水研機構研報，第45号，113－121，平成29年
Bull. Jap. Fish. Res. Edu. Agen. No. 45, 113－121, 2017

Development of Improved Catfish Germplasm at the Warmwater Aquaculture Research Unit, DSDA - ARS

Brian BOSWORTH* and Geoffrey WALDBIESER*

Abstract: Farm-raised catfish is the largest aquaculture enterprise in the U.S. in terms of both production volume and value. The USDA-ARS Warmwater Aquaculture Research Unit (WARU) mission includes development and release to farmers of catfish germplasm improved for economically important traits. Historically, the channel catfish (*Ictalurus punctatus*) comprised nearly all U.S. farm-raised catfish production, but in the last 10 years, production of the F1 hybrid between the channel catfish and blue catfish (*Ictalurus furcatus*) has increased to about 50% of total production. Therefore, the WARU breeding program is focused on genetic improvement of purebred channel catfish and F1 hybrid catfish performance. The channel catfish improvement program has used selection on BLUP breeding value estimates to improve growth rate and carcass yield. We started with a diverse population of channel catfish derived from 10 commercial farms in 2006 and have evaluated over 21,000 animals from 750 full-sib families produced by 408 sires and 624 dams between 2008 and 2015. Heritabilities for harvest weight and residual carcass weight are 0.29 and 0.36, respectively, and fish are selected based on an index that puts equal weight on individual breeding values for growth and family average breeding values for residual carcass weight. Improvements in growth have been 8 - 10% per generation and are in agreement with expected improvements. Increases in residual carcass weight have been less substantial (-2 g per generation) than those for harvest weight due, at least in part, to the necessity for selection on less accurate family average breeding values for carcass weight.

The hybrid catfish improvement program has focused on evaluation, identification and selection of blue catfish sires that produce superior performing hybrid progeny. We initiated a program to collect several blue catfish populations and evaluate performance of their purebred and hybrid progeny. Initial evaluations suggest the majority of genetic variance for growth in hybrid progeny is additive in nature, and populations and individual sires that produce purebred blue catfish progeny with faster growth also produce hybrid progeny with faster growth. We have ongoing experiments to estimate heritabilities and genetic correlations in the purebred blue and hybrid catfish, which will give us direction in selecting purebred blue catfish for improved hybrid catfish performance. We use DNA markers to identify parentage and establish pedigrees in our populations and are developing a SNP chip to be used for genomic selection to improve our breeding value accuracy and rate of improvement, particularly for carcass yield. We are evaluating other traits for inclusion in our selection index, and are collecting and cryopreserving sperm from superior channel and blue catfish sires for future use. This combination of traditional animal breeding, genomic selection and cryopreservation will result in improved catfish germplasm, improved production efficiency and greater profitability for catfish farmers.

Key words: Channel catfish, blue catfish, genetic improvement

2017年2月28日受理（Received on February 28, 2017）
*1 Warmwater Aquaculture Research Unit, USDA-ARS, P.O. Box 38, Stoneville, MS 38776, U.S.A
E-mail: brian.bosworth@ars.usda.gov

Introduction

Catfish farming is the largest aquaculture enterprise in the U.S. in terms of both production volume and value (National Agricultural Statistic Service 2012). Approximately 150 million kg of catfish were produced and processed in the U.S. in 2015. Most of the production occurs in the southeastern U.S. and the vast majority of product is consumed domestically. Prior to 2005, nearly all production consisted of purebred channel catfish, *Ictalurus punctatus*, but in the last 10 years, production of hybrid catfish (F1 hybrid between female channel catfish and male blue catfish, *Ictalurus furcatus*) has increased dramatically and represented about 50% of catfish production in 2015. Although catfish aquaculture represents the majority of U.S. aquaculture production, current production is about half of what it was at its peak in 2003. The reduced production of catfish in the U.S. is related to increased production costs (particularly feed), competition from lower-priced imported fillets (*Pangasius* and *Tilapia*) targeted at similar markets, and the subsequent conversion of catfish ponds to more profitable row-crop production. The USDA-ARS Warmwater Aquaculture Research Unit (WARU) mission includes development and release of improved catfish germplasm to U.S. farmers that will improve production efficiency and help U.S. farmers remain competitive in a global seafood market.

The process of genetic selection to develop improved germplasm for release to the industry requires production and performance evaluation of purebred blue catfish, purebred channel catfish and hybrid catfish. Mating designs used for genetic merit estimation require collection of performance data on traits targeted for selection in large, pedigreed populations. Development of improved germplasm is a recurrent process of broodfish selection, offspring production and evaluation, genetic merit estimation and selection of the next generation of broodfish. Breeding projects at WARU are focused on selection to improve performance of purebred channel catfish and selection of purebred blue and channel catfish to improve hybrid catfish performance. The WARU's current catfish breeding program and future directions are summarized in this paper.

Materials and Methods

Purebred channel catfish

In 2006, 10 to 12 spawns (full-sib families) were collected from eight commercial farms where farm owners indicated fish were from unique base populations. Spawns were hatched and raised in separate family tanks. Fish were fed commercial diets of appropriate size and composition for their developmental stage. Fish densities in tanks were periodically reduced and equalized in all tanks. When fish averaged greater than 40 g, 100 fish per full-sib family were tagged with individually coded passive integrated transponders (PIT) tags (BioMark, ID, USA). Fish were then transferred to replicate earthen ponds and families reared communally. Fish were fed a 32% protein commercial catfish diet to apparent satiation once daily until the majority of the fish were of market weight (0.5 to 1.0 kg). Fish were then harvested, and measured for total weight and gender. The largest 3 to 6 males and 4 to 7 females from each full-sib family were retained as broodfish and an additional 80 mature broodfish of unknown age were obtained from each of two additional commercial farms and PIT tagged. An initial pedigree file was established with an additive relationship of 0.5 among individuals within full-sib families and assuming all other fish were unrelated. Fish derived from this base population are referred to as the Delta Select strain of channel catfish. Blood samples were collected from all broodfish (835 females and 638 males) for DNA isolation and then broodfish were stocked in the spring of 2008 in earthen ponds at 800 kg/ha and allowed to mate at random. Spawns were collected from ponds every 2 to 3 days and moved to the hatchery from mid-April through early August. Fry were hatched and treated as described above and a sample of 8 to 10 fry were collected from each spawn for DNA isolation. Microsatellite genotypes of fry from each spawn and potential parents were compared to determine parentage of spawns (Waldbieser and Bosworth, 2013). Sixty to 75 fish per family were tagged, stocked communally in earthen ponds and grown to market weight as described previously. Fish were harvested in late October to November when water

temperatures cooled and feeding activity declined. Fish were harvested by seining the ponds, then anesthetized with 200 ppm MS-222 and gender, PIT tag number and weight to the nearest 0.5 g were recorded for each fish. A sample of 4 to 5 males and 4 to 5 females from each full-sib family in the weight range typically processed at commercial facilities (0.4 to 1.0 kg) were electrically stunned, decapitated (Baader 166 heading machine, Baader North America Corporation, Auburn, WA, USA), eviscerated by hand and the carcasses were weighed.

Broodfish used in the 2008 spawning season were held over winter, inventoried, weighed and restocked into spawning ponds spring of 2009. The percentage of male and female channel catfish that are mature and spawn is only about 25% at two years old but increases to over 50% at three years old. Therefore, to increase the number of broodfish that spawn and maintain a higher effective population size, selected broodfish were typically spawned as two year olds and again as three year olds. This process has been repeated with selected broodfish being spawned in 2011 and 2012, and 2014 and 2015.

Phenotypic variance, additive genetic variance, heritablilities and breeding values were estimated for each trait (harvest weight and carcass weight) with linear single-trait animal models using MTDFREML (Boldman *et al*., 1995). The model for harvest weight included fixed effects of pond, year, and gender; age within year*gender as a linear covariate; and animal additive genetic and common environment (confounded effects of full-sib family and fingerling rearing tank) as random effects. Carcass yield (the percentage of whole weight that is comprised of carcass weight) is a trait of high value to catfish processors. However, because of statistical issues related to estimation of variance components for ratios, carcass data was analyzed as residual carcass weight (carcass weight adjusted to a common whole animal weight by using whole weight as a linear covariate). The model for residual carcass weight included fixed effects of pond, year, gender and day of processing; whole weight within year*gender as a linear covariate; and random effects of animal additive genetic and common environment. Genetic correlations between harvest weight and carcass weight were not analyzed using a multi-trait model because animals measured for carcass weight were selected based on a size range required to fit the processing equipment and therefore were not a random sample, which would have biased the correlation estimate. Instead, the genetic correlation between harvest weight and carcass weight was estimated as the correlation between full-sib family average breeding values for harvest weight and residual carcass weight.

Breeding values for harvest weight and residual carcass weight were estimated with MTDFREML and approximately the top 10% of fish from each year-class were selected as broodfish based on an index placing equal weight on individual's breeding value for harvest weight and full-sib family value for residual carcass weight. Response to selection for harvest weight and residual carcass weight was evaluated by estimating the correlation between mid-parent breeding value (average breeding value of a sire and dam) and the phenotypic means of their corresponding full-sib progeny family means after adjustment for relevant fixed effects (year, pond, sex). Genetic trends (changes in mean breeding value of the population over time) were also estimated for harvest weight and residual carcass weight.

Blue and hybrid catfish

There is little commercial production of blue catfish and little data relevant to genetic effects of blue catfish on purebred or hybrid catfish performance. Therefore, our initial goal was to gather blue catfish germplasm from diverse sources and evaluate the effects of these populations on harvest weight and carcass yield in their purebred and hybrid progeny. Because blue catfish mature at a late age (typically five years or older) and shipping large fish is costly and difficult, we obtained fish from some sources as larvae, some as juveniles and some as mature adults. Our initial evaluations of blue catfish focused on comparisons on the population level rather than evaluations of individual males within populations due to the fact that obtaining sperm from blue catfish males to produce hybrids requires killing the male and storage of fresh sperm is limited to about five days.

We conducted a series of studies comparing effects of blue catfish populations on purebred blue catfish

and hybrid catfish progeny growth. Typically, blue catfish are pond- spawned, reared in family tanks, PIT-tagged and then stocked in ponds and reared communally as described previously for channel catfish. Hybrids are produced by hormone (LHRHa or pituitary extract) induced ovulation of female channel catfish and fertilization with blue catfish sperm obtained by maceration of testes (Bosworth *et al*., 2005). Hybrid catfish larvae are reared in family tanks, PIT-tagged and evaluated for performance in earthen ponds as described previously.

Data from five growth trials are presented. The first trial (2009 year-class) compared effects of 4 to 5 sires from each of two blue catfish populations on harvest weight of their hybrid catfish progeny; the second trial (2010 year-class) compared effects of 7 to 10 sires from each of five blue catfish populations on harvest weight of their hybrid catfish progeny; the third trial (2012 year-class) compared effects of 5 to 15 full-sib families from each of three blue catfish populations on harvest weight of their purebred blue catfish progeny; the fourth trial (2014) compared effects of 3 to 15 full-sib families from each of four blue catfish populations on fingerling weight of their purebred blue catfish progeny; and the fifth trial compared effects of 9 to 27 full-sib families from each of three blue catfish populations on fingerling weight of their purebred blue catfish progeny. Two trials (2014 and 2015 year-classes) are ongoing and, therefore, only weights of fingerlings at stocking are presented.

Mean harvest weight of hybrids and purebred blues produced from blue catfish populations were compared within each trial using the Mixed Procedure of SAS (SAS Institute, Cary, NC, USA). Models for harvest weight included pond and sex as fixed effects, age as a covariate and full-sib family within population as a random effect. Models for fingerling weight included age as a covariate and full-sib family within population as a random effect. Full-sib family was used as the error term in comparisons of population means. Correlations between mean weight of purebreds and hybrids produced using each population were estimated for each trial and the mean of these correlations was determined and provided an estimate of the relationship between purebred and hybrid growth of the various populations tested.

Results

Channel catfish

A total of 21,055 progeny from 750 full-sib families produced by 624 dams and 408 sires have been measured for harvest weight; 4,060 progeny from 585 families produced by 494 dams and 342 sires have been measured for carcass weight (Table 1). The heritability estimates for harvest weight and residual carcass weight are 0.29 (± 0.03) and 0.35 (± 0.05), respectively. Values for phenotypic, additive genetic and common environmental variance and heritabilities for harvest weight and residual carcass weight are listed in Table 2. The correlation between full-sib family mean breeding values for harvest weight and carcass yield was -0.11. Correlations among mid-parent breeding values and corresponding full-sib family means were 0.50 ($p < 0.0001$) for harvest weight and 0.41 ($p < 0.0001$) for residual carcass weight. The mean breeding values for harvest weight were 0 g for the base population, 78 g for the 2011 and 2012 year-classes, and 140 g for the 2014 year-class; mean breeding values for residual carcass weight were 0 g for the base population, 2.2 g for the 2011 and 2012 year-classes, and 4.8 g for the 2014 year-class.

Blue and hybrid catfish

Blue catfish population had a significant effect on purebred blue catfish and hybrid catfish progeny growth in each of the five trials presented (Table 3). Purebred and hybrid catfish progeny produced from Rio Grande population parents consistently had the highest progeny harvest weight. The overall mean correlations across studies between mean harvest weight for hybrid and purebred progeny produced by the various populations tested was 0.98 ($p < 0.001$), indicating the effect of blue catfish population on progeny growth is consistent across hybrid and purebred progeny.

Discussion

Heritabilities for harvest weight (0.29) and residual carcass weight (0.35) in the Delta Select strain of

Table 1. Number of full-sib families, sire and dams and means (+ SD) and number of fish measured for harvest weight and carcass yield for 2008, 2009, 2011, 2012 and 2014 year-classes of Delta Select channel catfish

Year-class	Full-sib families	Sires[1]	Dams[1]	Harvest Weight			Carcass Yield %		
				Mean	SD	n	Mean	SD	n
2008	161	107	149	777.4	284.9	4,762	58.3	1.7	829
2009	186	113	181	614.7	225.3	5,686	58.0	1.8	1,352
2011[3]	170	89	161	702.2	263.7	1,982	--	--	--
2012	104	67	90	814.6	281.0	4,484	64.4	1.7	924
2014	113	73	109	881.4	287.5	4,141	64.3	1.7	955
Total n									
Harvest weight	750	408	624			21,055			
Carcass yield	585	342	494						4,060

[1] The total number of sires and dams is less than the sum of sires and dams across years because some sire and dams spawned in consecutive years.

[2] Carcass data were analyzed as residuals carcass weight after covariate adjustment to a common whole weight, but values presented in Table 1 are carcass yield (100*carcass weight/whole weight) to be more meaningful to the reader. 2008 and 2009 carcass yield data were calculated based on skin-off carcass weights, 2012 and 2014 carcass yield data were calculated based on skin-on carcass weight.

[3] A severe outbreak of proliferative gill disease resulted in substantial mortalities in 2011 and, therefore, no fish were processed.

Table 2. Phenotypic, additive genetic and common environmental (tank and full-sib family) variance and heritabilities (+ SE) for harvest weight and residual carcass weight in the Delta Select strain of channel catfish

Trait	Variance Component				
	Phenotypic	Additive Genetic	Common Environment	Heritability	SE
Harvest weight g	58,302	16,965	4,797	0.29	0.03
Residual Carcass weight g	114.4	40.5	6.5	0.35	0.05

Table 3. Effect of blue catfish sire population on least square means1 for harvest and fingerling weight of purebred and hybrid catfish offspring

Year-Class	Hybrid/ Purebred	Trait	Blue Catfish Population					
			Rio Grande	D&B	MS River	MO River	Kentucky	SE
2009	Hybrid	Harvest Weight g	---	362.0[a]	---	---	278.3[b]	23.1
2010	Hybrid	Harvest Weight g	572.2[a]	525.0[a,b]	506.7[b]	459.6[c]	442.0[c]	26.2
2012	Purebred	Harvest Weight g	489.2[a]	309.9[b]	286.2[b]	---	---	50.5
2014	Purebred	Fingerling Weight g	45.2[a]	38.9[a,b]	31.5[b]	16.1[c]	---	5.5
2015	Purebred	Fingerling Weight g	143.8[a]	95.4[b]	91.3[b]	---	---	8.1

[1] Means within row are significantly different at $P < 0.05$

channel catfish are similar to those for growth and carcass yield observed in other farmed fish species (Navarro *et al*., 2009; Nguyen *et al*., 2010) and terrestrial livestock (Hermesch *et al*., 2000; Aslam *et al*., 2011). The positive correlation between mid-parent estimated breeding values (EBVs) and mean harvest weight of their full-sib progeny (r = 0.5) and increased genetic trend over time indicate that the response to selection for harvest weight is in agreement with expectations. Data from the first two generations of selection demonstrated an increase of about 8 to 10% in average breeding values for harvest weight each generation, similar to response reported for farmed carp (Dong *et al*., 2015), tilapia (Hamzah *et al*., 2014), trout (Kause *et al*., 2005) and salmon (Gjedrem, 2000). Response to selection for carcass weight was positive but less than expected. The lower response to selection for carcass weight relative to harvest weight is due, at least in part, to the necessity to select on full-sib family mean EBVs for carcass weight, which are less accurate than the individual EBVs used to select for harvest weight. However, the correlation between mid-parent EBVs and offspring carcass weight (r = 0.41) and increased genetic trend over generations suggest positive gain in carcass weight is being made. Even small increases in carcass yield have a large effect of profitability of catfish processors.

The high correlation between mean growth of blue catfish and hybrid catfish progeny produced by the same blue catfish sire populations, along with earlier published data demonstrating much higher variation for general combining ability than for specific combining ability for effects of blue catfish sires on hybrid progeny growth (Bosworth and Waldbieser, 2014), suggest that much of the genetic influence of blue catfish on growth in hybrid progeny is additive. This may be due to genes acting in an additive genetic manner or common dominance deviations between the blue catfish populations and channel catfish we have evaluated. The current data suggests that purebred blue catfish population performance is predictive of hybrid catfish performance and that we can substantially improve hybrid growth simply by selecting for increased purebred blue catfish growth. We have a large on-going project with 120 blue catfish sires from four populations each mated to two blue catfish females and 2 to 3 channel catfish females in a series of factorial matings. Offspring from these matings are being evaluated for growth and carcass weight and the data will be used to estimate heritabilities of these traits in purebred blue catfish and hybrid catfish, genetic correlations among traits in purebred blue and hybrid catfish, and relative importance of additive and dominance genetic variation for traits. This information will provide details on the optimal approach to selecting purebred catfish for improvement of hybrid catfish.

Current germplasm development has focused on improving catfish growth and meat yield because these traits are economically important to catfish farmers and processors and because they can be measured accurately and relatively inexpensively on the large numbers of animals required for accurate estimation of heritabilities and breeding values. However, we have been collecting data on reproductive traits, disease resistance and meat quality and may include additional traits in future selection indices, if the heritabilities and economic values of the traits indicate that it would benefit catfish farmers and processors.

The use of microsatellite DNA polymorphisms to identify parentage in channel, blue and hybrid catfish populations has played an important role in our genetic evaluations by providing pedigree information required for heritability and breeding value estimation (Waldbieser and Bosworth, 2015). However, we are now planning to expand use of DNA technology in our breeding program by evaluating the use of SNP markers for genomic selection in the Delta Select channel catfish population and in evaluations related to improvement of hybrid catfish performance. We are near completion of a 50 K SNP chip (Affymetrix, Santa Clara, CA, USA) based on markers that segregate in the Delta Select population and will be evaluating approaches to using genomic selection to improve accuracy of breeding value estimates. Genomic selection should be particularly beneficial for improving accuracy of breeding value estimates and the rate of genetic gain for traits like carcass yield, which have high heritability and large economic value but cannot be measured on live animals (Daetwyler *et al*., 2012).

Ultimately, one of our primary missions at the WARU is to release improved catfish germplasm to U.S. catfish farmers for commercial production. The role of development and release of commercial germplasm is a unique situation for a research agency and requires considerable planning to allow equitable distribution of germplasm, evaluation of performance and determination of impact after release. We are currently evaluating Delta Select channel catfish from our third generation of selection and are discussing options for a commercial release with industry stakeholders. The data collected to date indicate that the selected population should have substantially faster growth and higher carcass yield than the base population, which represented fish from hatcheries providing greater than 50% of industry production at the time the base population was formed. However, at this time, no direct comparisons of performance of the Delta Select and channel catfish currently being used by the industry have been conducted. Attempting to replicate the multitude of management strategies employed by farmers (stocking densities, feeding strategies, aeration management, etc.) and compare the Delta Select and industry fish in a research setting is likely impossible. Therefore, a scenario in which the fish are initially released to a small number of producers willing to provide accurate feedback on commercial performance, including growth, survival, feed conversion and processing yield, prior to large scale release may be the best approach. If performance data from the initial release is favorable, the high reproductive capacity of catfish would allow rapid expansion and additional widespread release of the Delta Selects to commercial producers. Releases could be made every couple of generations to distribute fish with additional improvements to farmers if the initial release is favorable.

The blue catfish breeding program is not as advanced as the channel catfish program for various reasons, including a lack of domesticated populations, the time involved in testing blue catfish due to the later age at maturity of blue catfish compared to channel catfish, and the requirement to kill blue catfish males to obtain sperm for hybrid catfish production. However, the potential for industry impact through development and release of improved blue catfish germplasm is tremendous. Calculations based on discussion with commercial hybrid hatchery operators suggest 3,000 to 4,000 male blue catfish would suffice for current levels of hybrid catfish fry production. Even if hybrid catfish production doubles, that is still less than 10,000 males a year, which is substantially less than the male offspring produced from a single large blue catfish full-sib family. Therefore, identification and development of improved blue catfish germplasm, with subsequent rapid expansion to commercial industry production, has the potential to have a rapid and dramatic positive benefit on hybrid catfish performance.

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Commonly used cow evaluation methods apply principles of the selection index to herdmate deviations on the cow and close relatives. In contrast, best linear unbiased prediction adjusts records by best linear unbiased estimates of all fixed effects in the model and simultaneously weights those adjusted records by selection index principles. It would be advantageous to utilize all known relationships among animals in the herd in the latter method, but computations have been too laborious, requiring the inverse of the numerator relationship matrix. By a method of writing this inverse rapidly without computing the relationship matrix itself, all relationships can now be used in intraherd cow evaluation. Further, tests of progeny by artificial insemination on sires used in the herd can be incorporated.

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A combined crossbred and purebred selection (CCPS) method, i.e. using crossbred and purebred information, was proposed to achieve genetic response in crossbred animals. Selection index theory was applied to establish a CCPS index. The CCPS was compared with pure-line selection (PLS) and crossbred selection (CS) methods. The genetic correlation between purebred and crossbred performance (r_{pc}) and crossbred heritability (h_c^2) are crucial factors in the comparison. The CCPS is always

better than PLS or CS when a fixed number of purebred progeny is tested. With a fixed total number of purebred and crossbred tested progeny, CCPS is only worse than PLS for very high values of rpc (> 0.8). Superiority of CCPS over PLS increases and over CS decreases with decreasing r_{pc}. The larger h_c^2 is relative to purebred heritability,the more response CS and CCPS will achieve. The robustness of CCPS against inappropriate assumptions on r_{pc} and h_c^2 values was investigated. The expected response is always an overestimate, and the actual response is smaller than the optimal response when r_{pc} is assumed one but the true r_{pc} is smaller. The difference between actual and optimal response increases as r_{pc} decreases, but it is small for large r_{pc} values (e.g. < 3% for r_{pc} > 0.7). The expected response is smaller than the actual response when r_{pc} is large and $h_c^2 > h_p^2$. Finally, the actual response to CCPS is larger than the optimal response to PLS for positive values for r_{pc}. The main conclusions are: (1) CCPS method is optimal for obtaining genetic response in crossbreds and (2) CCPS with inappropriate assumptions on r_{pc} and h_c^2 values (e.g. recognizing crossbreds as purebreds) achieves more genetic response than PLS for common values of r_{pc} and crossbred heritability.

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Recent advances in molecular genetic techniques will make dense marker maps available and genotyping many individuals for these markers feasible. Here, we attempted to estimate the effects of z50,000 marker haplotypes simultaneously from a limited number of phenotypic records. A genome of 1000 cM was simulated with a marker spacing of 1 cM. The markers surrounding every 1-cM region were combined into marker haplotypes. Due to finite population size (Ne 5 100), the marker haplotypes were in linkage disequilibrium with the QTL located between the markers. Using least squares, all haplotype effects could not be estimated simultaneously. When only the biggest effects were included, they were overestimated and the accuracy of predicting genetic values of the offspring of the recorded animals was only 0.32. Best linear unbiased prediction of haplotype effects assumed equal variances associated to each 1-cM chromosomal segment, which yielded an accuracy of 0.73, although this assumption was far from true. Bayesian methods that assumed a prior distribution of the variance associated with each chromosome segment increased this accuracy to 0.85, even when the prior was not correct. It was concluded that selection on genetic values predicted from markers could substantially increase the rate of genetic gain in animals and plants, especially if combined with reproductive techniques to shorten the generation interval.

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Genomic evaluation methods assume that the reference population is genotyped and phenotyped. This is most often false and the generation of pseudo-phenotypes is uncertain and inaccurate. However, markers obey transmission rules and therefore the covariances of marker genotypes across individuals can be modelled using pedigree relationships. Based on this, an extension of the genomic relationship matrix can be constructed in which genomic relationships are propagated to all individuals, resulting in a combined relationship matrix, which can be used in a BLUP procedure called the Single Step Genomic BLUP. This procedure provides so far the most comprehensive option for genomic evaluation. Several extensions, options and details are described: compatibility of genomic and pedigree relationships, Bayesian regressions, multiple trait models, computational aspects, etc. Many details scattered through a series of papers are put together into this paper.