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ECONOMIC ASPECTS OF SELECTION IN THE DAIRY HERD IN ISRAEL*

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The paper reports a study of the operation of the breeding system in the milk herd in Israel. Basic notions in quantitative genetics are explained and incorporated in a simulation model which is used to illustrate and analyse the selection process. Particularly emphasised are the traits common to selection and other research and development effort; among them, search, limited information, and biological and technical constraints. Differential technical changes affected the structure of the milk producing industry and its measured productivity; these effects are discussed in the last part of the paper.

Introduction

Economic analysis of agricultural research has greatly enhanced our understanding of the process of technological change (Hayami and Peterson 1973), but it has mostly treated the research activity itself as a black box with resources as input and productivity as output. Further advancements in this area will have to rely on closer examination of the production function of technical change. As a step in this direction, we offer a survey and an analysis of selection for milk production in the dairy herd in Israel. In a sense the paper is very specific; it is a case study, but all applied varietal research—even if not actually conducted in these terms—operates, like selection, within the general rules of quantitative genetics. Moreover, the main attributes of selection—search, limited information, natural and technical constraints on the rate of progress—are common to most research and development efforts (the term used in pharmaceutics is *molecular roulette*). A more detailed examination of one such process can enrich our insight in considering others.

Breeding is a stochastic process but in some cases, when working with large numbers, its average rate of progress can be quite accurately predicted once the appropriate genetic parameters are known. This property is utilised in the paper to conduct the core of the analysis with the help of a simulation model incorporating the basic laws of quantitative genetics. With the aid of this model, we illustrate genetic gain, value of information, cost of test and—in combination with a more general

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search model—the biological and technical factors that determine and limit the rate of genetic progress.

The available data seem to indicate that, in Israel, the effectiveness of the selection process has been limited to the herd-book dairies. These dairies, which constitute less than one-half of the national herd, exhibit both higher yields and higher growth in yields than do the other dairies in the country. The outcome of this development has been a continued widening of the gap between the two groups resulting in changes in the structure and productivity of the industry. These aspects of the breeding program are discussed in the last sections of the paper.

Development and Selection in the Israeli Dairy Herd

Israel's milking herd consists of one breed of black and white Holstein cows originally imported from Europe and North America (Bar-Anan 1971). The main features of the development of the dairy herd since 1949 are summarised graphically in Figure 1. The number of cows grew from approximately 18 000 in 1949 to 102 000 in 1974. The larger and better enterprises are registered in the herd-book; milk production of these cows is officially recorded each month and the accumulated information utilised for management and selection purposes. Figure 1 depicts the share of registered, herd-book, cows in the national herd and average annual milk yields for the registered and the non-registered herds. While the yield in the registered herd rose continuously over the period, it has been effectively stagnant in the non-registered herd (Figure 1). This raises the issue of the interaction of breeding and management to which we shall return below.

A cow gives birth in her lifetime to only 2 or 3 female calves, and genetic improvement through the selection of better cows is therefore impractical. The identification of improving, above-average bulls is, in traditional agriculture, subject to large errors, and if such a bull is discovered, its effect is quite limited. The innovation that revolutionised breeding in the dairy herd has been artificial insemination. With this method a selected sire can be mated to a large number of cows—up to 20 000 annually, against less than 100 when breeding is natural. Consequently, the method permits fast and statistically reliable testing and identification of yield-improving sires, which affect, with artificial insemination, a large number of offspring.

Artificial insemination was introduced to Israel in 1938 and by the early 1950s the service covered 85 per cent of the dairy cattle. Today virtually all cows are artificially bred. Selection in the dairy herd is conducted by the insemination system and done in two stages: in the first, high-yielding cows are designated as bull-dams; in the second stage their male calves go through series of tests and the best join the team of the breeding sires.

Information on the bull-dams comes from the herd-book. All cows with milk yields higher than 2 standard deviations of their herd's average are screened; of these some 500 (1 per cent of the registered cows) are designated as bull-dams. Each year approximately 400 of the bull-dams are inseminated by the best 4 sires in the country and 100 are bred with imported semen. Forty-five male calves, 25 per cent of the sons of the bull-dams, are purchased annually by the artificial insemination services. The selection at this stage (of 45 out of some 200) is according to ex-

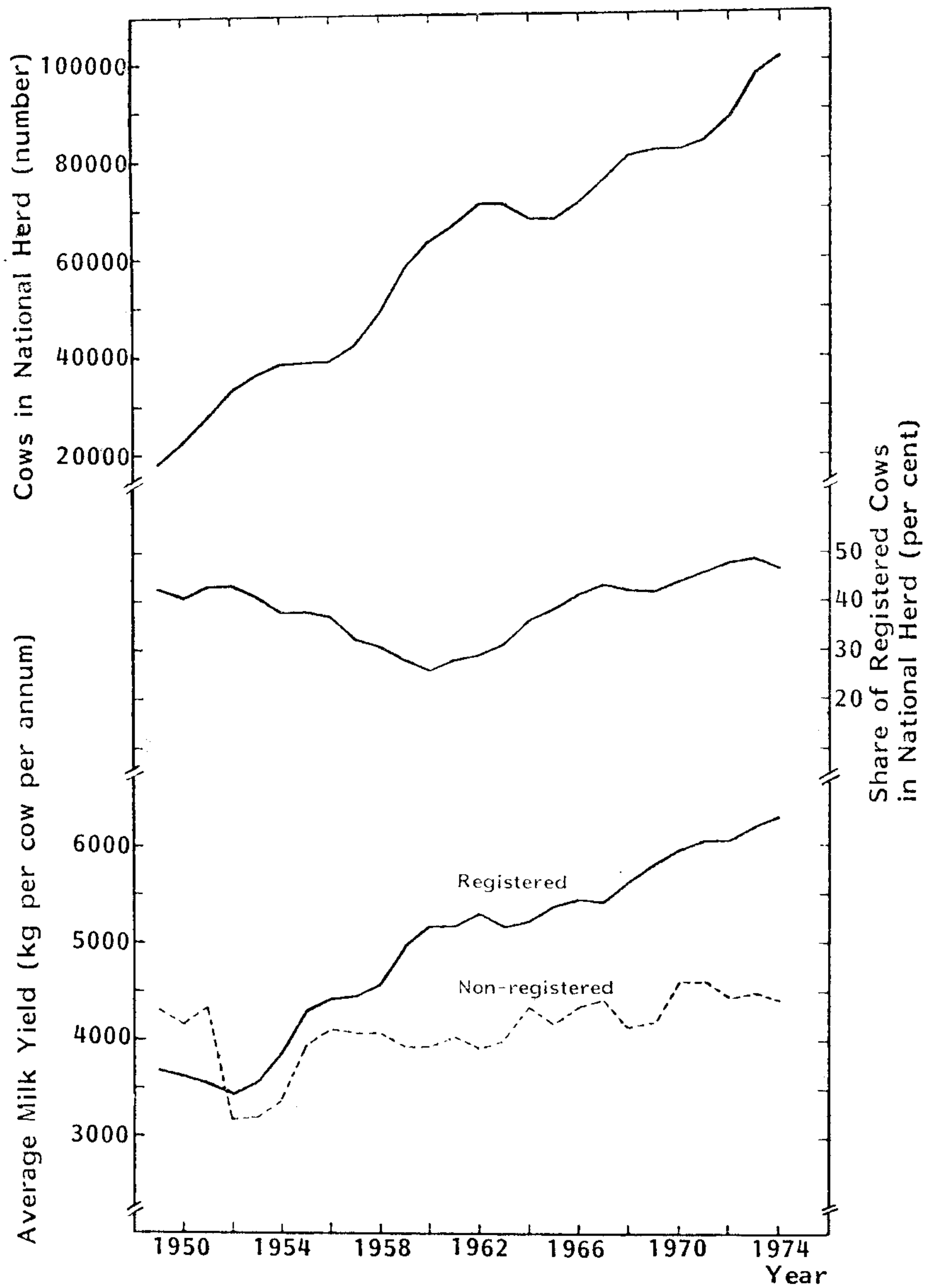

FIGURE 1—The Israeli dairy herd.

perts' rating of the bull's potential. When they are one year old, the young bulls are checked for growth rate and quality of semen; 30 are put to progeny tests.

A progeny test is conducted in the following way. Semen from each young bull is used to inseminate 400 cows to get approximately 100 female calves (the rate of successful insemination is 1:2). The bull then enters a waiting period of 2·5 years. The first test is conducted after the daughters have yielded for 122 lactation days. Milk production of these heifers is then compared to that of their contemporaries in the herds. On the average, 5 out of 30 tested bulls are proven, the rest are culled, most of them for comparatively low milk yields, others for different characteristics of their daughters, such as udder structure, stillborns, low fertility and similar attributes.

The proven sires enter the regular service. The contribution to milk production is constantly estimated. Since, in general, every generation of bulls is better than the previous one, the sires decline in their comparative position. The group of the 40 sires in operation is the group of the 40 best out of the old and the newly proven bulls. On the average, a sire operates up to the age of 10 when its comparative contribution is lower than that of the young vintage sires. The exceptional may maintain a superior position for a longer period.

As milk yields differ between enterprises, the genetic contribution of a sire is estimated by comparing the yield of his daughters to that of their mothers and their contemporaries in the same herds. Averaging over the group of operating sires, the general contribution of genetic improvement can be calculated. It was estimated (Soller and Bar-Anan 1973) to be 60-70 kg a year for milk production of heifers (cows in first lactation).[1]

Measurement of Benefits

Dairy selection is complex and multi-dimensional. Breeding affects meat production, milk composition, health, adaptability to machine milking and other attributes of the animals. Still, the major, dominant trait selected for is milk yield. We therefore concentrate on yield and mention other traits only in passing.

The exact relation between genetic improvement and feed requirement is not known (see, for example, Brown, Chandler and Holter 1977; Hooven, Miller and Plowman 1968). The practice in the industry is to assume constant marginal input-output coefficients (e.g. Oltenacu and Young 1974). Constancy of the marginal feed-milk ratio allows the economic gains of selection to be expressed in terms of milk. This procedure may exaggerate the value of the gains, but the extent of the exaggeration, which breeders and operators disregard, is not known.

The measurement of genetic gains in milk units is consistent with farm-level benefits. At the national level the issue is complicated by protection and subsidisation policies. Under a strict marketing-quota regime, increased yield enables saving of resources—capital, maintenance feed, labour—whose value is, to a first approximation at least, proportional to the additional milk production per cow. However, increased productivity and profitability, particularly for the better pro-

[1] The University of Minnesota has conducted, since the mid-1960s, an experiment that facilitates direct measurement of genetic gains. Pairs of half sisters of the Holstein breed were collected and separated into two herds which are kept together under identical animal husbandry regimes. One herd is bred by the current operating sires in the region, the control herd is bred by frozen semen from the mid-1960s vintage sires. The yield difference between the herds has been growing at about 100 kg a year, of which 80 kg can be attributed to genetic gain (Hansen, Young, Miller and Touchberry 1978 and personal communication with Dr Young 1979).

ducers, may increase the political pressure for further protection. Since we concentrate mainly in this paper on the technology of biological productivity generation, we do not here go into these important policy issues.[2]

An Abstract Model

Selection for milk production is essentially a search process—search for bull-dams and testing, screening and identification of the best sires. Technological research and development projects also often consist of testing of collections of technologies (methods, formulas, timings, varieties) to find the best. At an abstract level, each such collection can be regarded as a sample drawn—not always completely at random—from all possible technologies. Research is then a search process (Evenson and Kislev 1976). In this section such a process is formulated in relatively simple mathematical terms. Apart from serving as a background, the model is also used below in calculating a theoretical, ideal rate of genetic progress.

Assume that technologies are characterised by a single-dimensional variable—net income (in this study represented by milk yield). If economies of scale are disregarded, it can be net income per unit of operation. Define:

x_i = net income associated with technology i;
y = net income of the currently practised technology.

In conducting an experiment, the scientist draws a sample of n observations on x_i. Let $F(x)$ be the accumulated probability distribution of x

$$F(x) = \Pr(x_i \leqslant x).$$

Let z be the largest observation in a sample of technologies. Then the cumulative distribution of z is:

$$F^n(z) = \Pr(z = \text{largest value of } x_i,\ i = 1, 2, \ldots, n).$$

The best technology observed in an experiment, defined by z, is the outcome of that experiment. Assume that, if it is superior to the currently practised technology, the new technology is put to use and y increases. If not, y does not change. Hence

$$\Delta y = z - y \qquad z > y$$
$$\Delta y = 0 \qquad \text{otherwise.}$$

The expected value of the technological increment—of the improvement in income due to a drawing of one sample of n observations—is:

$$(1) \qquad E_n(\Delta y) = \int_y^{\infty} [1 - F^n(z)]dz.$$

$E_n(\Delta y)$ increases with n but at a diminishing rate and it decreases with

[2] Whatever the appropriate measure, selection is probably a worthwhile public undertaking, as, once artificial insemination is instituted and so long as milk registration is practised for management purposes, breeding is almost costless. Estimates also indicate (Rabiner 1975) that both the value of the additional milk (at market price net of marginal cost) and the value of the resources saved (on the assumption of constant national marketing quota) far exceed the cost of the insemination and selection services.

y. Coupled with assumptions on the cost of experimentation, this leads to the derivation of conditions for optimal search in Evenson and Kislev (1976).

Selection

In this section we present, in a simple form, the basic model of quantitative genetics. For a basic text, see Falconer (1961).

A basic distinction is between the genotype—the true genetic attributes of the individual, and the phenotype—its revealed characteristics. The genotype is unobservable directly but it is only genotypic properties that the individual transmits to its offspring; the phenotype can be affected to a significant extent by the environment.

In our discussion the individual animal is defined genotypically and phenotypically in a single dimension: milk yield (of course, for bulls this attribute is phenotypically meaningless). Accordingly, let S_i, M_j and G_{ij} be the genetic additive value of the sire i, the dam j and their offspring, respectively. The value of the offspring is the average of the additive components of its parents, plus a random genetic effect g_{ij}:

(2) $$G_{ij} = \tfrac{1}{2}S_i + \tfrac{1}{2}M_j + g_{ij}.$$

The phenotype, P_{ij}, is the sum of the genotypic value plus a random environmental effect, e_{ij}:

(3) $$P_{ij} = G_{ij} + e_{ij}.$$

The following are the basic assumptions of the model.

(a) The distribution of the genetic properties is normal with means $E(S_i) = \mu_s$, $E(M_j) = \mu_m$, and with an identical variance for cows and bulls, $V(G_{ij}) = \sigma_g^2$.

(b) $E(g_{ij}) = E(e_{ij}) = 0$; $V(e_{ij}) = \sigma_g^2$.

(c) Sires and dams, and genetic and environmental effects are independent:
$\operatorname{cov}(S, M) = 0$, $\operatorname{cov}(g, e) = 0$.

(d) The genetic variance σ_g^2 is constant.

In regard to assumption (c), recent studies (Fuchs 1977; Raz 1978) reached conflicting conclusions about the existence of a genetic-environmental interaction in the registered herd. This possibility is disregarded by the breeding program. Even if it were significant, it would not have affected substantially the average magnitudes of the breeding parameters in the registered herd, and these are the magnitudes illustrated in the simulation model of the next three sections. We shall return below to the difference between the registered and the non-registered parts of the national herd.

The last assumption is a crucial one. It means that genetic improvement in the selection process is assumed not to deteriorate with time. Theoretically, it is reasonable to expect the genetic variance and heritability to decline as the selection process proceeds and the population approaches the potential ceiling of the selected attribute. Such a ceiling must exist since the selection process is just a search in a given distribution of all conceivable genetic combinations with no basic improvements. However, no reduction has yet been found in the heritability of the milk-yield characteristics in the Israeli herd. One explanation could be that, since the number of genes controlling milk productivity is very large, the number of genetic combinations is very big; selection has been conducted for only a few generations and the process can be expected to continue for many more years with no visible decline in the variance.

With these assumptions, the expected phenotypic value of the offspring is the average of the parents' genotypes:

$$E(P_{ij}) = E(G_{ij}) = (\mu_s + \mu_m)/2.$$

By (3), the phenotypic variance of the offspring will be

$$(4) \qquad \sigma_p^2 = \sigma_g^2 + \sigma_e^2.$$

The assumption of a constant genetic variance, σ_g^2, together with equation (2) means that the variance of the random genetic effect g_{ij} is half that magnitude. To see this, write the variance of equation (2)

$$(5) \qquad V(G_{ij}) = \tfrac{1}{4} V(S_i) + \tfrac{1}{4} V(M_j) + V(g_{ij}) = \tfrac{1}{2} \sigma_g^2 + V(g_{ij}),$$

hence,

$$(6) \qquad V(g_{ij}) = \tfrac{1}{2} \sigma_g^2.$$

Equation (6) follows from the definition of assumption (a). It will be used in the simulation below.

Heritability (denoted by h^2) is the coefficient of inheritance of quantitative traits—the expected deviation of the offspring from the species' average, given the parents' deviation. It is defined with respect to midparents (hermaphrodites are an exception) and calculated from a regression of offsprings' on parents' traits. The systematic, genotypic component of the parent and the offspring are identical; therefore the covariance parent-offspring is the phenotype-genotype covariance. Given the assumptions (a) and (b), this covariance is the genetic variance, and heritability is the ratio of the genetic to the phenotypic variance:

$$(7) \qquad h^2 = [\text{cov}(P, G)]/\sigma_p^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2).$$

The fact that $h^2 < 1$ is the historical source for the term regression. If, as assumed, $\sigma_g^2 =$ constant and $\sigma_e^2 =$ constant, it follows that $h^2 =$ constant.

The phenotypic variance, σ_p^2, and the heritability, h^2, are routinely estimated directly from herd-book data. The first is simply the variance of milk yield per cow and the second parameter is estimated in regressions of heifers' yields on the yields of their mothers. The genetic and environmental variances are then calculated:

$$(8) \qquad \sigma_g^2 = h^2\sigma_p^2, \quad \sigma_e^2 = (1 - h^2)\sigma_p^2.$$

Equation (8) will be incorporated into the simulation process.

The Simulation Model

The model simulates selection for milk and reflects the operation of the breeding system in the registered herd. It starts with a herd whose average, per cow, milk production is 5000 kg a year. The initial herd is constructed by the simulation process in two stages. In the first, genotypes of cows and bulls are drawn from the normal distribution:

$$(9) \qquad \text{for cows} \quad M_j\text{: } N(\mu_m, h^2\sigma_p^2)$$
$$\text{for bulls} \quad S_i\text{: } N(\mu_s, h^2\sigma_p^2).$$

The numerical values in the calculations are: $\mu_m = \mu_s = 5000$, $h^2 = 0{\cdot}22$, $\sigma_p{}^2 = 700^2$; hence, by equation (8), the genetic variance $\sigma_g{}^2 = (h^2\sigma_p{}^2) = 328{\cdot}3^2$. These are the current estimates of variance and heritability parameters in the Israeli registered herd.

In the second stage, cows' phenotypes are constructed from

$$(10) \qquad P(M_j) = M_j + z(1 - h^2)^{0{\cdot}5}\,\sigma_p,$$

where the z values are randomly drawn from the standard normal distribution

$$(11) \qquad z : N(0, 1).$$

Offspring are created, in the simulation model, by equations (2), (6), and (3) as a result of mating of cows and bulls:

$$(12) \qquad \text{genotype} \quad G_{ij} = \tfrac{1}{2}(S_i + M_j) + z\sqrt{0{\cdot}5}\,\sigma_g$$
$$\text{phenotype} \quad P_{ij} = G_{ij} + z\sigma_e\,.$$

Exit of cows is random at the rate of 30 per cent per annum. Cows deliver once a year, first time at the age of two. Live births are 90 per cent of the total, and the calf's sex is determined randomly with males 51 per cent of total. Exiting cows are replaced by one-year-old heifers, chosen randomly; the remaining heifers are culled. Bulls are kept only to the extent required for reproduction and selection. They are fertile from the age of one year and can live, if not culled, up to 11 years.

Breeding starts with random mating—information on milk yields is unavailable, in practice, before first lactation. Selection of bull-dams—cows with relatively high milk yield—starts after first lactation. Their male calves are subjected to progeny test in the model: mated when they are one year old, wait for a period of 2·5 years and then ordered by yield level of their daughters. The best form the group of the proven sires. Once such a group has been created, bull-dams are mated with the very best of the proven sires.

The Basic Run

The simulation model was run with several parametric modifications to form alternative experimental breeding policies. Each run consisted of one process of 25 years and each was conducted with 10 repetitions, the average of which was taken as the experiment's result. In this section the findings of the first set of experiments—the basic run—are reported. Further experiments are discussed in the following section.

The basic run was conducted with a herd of 3000 cows and its findings exemplify the properties of the model and illuminated two economic issues. The first is the issue of returns to intensity of technological research, here discussed in terms of the size of the groups subjected to the progeny test. Two cases are compared: in one, a group of 16 young bulls is included in the progeny test every year; in the second, the group tested consists of 32 bulls. We shall also consider, in the next section, the cost of the test and its change with group size.

The other issue is related to the value of the unknown information about the true genetic structure of the cows. In the real world it is only the phenotype that can be observed, but in the model the computer carries also the genotypic information of the animal. [This is necessary for the creation of the offspring in equation. (12)] The experiment conducted in the basic run compares milk yields once when bull-dams are selected, as in practice, by their phenotypic attributes, and once when they are selected by the genotypes. The difference is the economic value of the unknown genetic information expressed in terms of milk.

The findings of the basic run are summarised in Table 1 and Figure 2. The graphs in Figure 2 depict average milk yield of the group of heifers against time. The four graphs in the diagram correspond to the four different cases in Table 1. (The information in the table, however, relates to averages over 10 simulation runs for each case while the graphs depict single runs randomly picked.) The solid lines show milk yields when 16 bulls are tested every year. They both start at the same initial yield level and move together for the first period of the simulation run when the breeding bulls are picked randomly. Meanwhile, bull-dams are selected; these are the best milk producers in the herd. In

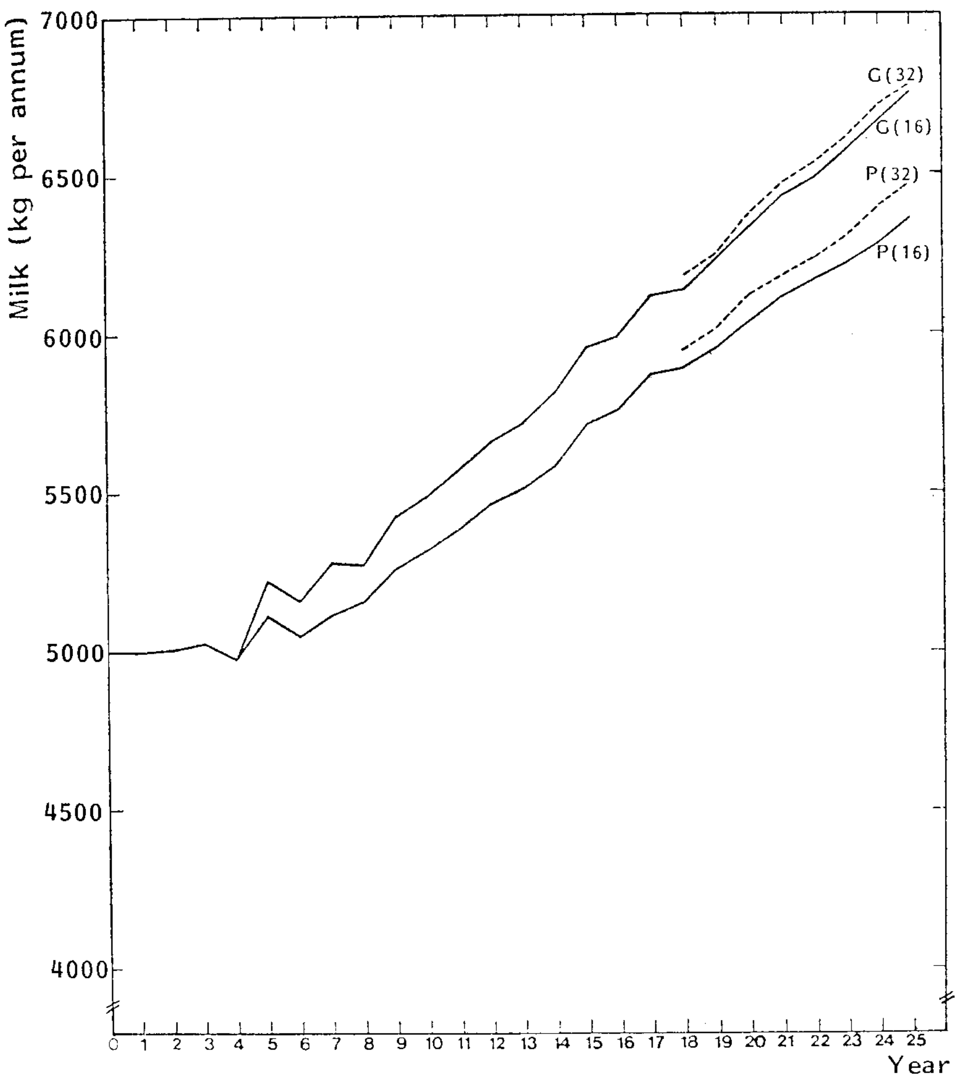

FIGURE 2—The simulation process—the basic run.

practice and in cases P of our simulation process, they are phenotypically selected—judged by their observed milk yields. In cases G they are genotypically selected. The sons of the bull-dams start breeding (first as a test group) at the end of the second year. From this point on mating is not random any more—only the best bulls and sons of bull-dams in the test are used for breeding—and milk yields rise. They rise faster for the case of the genotypic selection. The difference between the cases *P* and *G* is a measure of the value of the unobserved genetic information on the bull-dams.

The figure also shows (the broken lines) milk yields when 32, instead of 16, calves are tested every year. To keep the diagram clear, these last two cases are limited in Figure 2 to the last seven years of the simulation process. Increasing the sample size increases milk yields, but visibly less so when bull-dams are genotypically selected. A larger sample size is one way to get at better genetic information.

TABLE 1

First Experiment—The Basic Run

Bull-dams selection criteria	Case symbol	Number of tested calves	Present value of process[a]	Annual genetic improvement		Cost of test[b]
				Heifers	Breeding bulls	
		(1)	(2)	(3)	(4)	(5)
			kg milk per cow	kg per head	kg per head	kg per bull
Phenotype	P(16)	16	5917 (590)[c]	59·7 (4·8)	60·4 (5·2)	−2·6 (2·7)
	P(32)	32	6508 (489)	65·6 (3·9)	68·1 (7·2)	20·3 (4·0)
Genotype	G(16)	16	8218 (658)	73·9 (4·9)	74·1 (4·6)	−16·7 (2·4)
	G(32)	32	8649 (308)	79·2 (3·0)	81·6 (5·9)	−8·3 (2·9)

[a] Column (2): $V = \sum_{t=1}^{25} \frac{\Delta Y_t}{(1+r)^{t-1}}$ where ΔY_t is yield increment: difference in milk production of heifers in year t from base year and $r = 0{\cdot}05$, the discount rate.

[b] Column (5): Define A_1 as average milk contribution (difference from herd's mean) of 16 proven sires; A_2 as same average for breeding bulls and sires including tested calves; Cost of test in kilogram milk per bull: $C = A_1 - A_2$.

[c] Standard deviations in the simulation run are shown in parentheses.

The same four cases are summarised numerically in Table 1. Column (2) contains the capitalised values of the additional milk yields achieved through breeding, a practice which has recently become quite common in the breeding literature. This value is 5917 kg milk per cow if bull-dam selection is conducted by the phenotypes and 16 male calves are tested every year. If 32 are tested, this value is 6508 kg. The corresponding values for genotypic selection are 8218 and 8649 kg milk.

The difference of 2301 kg for the case of 16 calves is the value, in milk units, of the genetic information unknown to the breeder, who is confined to phenotypic observations. The increased size of the tested group from 16 to 32 calves permits better selection and higher returns to breeding. Prior genetic information and test group size are substitutes; a larger group compensates for lack of genetic information; so also the additional contribution of a larger group is smaller when selection is genotypically conducted: G(32) — G(16) = 431 kg; P(32) — P(16) = 591 kg.

Technological improvement is a random process with variable outcomes. The standard deviations of the outcomes (over 10 runs for each experiment) are reported (in parentheses) in Table 1. Again, genetic information reduces the variability, relatively at least. For column (2) the coefficients of variation are 0·099 and 0·080 for P(16) and G(16), respectively, and 0·075 and 0·035 for P(32) and G(32). More accurate genetic information cannot eliminate offspring variability altogether, but it reduces the effect of the phenotypic variance on the outcome of the process.

Annual genetic milk improvement for heifers is reported in column (3) and this variable (genotypically) for the breeding bulls is reported in column (4). The interpretation of the entries in these columns is similar to that of the entries of column (2) and they show similar characteristics. The simulated rate of yield improvement in P of column (3) corresponds well to the estimated genetic improvements reported for the Israeli registered herd—60-70 kg a year.

Cost of Test

The group of breeding bulls includes proven sires and male calves in the test. Eight tested male calves replace one sire and the group is composed of 16 'proven sires equivalent', that is, 14 sires and 16 calves or 12 sires and 32 calves. The inclusion of relatively unknown calves in the group of breeding bulls (the only way to find their actual genetic attributes) may lower the productivity contribution of the group. This productivity loss is, in addition to feed and care outlays, the cost of the test. This cost is reported in column (5). (The exact definition is given in the footnotes to the table.) The only case in which the cost is positive is when the tested group is of 32 calves and selection is phenotypic. The cost is then 20·3 kg milk per sire-equivalent. The negative cost in the other entries in the column is due to the constant productivity increase: the younger vintage calves are in general better than the older sires. When a tested group is included among the breeding bulls it is the lower productivity sires which are replaced. It is therefore possible that the average of the young calves will surmount the productivity value of the sires replaced. This is particularly true if selection is genotypic, since then the calves are sons of well-selected bull-dams.

In both cases, an increase in tested group size increases the cost of the test, by 22·9 kg per bull in phenotypic selection (22·9 = 2·6 + 20·3) and by 8·4 kg when selection is genotypically conducted. With a larger group the cost of the test would become positive even for genotypic selection. What we have here is one aspect of optimal testing. At the margin, the cost of the test, for the last group of eight calves replacing a proven sire, should be equal to the expected increment in genetic gains attributable to the inclusion of this group in the test. There has not been any attempt to find this optimum analytically for the Israeli breeding program and we do not know whether, at the optimum, the total cost of the test (again, disregarding feed and maintenance) would have been negative or positive.

Scale and Efficiency

This section includes two additional topics: the effect of the size of the registered herd on the rate of genetic progress, and construction of an efficiency index comparing real genetic improvements to a theoretic rate of technological advancement. This comparison will enable the identification and quantification of the decision variables and the natural constraints which limit the effectiveness of the selection process.

Table 2 reports the simulation experiments for four population sizes: 1500, 3000, 6000 and 12 000 cows in the herd. The table is of the same format as Table 1 with some columns omitted; columns (6) and (7) will be explained below. There are economies of scale in selection. Technological progress in a large herd is, in general, faster than in smaller ones; but these advantages are comparatively small and, considering the fact that selection cannot be practised effectively in very small herds, the scale effects are evidently diminishing. Moreover, since selection is a stochastic process, genetic improvement may turn out to be slower in a larger herd; in the table, for the case of 16 tested bulls, the rate of growth of output declines when herd size grows from 6000 to 12 000.

We turn now to an analysis of the laws of motion of the selection process—the factors determining its rate of progress. This analysis is conducted by specifying an *ideal* model and attributing the difference between it and the actual process to explanatory effects. This procedure is similar to the calculation in physics of the efficiency of a steam engine relative to an ideal, 100 per cent efficient, theoretical model (e.g. Halliday and Resnick 1965, p. 540).

Before we formulate the model, it is useful to note that the rate of turnover of cows does not affect yield improvement. Assume a steady-state, constant age distribution of cows, constant genetic yield increases —each year the incoming heifers yield Δ kg more than last year's heifers—and that the genetic yield differences are maintained through subsequent lactations. Under these assumptions, the increase in the herd's average yield is also Δ kg per year. Each cohort is Δ kg better than the cohort it replaces. Hence the herd's *rate* of genetic gain is independent of the rate of turnover of cows. (On this point, the discussion of the steady state in Evenson and Kislev 1976 may be helpful to the interested reader.)

The crucial attribute determining the progress of selection is the search for extreme values in the population. The theoretical, ideal rate of genetic improvement can be calculated by adopting the framework of the abstract model and equation (1). Assume that the population is distributed normally; each year the best animal is found; if its milk yield is higher than that of the currently yielding cows, the population is completely replaced by the new, better, genetic type (complete replace-

TABLE 2

The Effect of Population Size

Number of cows	Number of tested calves	Present value of process	Annual genetic improvement	Genetic improvement in milk production (standard deviations per annum)	
			Heifers	Simulation model[a]	Ideal case[b]
	(1)	(2)	(3)	(6)	(7)
		kg milk per cow	kg per head		
1 500	16	5693 (485)[c]	58·1 (2·4)	0·177	3·58
	32	6250 (500)	64·6 (1·9)	0·197	
3 000	16	6092 (498)	60·9 (7·0)	0·186	3·77
	32	6347 (402)	64·3 (5·2)	0·196	
6 000	16	6385 (546)	64·1 (4·4)	0·195	3·95
	32	6948 (475)	68·8 (2·5)	0·210	
12 000	16	6141 (452)	62·1 (4·6)	0·189	4·12
	32	7204 (427)	73·1 (5·6)	0·223	

[a] Column (6): Column (3) divided by the genetic standard deviation, 328 kg.

[b] Column (7): The expected value of the largest observation in a standardised normal population. Equation (1) is approximated by Gumbel (1958, p. 139). $E_n(z) \approx (2 \log (0{\cdot}4n))^{0{\cdot}5}$. Other values in Figure 3 and not reported in the table are $E_{500}(z) = 3{\cdot}26$
$E_{9000}(z) = 4{\cdot}05$;
$E_{24\,000}(z) = 4{\cdot}28$.

[c] Standard deviations in the simulation run are shown in parentheses.

ment is not a necessary assumption, it is adopted to crystallise the model); again search to find the best is conducted, and so the process continues.

The expected genetic improvement predicted by the ideal model is reported in column (7) of Table 2. The values in the column are annual rates of progress in terms of standard deviations. For milk production in the Israeli herd $\sigma_g = 328$ kg and the ideal rate of progress is approximately 20 times faster than the actual (simulated) rate σ_g in column (6).

The ideal model abstracts from real-world attributes of the selection process, yet the model can be taken as the upper bound, the 'unachievable' 100 per cent efficiency case, of the selection process. The gap between actual and ideal results can then be explained by the characteristics of selection. This is done in Figure 3 and Table 3. The figure shows yield progress in the ideal model and in the simulation run. It also partitions this progress for a herd of 12 000 cows to its components. This is done numerically in Table 3, which explains the efficiency gap between the simulated and the ideal model almost completely. Two major factors affect the genetic progress: the genetic laws of inheritance and the generation gap. The first is a law of nature and cannot be changed, the second can be affected by making wider use of young, yet untested, but potentially promising bulls—perhaps at the cost of a larger variability in the results and a higher cost of test—but this takes us outside the scope of the present paper.

Another, practical, conclusion from this discussion is that sample size is, at these orders of magnitude, of little importance. In our case, the

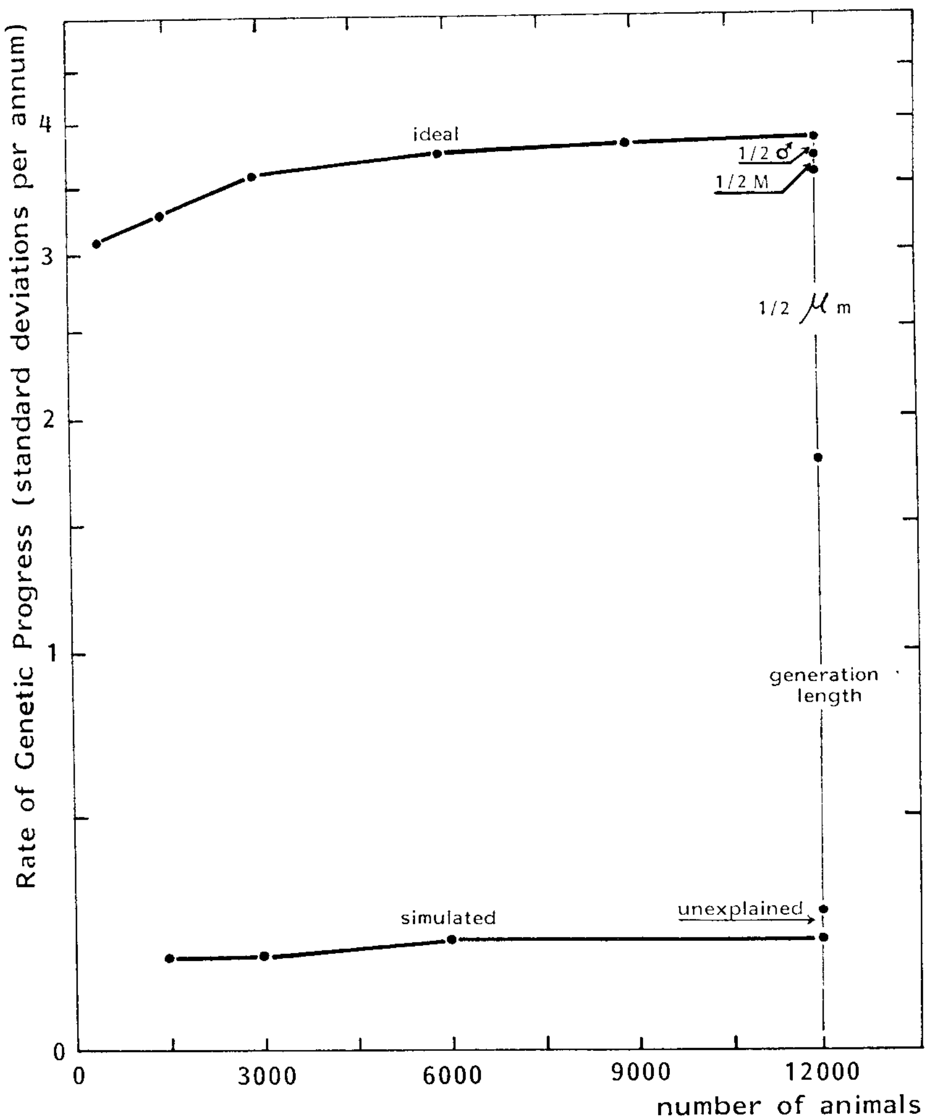

FIGURE 3—Rates of genetic progress—ideal and simulated. (semi-logarithmic scale)

TABLE 3

The Components of the Gap between the Ideal and Actual (Simulated) Genetic Progress

	Standard deviation per annum	Per cent
The ideal rate of progress for a herd of 12 000 cows	4·12	100·00
Actual selection is limited to males, this reduces the affected population by one-half to 6 000 (½♂ in the figure)	3·95	95·87
About half the bulls are culled for other than milk-productivity attributes of their daughters; this reduces the population subjected to selection for milk to 3 000 (½ M)	3·77	91·50
A sire transmits to its offspring only half its genetic advantage ($\frac{1}{2}\mu_m$)	1·89	45·87
The time between the birth of a sire and the birth of his replacing son is 7·75 years (Owen 1975, Table 1): the annual genetic progress is the average over this period (generation length)	0·24	5·83
The actual (simulated) rate of progress is 68/328 standard deviation[a]	0·20	4·85
Unexplained	0·04	0·97

[a] The average in Table 2, for a herd of 12 000, is 68 kg a year per heifer. The genetic standard deviation is $\sigma_g = 328$ kg.

registered herd, which is screened in search of bull-dams, can be viewed as a sample from the population of all potential genetic combinations of milking cows. The registered herd in Israel consists of 50 000 cows. The increase of the sample size from extension of the coverage of the herd-book to include a larger number of registered cows would have virtually no effect on the performance of the selection process.

With this section we conclude the discussions of the breeding process. Before turning to other related issues, note that, in the dairy herd, genetic theory, with readily estimated parameters, can predict a major component of productivity increases (a third in Israel, see Table 4). In principle, it should also be possible to predict progress in other genetic work; for example, in crop improvement, where the size of the group of breeders working on a crop determines the sample size.[3] We do not know of any attempt in this direction.

Breeding and Management

There are large and puzzling differences in the realisation of genetic potentials in the dairies in Israel. The breeding program utilises data and livestock from the registered herd and the simulation model of the last three sections reflected, therefore, average developments in this

[3] We are indebted to Y. Mundlak for stressing this point.

herd. However, the insemination service, which distributes the productivity gains generated by selection and embodied in the genetic material, operates in all dairies in the country. As a result, all herds in the country are of similar genetic potential; genetic differences between cows do exist but they wash out at the herd's average. This basic genetic uniformity is vividly illustrated by the practice of the better operators to export heifers and buy replacements from lower yielding, sometimes non-registered, dairies. In most cases, the newcomers reach, after several months, the yield level of the adopting herds.

However, yields in the individual herds vary greatly with management. In 1974 the record registered dairy (with 225 cows) had an average milk yield of 9467 kg per cow, while the lowest of the registered dairies had an average yield of less than 60 per cent of that level—5439 kg (196 cows). The difference between the registered and the non-registered group is even more striking (Figure 1). Despite the continuous genetic improvement, there was virtually no visible increase in yield in the non-registered herd. Realisation of genetic gains could not be detected in more than half of the national herd.[4]

As indicated in the section on selection, the evidence supporting the existence of interaction between genetic and environmental effects within the registered herd is weak and this possibility is disregarded by the breeding system. The non-registered herd, on the other hand, either offers a significantly different environment in which selection is ineffective or features developments that nullify whatever positive effects genetic improvement might have had. A major difference between the two herds is in organisation and management. The registered dairies are comparatively large, operated by specialised teams in the communal *kibbutzim*. The others are mostly family operations of 10-40 cows (15 is the average) on diversified farms.

We do not now whether these organisational differences actually cause the productivity gap. This is an important issue that may have bearing on the question of the adoption of new technologies in the course of agricultural development and on the distribution of gains from economic growth among farms of different attributes. The available information does not yield definite answers to this question. However, the growing productivity gap affects the structure of the milk-producing industry and the measured shifts in its production function. These issues are considered in the next section.

Components of Supply Increment

A recent detailed study (Chayat and Natan 1977) attributes a significant part of the differences in income from the dairy enterprise to milk yield. The better managers realise higher yields and higher incomes and, as these differences increase through time, their comparative position in the industry improves. As supply expands, even with government intervention (see next section), terms of trade change against the industry and the lagging operators have to exit. Production gradually concentrates in the hands of the better operators, this concentration itself

[4] Recall that yields in the registered herd are measured monthly for each cow individually. For the non-registered herd the yield was calculated by substracting the production of the herd-book dairies from national supply and dividing by the number of cows.

adding further to supply and to the deterioration of the relative position of the less skilled managers.

Supply (actually, quantity supplied) increases can be partitioned to an expansion effect—changes in the number of cows—and to a productivity effect, the last subdivided again into three terms: genetic improvement (limited in our case to the registered herd), concentration (changes in the relative share of the registered herd) and a general technological improvement term, measured as the residual, and which stands for changes in management, animal husbandry and feeding methods.

Formally, let:

Q_t = quantity of milk supplied in year t;
M_t = number of cows in country;
Y_t = country average milk yield per cow;
G_t = genetic annual yield increment; and
$\Delta Q_t \equiv Q_t - Q_{t-1}$ etc.

The superscript r (Y_t^r) marks the registered herd and superscript n marks the non-registered. Then

(13) $\Delta Q_t =$	supply increment
$\Delta M_t Y_{t-1}$	expansion effect
$+ G_t M_t^r$	selection effect
$+ M_t^r \left(\frac{\Delta M_t^r}{M_t^r} - \frac{\Delta M_i}{M_t} \right) (Y_t^r - Y_t^n)$	concentration effect
$+ R_t$	residual.

Table 4 presents our analysis of the supply increments. In the calculation, we took G_t as 60 kg per annum per heifer (Bar-Anan 1975). Note also that the selection effect is limited to the registered herd and the concentration effect is limited to the increases in the registered herd over and above proportional expansion. The entries in the table are differences in milk supply between the listed years. For example, the country's milk supply increased, between 1950 and 1954, by 64·8 kt per annum. If milk yields were to stay constant between these two points in time, the mere expansion of the number of cows (from 26 000 to 38 000) would have increased the quantity supplied by 71·5 kt per annum (yields declined over this period, see Figure 1).

The dominant factor in Table 4 is the expansion effect which explains 55 to more than 100 per cent of the additional supply. The other three components account for shifts in productivity. The selection effect may be overestimated for the first two periods when the artificial insemination system and the associated selection machinery were in their infancy (though some excellent Canadian bulls were imported during this period). The concentration effect, on the other hand, is probably underestimated since its calculation neglects concentration of production in the hands of the better operators within the sectors—the registered and non-registered groups. On the average, for the last 15 years (1960-1974) during which the present selection process has been operating routinely, our effects—selection, concentration and the residual technical change—explain close to 30 per cent of supply increment with each of them contributing approximately equally to supply.

TABLE 4

Components of Milk Supply Increments[a]

Period	Supply increment (1)	Expansion effect (2)	Selection effect (3)	Concentration effect (4)	Residual (5)
	kt	kt	kt	kt	kt
1950-54	64·8	71·5	3·87	0·33	−10·90
1955-59	110·5	76·0	4·67	−2·68	32·71
1960-64	62·5	34·6	6·15	8·70	12·95
1965-69	76·6	66·9	9·38	5·77	−5·45
1970-74	139·7	103·5	12·27	6·27	17·66
	%	%	%	%	%
1950-54	100	110·3	6·0	0·05	−16·35
1955-59	100	68·8	4·2	−2·4	29·4
1960-64	100	55·4	9·8	13·9	20·9
1965-69	100	87·3	12·2	7·5	−7·0
1970-74	100	74·1	8·9	4·5	12·5
Average 1960-74	100	72·3	10·3	8·6	8·8

[a] For definitions see equation (13) in the text. Column (5) = (1) − [(2) + (3) + (4)]. The entries in the table were calculated annually and added for the periods.

A Concluding Note

Breeding, the major technological improvement process in the Israeli dairy industry (outside of mechanical, mostly labour saving, innovations), has been conducted in a favourable economic atmosphere. Milk is subsidised and producer prices have generally been higher than in Europe, for example. Feed grains were also often sold at prices lower than in world markets. However, increased productivity permitted a gradual deterioration in terms of trade in the industry; the milk-feed price ratio is today less than 70 per cent of its 1950 level. After a period of food supply shortage in the 1950s, the Israeli agricultural sector 'matured' into the surplus stage and milk production quotas were imposed in 1960. The system was designed to protect the small farmer and the family operated dairy; but it achieved this goal with only partial success: as a rule, the industry's milk production fell short of the national quota allotment, with big producers (in the *kibbutzim*) exceeding their quota and family farms failing to meet theirs. Moreover, the number of family operated dairies declined by more than 30 per cent over the last decade, creating a gap in supply into which the bigger enterprises could expand—though perhaps slower under the quota system than could be realised under a free market structure. This expansion was aided by credit availability which the big producers (again, particularly the *kibbutzim*) have always been in a better position to exploit.

Thus, the economic selection environment has been tight enough to force the technological laggards to exit gradually, while offering the more efficient, advancing operators opportunities to realise handsome returns on their efforts. This, evidently, encouraged the operation of the strong producers' organisations which supported, together with the government, the co-operative artificial insemination and selection system, the benefits from whose operation were, as we have seen, limited mostly to the better enterprises. This last outcome was, no doubt, unintentional but effective measures to modify the nature of the distribution of the selection gains were not implemented either.

The milk production industry operates under protection from world competition. If free import of powder milk, butter and cheeses were allowed, prices would have had to be lowered and production curtailed, perhaps by as much as a third or even a half. It is impossible to tell now how the industry would have performed under drastically different circumstances and whether a breeding effort could have had any impact then.

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