The Open Access Israeli Journal of Aquaculture – Bamidgeh

As from **January 2010** The Israeli Journal of Aquaculture - Bamidgeh (IJA) will be published exclusively as **an on-line Open Access (OA)** quarterly accessible by all AquacultureHub (http://www.aquaculturehub.org) members and registered individuals and institutions. Please visit our website (http://siamb.org.il) for free registration form, further information and instructions.

This transformation from a subscription printed version to an on-line OA journal, aims at supporting the concept that scientific peer-reviewed publications should be made available to all, including those with limited resources. The OA IJA does not enforce author or subscription fees and will endeavor to obtain alternative sources of income to support this policy for as long as possible.

Published under auspices of
The Society of Israeli Aquaculture and Marine Biotechnology (SIAMB), University of Hawaii at Manoa Library
and
University of Hawaii Aquaculture Program in association with
AquacultureHub
http://www.aquaculturehub.org

ISSN 0792 - 156X

PUBLISHER:
Israeli Journal of Aquaculture - BAMIGDEH -
Kibbutz Ein Hamifratz, Mobile Post 25210,
ISRAEL
Phone: + 972 52 3965809
http://siamb.org.il

Lessons for Aquaculture Breeding from Livestock Breeding

Joel Ira Weller*

Department of Cattle and Genetics, Institute of Animal Sciences, A.R.O., The Volcani Center, P.O. Box 6, Bet Dagan, 50250 Israel

Key words: livestock breeding, animal breeding, biotechnology, genetic trends

Abstract

Investment in breeding is unique because genetic gains are eternal and cumulative. They are never “used up”, and never “wear out”. However, nearly all of the gain is transferred to the national economy. Very little stays with farmers or commercial breeders. Unlike genetic gains, costs are not cumulative. With a profit horizon of 20 years and a discount rate of 0.08, total discounted costs will equal total discounted gains if the value of the nominal annual genetic gains is 0.3 of the nominal annual costs. The rate of genetic gain for milk production in dairy cattle has been about 1% per year for the last 20 years. Since the 1950s, rates of genetic gain have increased due to better pedigree information, more traits recorded, more accurate recording, and better statistical methods. From the beginning of modern breeding programs, selection in dairy cattle focused on milk production. From 1985, breeding goals moved towards improving protein yield. In recent years, selection objectives were broadened to include “functional herdlife”, fertility, and health traits. The main reasons behind this shift were quotas and/or price constraints, and increasing concerns associated with the deterioration of the health and fertility of dairy cows. Modern technology complements traditional breeding but does not replace it. To date, nearly all progress in animal breeding has been obtained by traditional trait-based methodology. There is no substitute for accurate data and pedigree recording.

Introduction

Scientific breeding programs for livestock began in the 1950s. The most advanced and best organized breeding programs have been applied to dairy cattle, the most economically important species that is amenable to artificial selection. Therefore, most of this review will deal with dairy cattle results. Until 1970, rates of genetic gain were relatively low (Van Vleck, 1987). Rates of genetic gain increased due to better pedigree information (artificial insemination), more traits recorded, more accurate recording, and better statistical methods (BLUP, animal model, test day model).

Relative to most species of fish, livestock breeding has disadvantages in that the generation interval is long, each animal is very costly, and, although male fertility is nearly unlimited, female fertility is low for most species.

* Tel.: +972-8-9484430, fax: +972-8-9475075, e-mail: weller@agri.huji.ac.il

Furthermore, most traits of interest (e.g., milk production) can only be measured in females. Nevertheless, most breeding programs are based chiefly on selection of sires because of their nearly unlimited fertility via artificial insemination (AI). Genetic evaluation of the sires is derived from their female relatives, chiefly daughters.

In this paper I will first describe the Israeli and US dairy cattle breeding programs as examples of advanced dairy cattle breeding programs. I will then briefly describe methods for economic evaluation of breeding programs. Then I will review the evolution of dairy cattle breeding objectives in the important dairy producing countries. Finally, I will present results of realized and predicted genetic trends from Israel and the US, and evaluate the expected gain from application of biotechnology to livestock breeding. In the sections that include matrices, I follow the convention that vectors will be named using lower case letters, while matrices will be denoted with upper case letters. Both matrices and vectors appear in bold type.

The Israeli Breeding Program

There are currently about 120,000 dairy cows in Israel, nearly all of them Israeli Holstein breed. This number has been virtually constant for 25 years. About 90% of all dairy cows are in the national milk recording program. Dairy production is recorded monthly by milk inspectors and milk samples are sent to the central laboratory for fat, protein, and somatic cell concentration analysis. All breeding is by artificial insemination (AI). There is one AI institute, which is a nonprofit cooperative, owned by the farmers. The national breeding program is based on the “progeny test” scheme (Fig. 1). The Israeli program is cooperative, rather than competitive, and is based on the following principles.

1. About 300 cows are designated as potential bull dams. This number is decreasing slightly due to greater application of multiple ovulation and embryo transplant.

2. About 50 bull calves, sons of elite cows, are purchased by the AI institute yearly. Their price is fixed to current beef prices in Israel. Most of these calves are sons of local sires and the remainder are sired using imported semen, chiefly from the USA and the Netherlands.

3. All first parity cows are inseminated with semen from young bulls. About 1000 inseminations per bull are performed to produce 100 milk-recorded daughters of each sire.

4. About five elite sires are selected based on first-parity daughter evaluation and returned to general service.

5. These five sires are mated to about 1000 virgin heifers to test for dystocia and calf mortality.

6. All other virgin heifers are mated to proven sires with favorable evaluations for dystocia.

7. All later parity cows are inseminated with semen from proven bulls.

8. Farmers pay a flat rate per cow fixed to cover the operating costs of the AI institute and the milk recording system.

The US Dairy Cattle Breeding Program

The US breeding program is highly competitive, resulting in a reduction in the number of major AI institutes from 11 in 1981 to 5 in 2006 (Funk, 2006). The USA currently has approximately nine million dairy cows of which 85% are Holsteins. Most of the remainder are Jerseys. The number of cows has decreased from a high of 25 million in 1950 (Powell and Norman, 2006). Of the 3.5 million dairy cows entering production each year, the milk of about 700,000 (20%) is recorded by Dairy Records Processing Centers. Since 1980, the number of processing centers has fallen from 10 to 5. Approximately 1000 bulls are currently progeny tested each year (Funk, 2006). The mean number of daughters per bulls is approximately 50. Farmers are paid for inseminating cows with semen of young sires, thus the AI institutes invest about $30,000 to progeny test a bull. Similar to the Israeli program, only 12% of the progeny tested sires are returned to general service (Funk, 2006). Unlike the Israeli program, bull calves, sons of elite cows, are purchased by the AI institute at competitive prices and semen pricing is differential. Farmers pay more for semen of elite sires.

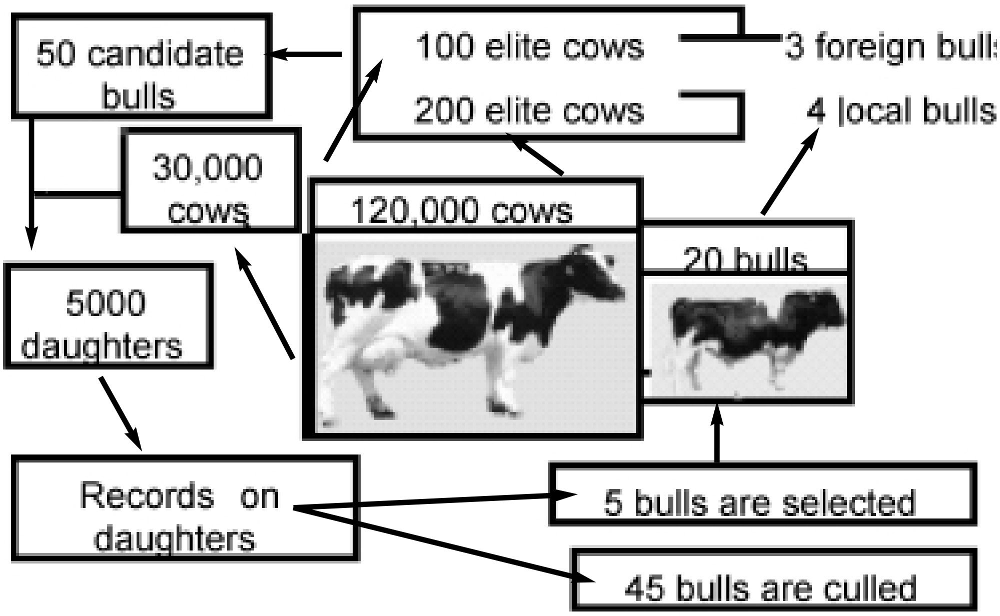

Fig. 1. The Israeli Holstein breeding program.

The US program has the advantage of greater selection of bull sires. Of the 1000 progeny tested bulls, only about ten bulls per year are widely used as bull sires. The Israeli program has the advantages that each young bull is progeny tested on more daughters and there is less incentive for preferential treatment of potential bull dams.

Expected Genetic Gain per Generation

Genetic gains of about 1% of the mean, or about 0.1-0.2 genetic standard deviations of the selection index per year, can be obtained by modern dairy cattle breeding programs (Nicholas and Smith, 1983). Genetic gain per year of the breeding program can be estimated as: $\Sigma\phi_j/\Sigma L_j$, where ϕ_j is the genetic gain per generation for the j^{th} genetic path and L_j is the respective mean generation interval, which will differ for each of the four paths of inheritance. For each of the four paths of inheritance: sire to sire, sire to dam, dam to sire, dam to dam, the genetic gain per generation, ϕ, is computed as $\phi = i\ \rho\ \sigma_a$, where i = selection intensity and is a function of the fraction of individuals selected as parents for the next generation, ρ = accuracy of the genetic evaluation and thus is dependent on heritability, and σ_a = additive genetic standard deviation. In the Israeli breeding index, $\sigma_a \approx 700$ units and the heritability ≈ 0.25. Both i and ρ differ among the four paths of inheritance. In the sire to dam path, about 10% of the sires are returned to general service. Thus i = 1.8. Since the genetic evaluation of each young sire is based on the performance of approximately 100 daughters, $\rho \approx 0.9$ for a trait with a heritability of 0.25. Thus, $i\rho\sigma_a = 1.8 \times 0.9 \times 700 = 1134$ units/generation.

Economic Evaluation of Breeding Programs

The main economic entities involved in breeding programs are farmers, breeders, food processors, consumers, and governments. Breeders can be either commercial or cooperative enterprises. Although genetic gain has resulted in major increases in efficiency of production, very little has remained with either farmers or breeders due to competition. Consumers have benefited from nearly all of the gain. Nevertheless, large investments in breeding programs are economically justified.

Unlike other investments, once a genetic gain is obtained, it is never lost. Although it does not "wear out," its value must be discounted in future years. Thus, the *cumulative* discounted return can be computed as the sum of a progression of the form $V[r^t + 2r^{t+1} + ... + (T-t+1)r^T]$, where V = the nominal value of the annual genetic gain, r = 1/(1+d), d = the discount rate, T = the profit horizon in years, and t = years until first returns are realized. The sum of this progression is computed as follows (Hill, 1971): $R = V([r^t - r^{T+1}]/([1 - r]^2 - [T - t+1]r^{T+1})/[1 - r])$. For example, with a discount rate of 0.08 (r = 0.926), a profit horizon of 20 years, and first returns after 5 years, R = 32.58V. Thus, with a nominal annual genetic gain of $10/animal, total returns to profit horizon will be $325.8/animal or $32,580,000 for a population of 100,000 animals. For an infinite profit horizon, this equation reduces to $R = Vr^t/(1 - r)^2 = V/d^2(1 + d)^{t-2}$, i.e., R = 124.04V. Thus, even with a relatively high discount rate, a little bit of genetic improvement goes a long way.

After initial start-up costs, annual costs tend to be constant. The main cost elements in traditional breeding programs are data recording (useful to farmers for herd management), maintenance of nonproductive animals (males) for future breeding, progeny testing of candidate males, and data analysis. Generally, in traditional breeding programs, total direct costs are small relative to the value of genetic gain. Unlike the genetic gain, the costs of a breeding program are not cumulative. With first costs in the following year, net present value of the cumulative costs (C) is computed as follows (Hill, 1971): $C = C_c r(1 - r^T)/(1 - r)$, where C_c = current annual costs, and the other terms are as defined previously. Using the same values of T = 20, d = 0.08; the net present value of the costs of the breeding program will be $9.82C_c$. Thus for t = 5, net profit will be positive if $V>0.31C_c$. Note that profit can be positive even if the yearly costs are greater than the revenue from the yearly genetic gain. Again, this is due to the fact that genetic gains are *cumulative*, while costs are not. Extended to an infinite profit horizon as above for the case R = 124V, $C = 12.5C_c$. Thus profit will be positive if $V>0.1C_c$.

Nearly all gain due to breeding is transferred to consumers. Thus breeding programs cannot be economically evaluated in terms of profit to the breeding enterprise. The only realistic criterion for the evaluation of breeding programs is the gain to the national economy (Weller, 1994). Considering the differential rates of accruement of profits and costs over time, three methods have been proposed to economically compare alternative breeding programs: (a) computation of aggregate profit with discount rate and profit horizon fixed, (b) computation of the discount rate required to obtain a cumulative profit of zero at the profit horizon, and (c) computation of the time required until zero profit is reached at a fixed discount rate.

Multitrait Selection Index Theory

In animal breeding, the selection objective nearly always includes several traits. Common practice is to compute genetic evaluations for each trait, and then combine these evaluations into a multitrait selection index. Henderson (1973) showed that if the economic value of each trait is constant, then maximum genetic progress is obtained by ranking on $\sum g_{ij}a_i$ where g_{ij} is the selection index genetic evaluation of animal j for the i^{th} trait, and a_i is the economic value of the i^{th} trait. Properties of an economic selection index were summarized by Weller (1994). Expected genetic gains of the component traits obtained by selection on a linear index can be computed by the following equation: $\phi = i\mathbf{Gb}/(sd_i)$, where ϕ = the vector of genetic gains of the component traits, i = the selection intensity, $\mathbf{G}$ = the genetic variance-covariance matrix among the traits included in the index, $\mathbf{b}$ = the vector of index coefficients, which will be the economic values, if selection is based on the genetic evaluations, and sd_i = the standard deviation of the index.

Note that $\mathbf{G}$ is fixed for any set of traits and

$i/(sd_i)$ will not affect the ratios among expected gains. Thus the ratios of the expected gains can only be changed by changing **b**, the vector of index coefficients. Similarly, the vector of index coefficients that should result in a specific vector of genetic changes can be derived by rearranging the previous equation as follows: $\mathbf{G}^{-1}\phi(sd_i)/i = \mathbf{b}$

This equation can be used to compare an "official" selection objective to the "realized" selection objective. Even if the economic values are not constant, maximum economic gain will be obtained by a linear selection index (Goddard, 1983). However, in this case there is no uniformly "best" selection index. Although it is only necessary to estimate the ratios among the economic values, not their absolute values, this is generally quite difficult. In addition, the economic values tend to change over time and place. Thus various alternative methods to compute selection indices have been proposed (reviewed by Weller, 1994). However, selection index is very robust. That is, relatively large changes in the relative economic values will have only very small effects on the predicted genetic gains in the component traits. Changes in dairy cattle selection indices over time, and differences across countries, are considered in the following sections.

Dairy Cattle Breeding Goals

As already noted, animal breeding, especially cattle, requires a long-term investment in which the mean generation interval is five years. However, breeding objectives tend to change with time. Changes in the US and Israeli selection indices since the 1970s are given in Table 1. Relative weights of the various traits are computed by multiplying the selection index coefficients of each trait by its genetic standard deviation and dividing the

Table 1. Changes in traits and relative economic weights in US and Israeli selection indices.

Country	*Trait*	*Year (% change)*					
USA		*1971*	*1976*	*1984*	*1994*	*2000*	*2003*
	Milk	52	27	-2	6	5	0
	Fat	48	46	45	25	21	22
	Protein		27	53	43	36	33
	Productive life				20	14	11
	Somatic cell score				-6	-9	-9
	Udder composite					7	7
	Feet/leg composite					4	4
	Size composite					-4	-3
	Daughter pregnancy rate						7
	Service sire calving difficulty						-2
	Daughter calving difficulty						-2
Israel		*1980*	*1985*	*1991*	*1996*	*2001*	*2004*
	Milk	65	50	-20	-17	-15	0
	Fat	35	50	17	15	13	16
	Protein			64	56	49	45
	Somatic cell score				-14	-11	-14
	Female fertility					13	16
	Productive life						10

sum of standardized units by the sum of their absolute values.

From the beginning of modern breeding programs, selection focused on milk production. From 1985, breeding goals moved towards improving protein yield. During this period, the Scandinavian countries selected for production together with health and fertility. Canada selected for conformation together with production. The main justification for selection for conformation traits, especially with respect to udder and legs, has been that these traits are correlated to cow survival, although results on this question are inconclusive. In recent years, selection objectives were broadened to include herd life, fertility, and health traits, especially somatic cell score (SCS), which is an indicator of udder health and the general level of herd management. The main reasons behind this shift were development of technology to accurately measure new traits in large numbers of animals, quotas and/or price constraints on milk, and increasing concerns associated with the deterioration of the health and fertility of dairy cows. Several studies showed that selection for production negatively effects udder health and reproduction (Lucy, 2001; Heringstad et al., 2003).

Relative emphasis on traits in national selection indices for the major dairy production countries in August 2003 are given in Table 2. Although there are major differences among countries, protein yield was given the greatest weight in all countries. All countries also include fat with positive economic values, although in some countries greater weight is given to longevity. Only Spain still has a positive value for milk production. Some countries have positive values for animal size, while others have negative. A larger animal produces more meat, but also requires more feed for maintenance.

Expected and Realized Genetic Trends

Actual and predicted annual genetic trends for the component traits during the last decade in Israel and actual US genetic trends are presented in Table 3. Israeli genetic trends were computed based on the regression of the cows' estimated breeding values, computed by the animal model, and on the birthdates of cows born between 1981 and 2001. US genetic trends were estimated as the difference between the mean breeding values of cows born in 2000 and 1990. US genetic trends were higher for all three milk production traits, especially milk. This reflects the fact that the index coefficient for milk was positive in the US during this period and negative in Israel. The negative coefficient for milk in Israel would also reduce progress for fat and protein, both of which are positively correlated to milk production. Genetic trend was "positive" (economically unfavorable) for SCS in the US and "negative" (economically favorable) in Israel. This reflects the fact that more weight was given to this trait in Israel. The genetic trend for female fertility was positive in Israel and negative in the US, reflecting the fact that this trait was only recently added to the US index.

The expected genetic trends based on the Israeli index and the index that should have given the observed genetic trends are also given in Table 3. Genetic trends for milk, fat, and fertility were lower than predicted. Trends for SCS (negative) and survival were higher than predicted. The trend for protein was very close to the expected value. The index that should have given the observed trends had a much greater negative coefficient for milk and a smaller coefficient for fat. This may reflect the farmers' response to the fact that the individual farm quota was in milk yield, even though payment was chiefly for protein content.

Genetic Evaluation Methods

Genetic evaluation of farm animals is generally based on analysis of very large numbers of commercial records. Thus it is necessary to correct for herd, year, and season effects. Also distribution of animals across herds is non-orthogonal and genetic evaluation methods must account for genetic trends over time. Thus, all analysis systems are based on the "mixed model" that takes into consideration fixed effects such as herd-year-season and genetic effects that are assumed to be ran-

Table 2. Relative emphasis on traits in national selection indices in August 2003[1].

	Production					Durability							Health and reproduction			
Country	*Milk yield*	*Fat yield*	*Protein yield*	*Fat content*	*Protein content*	*Longe-vity*	*Body size*	*Overall udder*	*Feet & legs*	*Final score*	*Temper-ament*	*Other*	*Udder health*	*Fertility*	*Calving ease*	*Other*
Australia	-18.6	12.0	36.3	-	-	8.5	-4.0	-	-	-	4.0	-	5.2	8.2	-	3.2[2]
Canada	-	14.3	42.7	-	-	7.6	3.8	15.2	11.4	-	-	-	5.0	-	-	-
Denmark	-3.4	10.2	20.4	-	-	6.0	-2.0	9.0	5.0	-	2.0	5.0[3]	14.0	9.0	6.0	8.0[4]
France	-	9.5	35.5	2.5	2.5	12.5	2.5	7.5	2.5	-	-	-	12.5	12.5	-	-
Germany	-	9.0	26.0	5.0	10.0	25.0	3.0	6.0	3.7	-	-	2.3[5]	5.0	5.0	-	-
Great Britain	-16.4	9.5	49.1	-	-	15.0	-	-	5.0	-	-	-	5.0	-	-	-
Ireland	-19.0	8.0	42.0	-	-	23.0	-	-	-	-	-	-	-	8.0	-	-
Israel	-11.0	18.0	51.0	-	-	-	-	-	-	-	-	-	11.0	9.0	-	-
Italy	-	12.0	42.0	2.0	3.0	8.0	-	13.0	6.0	4.0	-	-	10.0	-	-	-
Japan	-	20.3	54.7	-	-	-	-	21.3	3.7	-	-	-	-	-	-	-
Netherlands	-17.0	7.0	34.0	-	-	26.0	-	-	-	-	-	-	4.0	4.0	8.0	-
New Zealand	-17.0	8.0	41.0	-	-	5.0	-19.0	-	-	-	-	-	-	10.0	-	-
Spain	12.0	12.0	32.0	-	3.0	3.0	-	16.0	10.0	9.0	-	-	3.0	-	-	-
Switzerland	-	14.0	27.0	3.0	9.0	7.0	4.8	9.6	4.8	-	-	4.8[6]	10.0	6.0	-	-
USA	-	22.0	33.0	-	-	11.0	-3.0	7.0	4.0	-	-	-	9.0	7.0	4.0	-

[1] Based on Miglior et al. (2005)
[2] Milking speed
[3] Meat quality
[4] Milking speed (6%) and other health traits (2%)
[5] Dairy character
[6] Overall rump (2.4%) and dairy character (2.4%)

Table 3. Actual and predicted annual genetic trends, 1990 to 2000.

	Israeli indices				*Annual genetic trends*		
	Year beginning			*From genetic*	*Israel*		*US*[1]
Trait	*1991*	*1996*	*2001*	*trends*	*Predicted*[2]	*Actual*	
Milk (kg)	-0.274	-0.274	-0.274	-0.45	57.5	15.0	110.3
Fat (kg)	6.41	6.41	6.41	3.0	2.9	2.4	3.2
Protein (kg)	34.85	34.85	34.85	31	2.4	2.4	3.4
Somatic cell score	0	-300	-300	-129	-0.008	-0.023	0.004
% conception	0	0	26	19	0.22	0.09	-0.05
Survival (days)	0	0	0	0.26	12.3	17.6	3.9

[1] Shook (2006)
[2] Based on the 2001 selection index

dom (Henderson, 1973). Until the mid 1980s all genetic evaluation programs for dairy cattle were based on “sire models.” That is, genetic evaluations were computed only for sires and each daughter was considered a “sample” of her sire’s genotype. This allowed for models with a manageable number of effects for the computing capabilities available. Since 1985, “animal models” have been adopted in most advanced breeding programs. In these models a genetic effect is estimated for each animal. For animals without production records (i.e., males), genetic values are determined by including the inverse of the relationship matrix. Since 2000 several countries have adopted “multi-trait animal models” in which several traits are analyzed jointly (e.g., Weller and Ezra, 2004) and a few countries have adopted “test-day models” in which each monthly milk production record is the dependent variable.

Although analysis models have become more complex as computing capabilities have increased, there has been very little analysis as to the actual benefit derived from more complex analysis models. Generally, when a new method is adopted, correlations are computed between the new and old genetic evaluations, but these values cannot be translated into an economic measure of the advantage of the new methodology. All genetic evaluation methods in use assume that pedigree records are correct. Recently, several studies used genetic markers to estimate the frequency of incorrect paternity determinations in dairy cattle. These studies generally found error rates near 10% (Weller et al., 2004).

Biotechnology and Future Directions in Dairy Cattle Breeding

Recently, first steps have been made to incorporate biotechnological methods into the breeding program. Multiple ovulation and embryo transplant are being used to increase the potential number of bull calves from elite dams. Techniques have been developed to genotype and sex embryos prior to implantation. Genome scans to detect specific loci affecting economic factors have been completed for most major dairy cattle populations. Results for milk, fat, and protein production, fat and protein concentration, and SCS from most of the studies are summarized at http://www.vetsci.usyd.edu.au/reprogen/QTL_Map/. Results from these traits and many others including meat production are summarized at http://bovineqtl.tamu.edu. Significant effects were found on all 29 autosomes, but most effects were found only in single studies and have not been repeated. Khatkar et al. (2004) performed a meta-analysis combining data from most of these studies and found significant across-study effects on *Bos taurus* chromosomes 1, 3, 6, 9, 10, 14, and 20.

Methods are being developed to incorporate information on individual quantitative trait loci into the national breeding program. Two ongoing marker assisted selection (MAS) programs in dairy cattle have been reported so far, in French and German Holsteins (Boichard et al., 2002; Bennewitz et al., 2004). It should be possible to increase the rate of genetic progress by up to 25% using new methodologies. However, modern technology complements traditional breeding; it does not replace it! To date nearly all progress in animal breeding was obtained by traditional trait-based methodologies. There is no substitute for accurate data and pedigree recording, and data analysis.

Acknowledgements

This research was supported by a grant from the Israel Milk Marketing Board. I thank E. Ezra and M. Ron for useful discussions.

References

Bennewitz J., Reinsch N., Thomsen H., Szyda J., Reinhart F., Liu Z., Kuhn C., Tuchscherer A., Schwerin M., Weimann C., Erhardt G. and E. Kalm, 2003. Marker assisted selection in German Holstein dairy cattle breeding: outline of the program and marker assisted breeding value estimation. Session G1.9, *54th Ann. Meeting Eur. Assoc. Anim. Prod.*, Rome, Italy.

Boichard D., Fritz S., Rossignol M.N., Boscher M.Y., Malafosse A. and J.J. Colleau, 2002. Implementation of marker-assisted selection in French dairy cattle. *Proc. 7th World Cong. Genet. Appl. Livestock Prod.*, Montpellier, France. 33:19-22.

Funk D.A., 2006. Major advances in globalization and consolidation of the artificial insemination industry. *J. Dairy Sci*., 89(4): 1362-1368.

Goodard M.E., 1983. Selection indices for non-linear profit functions. *Theor. Appl. Genet*., 64(2):339-344.

Henderson C.R., 1973. Sire evaluation and genetic trends. pp. 10-41. In: *Proc. Anim. Breed. Genet. Symp. in Honor of Dr. D. L. Lush*. ASAS and ADSA, Champaign, IL, USA.

Heringstad B., Klemetsdal G. and T. Steine, 2003. Selection responses for clinical mastitis and protein yield in two Norwegian dairy cattle selection experiments. *J. Dairy Sci*., 86(9): 2990-2999.

Hill W.G., 1971. Investment appraisal for national breeding programmes. *Anim. Prod*., 13(1):37-50.

Khatkar M.S., Thomson P.C., Tammen I. and H.W. Raadsma, 2004. Quantitative trait loci mapping in dairy cattle: review and meta-analysis. *Genet. Sel. Evol*., 36(1):163-190.

Lucy M.C., 2001. Reproductive loss in high-producing dairy cattle: where will it end? *J. Dairy Sci*., 84(6):1277-1293.

Miglior F., Muir B.L. and B.J. Van Doormaal, 2005. Selection indices in Holstein cattle of various countries. *J. Dairy Sci.,* 88(3): 1255-1263.

Nicholas F.W. and C. Smith, 1983. Increased rates of genetic change in dairy cattle by embryo transfer and splitting. *Anim. Prod*., 36(2):341-353.

Powell R.L. and H.D. Norman, 2006. Major advances in genetic evaluation techniques. *J. Dairy Sci*., 89(4):1337-1348.

Shook G.E., 2006. Major advances in determining appropriate selection goals. *J. Dairy Sci.*, 89(4):1349-1361.

Van Raden P.M., 2004. Selection on net merit to improve lifetime profit. *J. Dairy Sci.*, 87(10):3125-3131.

Van Vleck L.D., 1987. Reduction in genetic gain for milk production due to economic emphasis on test and type. pp. 23-31. In: *Genetics Research Report to Eastern AI Coop*. Cornell Univ., Ithaca.

Weller J.I., 1994. *Economic Aspects of Animal Breeding.* Chapman & Hall. London, UK. 244 pp.

Weller J.I., 2001. *Quantitative Trait Loci Analysis in Animals*. CABI Publ., London, UK. 287 pp.