility to accord to the figures, I mention that they pertain to quite large numbers and thus were not vitiated by individual reaction to environment.

In the early years the numbers in milk were a few hundreds but from 1912 when the Government decided on expansion they increased rapidly until when I left the country there were some 4,500 dairy cattle in herds which I had myself established or of which I was then in control.

Naturally the total varied from time to time and similarly the proportions of the classes making up the herds. Something like one half were water buffaloes, which do not concern us today but the remaining members of the herds were cows, all native in the beginning but leavened with increasing numbers of crossbred cattle until these were in large preponderance.

These cows again fall into classes, the F1 generation, the F2, and the back crosses to both sides. It is the F1 generation with which I am concerned first, and though I have not now got exact figures for the pre-1914-1918 war period, it is safe to say that well over 1,200 cows contributed to the study; these being the progeny of over 100 imported bulls.

One possible criticism is that for purposes of evaluating one milk yield against another it is important that the plane of nutrition shall be the same. As to this we had no means of comparing the nutritional environment of the female ancestors of the bulls we imported with that of their progeny and that defect (if it is one) is, of course, insuperable. So far as there was a difference my belief is that our standard was higher. I visited many herds in Europe and America both privately owned and in Research Institutions and I saw nothing better. During the last twelve years of my career we had organised the feeding on a system by which every animal was individually rationed. Each was weighed at intervals, her milk was weighed night and morning and tested for fat and non-fatty solids weekly. She was rationed on a basis of weight and the net energy value of her milk. The ration was adjusted, if necessary, weekly. Similarly the yields we recorded were to some extent affected by nutritional studies and experiment which were carried on continuously. For instance, in regard to varying the intake of mineral constituents of the diet or of varying the ratio of these one to another and yet again the influence of heredity on resistance to disease, etc., etc., but I do not think that any of these things can have affected materially the broad significance of the figures I am about to give you.

Now in the sire survey we take so many bulls and grade them according to whether (a) they have raised the yields of their daughters over those of their daughters' dams or (b) have kept them about the same level, or (c) have produced daughters showing lower yields on the average.

Further in the field of Class (A) we can give a figure of merit to individual bulls according to the degree of increase shown by their daughters.

If one were to go the round of the pedigree herds in New Zealand and buy one hundred bulls no one would expect that every bull would beget daughters better than their dams, and not only that, but that <u>every</u> daughter would be better than her dam, but that is what happened in regard to all the bulls we imported to India. However, the yield of Indian native cows is very low. In the beginning all were purchased cows and the yields averaged 118 lbs. fat for one variety of cows, and 140 lbs. for another, though odd individuals were found, about 1 in 200, that gave as much as 300 lbs., and those purchased herds by culling were brought up to an average of 200 lbs. Per-

haps it is just possible that, if one bought 100 Jersey bulls in New Zealand and mated them with 1,000 of the worst Jersey cows, all of the daughters might be found better than their dams. But the Indian examples do not end there.

You would not expect your 1,000 worst cows to produce a proportion of daughters which not only gave more than their dams but substantially more than any female in their sire's ancestry. Yet again this is what happened. Not with absolute certainty in the case of every bull because in regard to early importations of bulls we could not always obtain milk yield pedigrees (though an abundance of show yard successes), but I was at some pains during periodical world tours to enquire into the history of herds from which those bulls, whose daughters gave extremely high yields, had come and I came to the conclusion that the best daughters had no ancestor on the side of the sire which had given as much.

It should be understood that the number of bulls purchased increased year by year as greater success was attained by cross breeding but a number of the progeny had only one or two lactations at the time I ceased compiling the record. Nevertheless, that record showed that every bull with 20 daughters of 6 years of age, and some with less daughters, had at least one with a yield in excess of anything in his own ancestry, so far as the latter could be determined.

I will describe one or two of the outstanding examples:-

1. PARBATTI:

Her highest yield, the fourth, was given in a long lactation of 481 days. In the first 300 days 19,536 lbs., 4.6% milk, i.e. (897 lb. fat) and in the whole lactation of 481 days 24,153 lbs. milk - 1127 lbs. of fat. The dam of this cow gave 270 lb. fat in 307 days (a relatively good yield for a native cow).

The sire was a Friesian purchased in America and the highest yield in his ancestry was 16,000 lbs. 3.65% milk or 584 lb. fat. That is to say, he had begotten a daughter 300% better than her dam and 40% better than any ancestor.

Another notable example of this cross - Edna, from a dam of another variety and herself a very inferior milker. This dam's highest yield was 2,200 lbs. 5% milk in 270 days or 110 lb. fat. The daughter 15,324 lbs. 4.7% milk or 719 lb. fat in 360 days.

As to the Ayrshires, the bulls which I obtained had milk records behind them stated in gallons without fat percentage, and they ran 900 to 1,100 gallons. If you take the Ayrshire fat percentage at 4.2% that means a range of 378 to 462 lb. of fat. Few of these bulls failed to produce a daughter which exceeded the higher quantity.

The outstanding Ayrshire half bred, named "Bhatori", gave 11,890 lb. of milk and 542 lb. fat in 300 days with her second calf and 16,850 lb. of milk and 772 lb. fat in 359 days with her third. Her dam 220 lb. fat in 307 days.

As to other European breeds, there were 3 Shorthorns imported at one time and another. They had no milk records and their daughters were practically on a level with the Ayrshire crosses.

An official report compiled by order of the Government of India a few months after I retired, states that the Shorthorn and Ayrshire crosses gave yields 75% higher than the average of their dams, while the Friesian crosses were 100% better.

These averages are, however, somewhat difficult to compute because India is so saturated with disease; without disease the cross bred average yields would have been higher. I made an approximation for the Ayrshires once as follows:-

	Lbs. Fat.
Average of selected Indian cow	200
" " Ayrshire herds from which bulls came	320
Mean	260
Average of F1 daughters	360
Average of F2	250

Nobody has yet worked out a satisfactory formula for standardizing milk yield in regard to the number of days in milk - the interval between calvings or the number of days dry preceding a lactation - to mention only some of the modifying factors - so these are a purely personal estimate. I could not repeat it for Friesians as, except in Holland, I was denied figures for all the cows in pedigree herds.

We have seen, therefore, that all of a large number of bulls increased the yields of all daughters.

The test of the permanence of the increase should be found when in turn the grand-daughters are studied. Here we found quite a different picture. Every imported bull mated to the first cross produced daughters giving substantially less on the average than their dams.

The Friesian 2nd Cross fell moderately, some 20%, the Ayrshire 2nd Cross were 50% down, but I should explain here that the Ayrshire 2nd Cross did not stand up to the climate nearly as well as the Friesian.

More illuminating is the result of mating the F1 or half-breds with each other. Broadly speaking, the F2 Ayrshire cross-cattle thus produced reverted to rather less than the mean of their parent races in regard to average yield. At the lower end the F2 were down to the level of the native cow, at the higher end while no cows reached the heights of the first cross, an odd cow gave 400 lb. fat and about 10% 300 lb. or over, that is to say, they were on a par with the average of the Ayrshire herds from which the bulls came. The Friesians F2 were better than the Ayrshires. They gave more milk and there was no discernible difference in test.

Now as to applying my interpretation of the Indian figures, my suggestion is that although the Indian case is extreme, in that the two parent races were so widely differentiated, yet Heterosis is in operation in varying degrees in front of our eyes all the time. For it is not limited to crosses of what we call breeds, but is likely to make its appearance whenever two strains with no common ancestor within a large number of preceding generations, are mated, and I suggest further that the degree of Heterosis displayed will be greater in cases where the two strains have been bred for many generations in widely differentiated environments. Even where there is little difference in environment there is always the idiosyncracy of the breeder at work eliminating individual animals which do not please his fancy.

It would follow that the figure of merit accorded to bulls whose daughters improve on their dams needs to be judged in the light of the co-efficient of inbreeding of the parents. If the same ancestors appear here and there in the pedigree of both, the increase is probably reliable and may be expected to persist, but if there is no common ancestor it is probable that an increase will be limited, wholly or in part, to that generation, and this can only be determined as succeeding generations come under observation. I suggest that instances will be frequent where a moderate increase in the first generation turns to a

definite decrease in later ones.

Some of you may have noticed an article in the Exporter for April which describes an Ayrshire herd in Southland to which a Friesian bull, that is to say, with no common ancestry, was introduced and gave an increase of 35 lb. fat in his daughters. The whole credit of this is given to the bull's assumed inherited and transmissible milking capacity. In the light of what I have described I would ascribe it, until later generations confirm the figures, simply to the outcross. There is this further danger in such a case, that if now another Ayrshire bull is brought in and produces daughters giving 25 lb. less than the Friesian half breds he will be blamed for reducing the yield, though actually his daughters will be 10 lb. better than the grand-dams.

Many of the cases where an imported bull has begotten high yielding daughters followed by a slump in grand-daughters, seem to me ascribable to Heterosis in the first cross. But I wish to guard myself against being understood to deprecate importation. I do not suggest that our farm animals are so perfect that they cannot be improved by importation.

At this point I wish to go back to the 2nd Cross to the imported bull. As stated the daughter from every bull showed a fall, but this is the point, the degree of fall varied between different bulls and then it was possible to distinguish between them.

The suggestion is not new but it is very clear that with a group of herds at command and interchange of bulls a reasonable reliable estimate of the concentration of favourable genes in different bulls can be arrived at and this intrinsic benefit of the progeny test obtained.

There were many other most interesting results of the crossing in India, first in regard to the variations between the crosses according to which of the 3 basic types of native cattle were used - these types differ more widely one from another than do European cattle in general from those of India, and secondly in the curious variations in the result of breeding these types as pure strains, but it is not possible to enlarge on these things today.

DISCUSSION ON COL. MATSON'S PAPER:

COL. MATSON: There are four, what may be called basic types of cattle in India. They differ amongst themselves as widely as Indian Cattle in general differ from the European; even the universal hump is barely visible on individuals of one type whose habitat is the Western Punjab. Studies of Archeological discoveries and historical records suggest that these animals developed from cattle brought in, in the wake of invasions from the West as far back as that of Alexander the Great.

These cattle are the only ones which are kept purely for milking qualities and they appear to carry genes governing the milk production mechanism identical with those carried by the imported cattle. Against that, in the South, the cattle around Mysore are almost devoid of milking capacity, one could enclose many of their udders with two hands.

DR. CAMPBELL: There is one point I would like cleared up. Under the conditions of Col. Matson's work in India what was the environment like for pure-bred European cattle? If the environment was not good, the change in the production from F1 to F2 in those generations would probably be due to the concentration of the European blood at the expense of the Indian blood, in which case the factors which enabled the cattle to produce in that environment unsuitable to European cattle would be reduced, and thus although they had the genes for milk production,

those would not come into full production because of the lack of facilities to produce under the conditions. It is a well known fact that European cattle do not produce to their inherited capacity under conditions of temperature unsuited to them, and that would not apply in countries such as New Zealand.

COL. MATSON: The Ayrshire second cross, i.e., the back cross to Ayrshire could not be condemned for lack of genes favourable to milk production. She was not resistant to the climate. The Friesian back crosses were troublesome also in the first generation but not in later ones. Admittedly the genes for black colour would be dominant while the whole colour of the particular variety of Indian cattle in use would also be dominant so the crosses were black and this black conferred an ability to withstand the climate. That was the trouble with the Ayrshire and Shorthorn crosses - lack of pigment. However, the Friesians, as I say, were troublesome at first but that was due to disease. We had reason to suppose that the diseases were largely carried by insects so during the last twelve years we dipped the whole of the cattle regularly from which time the Friesian second cross was entirely satisfactory. They fell about 20% in yield on their first cross mothers - not 20% of the increase shown by those mothers - but of the whole yield. I do not think lack of resistance to climate affected the Friesian.

I did try to breed and keep pure European cattle and failed completely with Shorthorns. I succeeded with Friesians but the locality was rather better as to climate than most of the other plains stations and anyway it was so late in my career that I could not say how some of the young stock continued in later life.

MR. DICK: While I was in Egypt last year, another member of this Society and I were in Maadi together, and by the liberal use of "backsheesh" got on good terms with the Secretary of the Egyptian Minister of Agriculture, and through his services we had a most interesting stay on one of King Farouk's experimental farms. I was most interested in the Colonel's paper, because on this station they were doing extensive work on the crossing of English and imported dairy breeds - Friesian, Shorthorn and Jersey - with the Egyptian animal. I do not know how closely the Egyptian animal resembles the Indian.

COL. MATSON: The geographical distribution of the Zebu extends to North East Africa so no doubt there is considerable admixture with the cattle of Egypt.

MR. DICK: The experience of Dr. Maki, whom I think is about the best native Egyptian scientist in Egypt, and who studied under Crewe of Edinburgh, was that he got considerable improvement on the first cross. He was trying to retain the high fat test of the gamoosa - 28 per cent - and improve the milk yield, which is low, by crossing with English breeds, but he ran up against the same trouble, and found that for maximum or optimum disease resistance, he had to reduce the English blood to a minimum. He has been working on that project for only about the last five years, and consequently has not nearly as extensive observations as the Colonel, but the evidence is such that the percentage of English blood will have to be fairly low, but even within that limitation he was making increases in the first cross.

COL. MATSON: Regarding resistance to disease no Indian commercial farmer could have done the things that I did to control the incidence. He could not have provided expensive concrete dips or a host of other things; he could not have had a veterinary surgeon on his staff to advise him all the time and so on but although the East is riddled with disease no doubt in the long run measures will be found to protect the more susceptible but functionally more efficient European cattle.

DR. FILMER: I would ask whether the question of the resistance of the animals to the climate, as against disease has been carefully taken into account. A considerable amount of work has been done recently in the tropics in regard to the effect of temperature on European breeds of cattle, and it has been shown in the Philippines and elsewhere that many of the European breeds do not stand up to high temperatures as well as some of the native breeds. Without going into too many details, one could mention that respiration and heart beat and so on, are generally faster in the high temperatures in European cattle, than they are in the native cattle, and it has been suggested that that is, in part at least, due to the greater number of sweat glands in some of the native cattle than European cattle. So it would not necessarily be a question of resistance to disease, but adaptability to climate. I am wondering whether some of the results the Colonel has quoted could not be explained on that ground, without reference to disease. Turning it about the other way, I am wondering if any one has any real data about the effect of crossing between European breeds in a European type of climate, and whether there is any real evidence to show that heterosis does lift yield under those conditions.

COL. MATSON: We pursued studies very extensively into the question of resistance to heat and concluded that the Shorthorn and Ayrshire crosses with which we began were unable to withstand heat irrespective of other things but the Friesian crosses, when they were produced, puzzled us as they appeared to endure it quite well. So then the question arose, had they a more efficient sweating system? On a visit to London I consulted various authorities but they were not prepared to commit themselves. Later I referred the point to a histologist who was collaborating with us in other studies but he was unable to discover anything that appeared significant. It was left an open question.

Regarding crosses between European breeds I venture to suggest that there is a great deal of evidence of an immediate increase after crossing two European breeds; in fact, my neighbouring farmers within 100 miles are constantly crossing Shorthorns on Jerseys getting a yield which is higher than that of the parent cow or of the dam of the Shorthorn bull.

MR. HANCOCK: I fail to see how the black colour of the Friesian after one cross, could have made it more resistant to the heat. South African workers have shown that the black coat will absorb 60% of all radiated energy, whereas a pure white coat does not absorb more than 25%. Dr. Filmer has suggested that the resistance of some native breeds was due to the greater number of sweat glands in the native cattle. I venture to say that that also is wrong, because these native cattle have not got more sweat glands. It is true that they lose more water through the skin - and that is the main mechanism by which cows get rid of accumulated heat. But the South African workers have proved that it is not sweat, but pure water, that is lost.

MR. RANSTEAD: There are more things than heat in sunshine. We have the dark races who inhabit those areas, and if the dark colour were an advantage to them, and if they absorbed more heat under the African sun, which is a disadvantage there would be nothing in it, but certainly they would not suffer from the actinic rays, and that has been overlooked. You do not get sunburn when you are black, but you do when you are white, although you reflect more of the heat rays from a white surface.

COL. MATSON: I remember Leonard Hill, F.R.S., in London, suggesting the case was simply that of the Negro who, through his skin pigmentation, can stand any amount of sun and thought it might be the same with a black cow. But there was another character developed by the Friesian cross. The Ayrshire second