SERVING SEVERAL SPECIES WITH ANIMAL MODELS

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SUMMARY

Animal-model best linear unbiased prediction (BLUP) is more accurate for estimating breeding values than are other models and evaluation procedures. Implementation of the animal model has been researched most extensively for dairy cattle breeding. However, its desirable properties have resulted in its application to many other species. Since 1983, an animal model has been used for calculating national evaluations of horses, swine, beef cattle, sheep, and goats in several countries. The use of the animal model has enabled breeding schemes to become more flexible by increasing the number of animals available for selection. However, a well-organized data recording system is required to establish genetic links among herds.

INTRODUCTION

Animal models used in prediction of breeding values by BLUP methodology have been recognized as preferable to other traditional models because they better describe genetic and environmental effects that determine an animal's performance. They allow more accurate genetic evaluation by considering nonrandom matings and including all available pedigree information. Application of an animal model also provides tools such as genetic trends and female evaluations for within-herd selection. One potential drawback to implementation of an animal model is increased computational demands. Application of the animal model has been made possible in many cases by development of computing strategies to reduce computing time and memory requirements (Quaas and Pollak, 1980; Hudson, 1984; Schaeffer and Kennedy, 1986; Ducrocq *et al.*, 1990). Another disadvantage of the animal model is the possibility of increasing the level of inbreeding in a population because animals used as breeding stock (those with higher evaluations as a result of including more information from relatives) are more likely to be related to each other (Toro *et al.*, 1988; Wray, 1989).

Although the most extensive use of animal models has been for genetic evaluation of dairy cattle, their desirable properties have resulted in expanded applications to many other species. Animal model methodology is influencing breeding schemes and may lower costs per unit of genetic gain. This paper reviews and updates information on implementation of the animal model by several countries for genetic evaluation of horses, swine, beef cattle, sheep, and goats.

HORSE BREEDING

The main objectives in horse breeding are success in riding and racing competitions. Specific circumstances of horse production define horse breeding schemes. In many cases, herds are of extremely small size. For example, in Germany, more than 80% of the breeders only have one or two mares (Priesinger, 1989, personal communication). Population size also is frequently small with risk of inbreeding. Some breeds, especially riding horses, are selected for several purposes, such as sport (show jumping and dressage) and leisure riding. Restricted use of artificial insemination (AI) in horse breeding and a low reproductive rate due to a low foaling rate result in small numbers of progeny per parent. For example, in France, a stallion may serve only 100 mates per year (Tavernier, 1988). A significant amount of nonrandom mating occurs and usually is associated with well-known pedigree information. As in other species, animals of both sexes are selected at various stages, and young individuals without their own performance records have to be selected as parents. Interactions involving animal and other effects such as rider, trainer, and race distance or mare-by-herd interactions may be of importance (Langlois and Chico, 1989; Priesinger, 1989, personal communication).

Most of the conditions particular to horse breeding are more efficiently handled with an animal model as discussed by Tavernier (1988) and Philipsson (1989). Multiherd evaluations are necessary to provide comparable breeding value estimates of animals in different herds connected through common sires and to enlarge possibilities for selecting animals beyond the reduced herd level. Multitrait situations are handled efficiently by mixed model methodology. In addition, use of all relationships corrects for nonrandom matings, increases amount of pedigree information other than that for parent-offspring utilized in analysis, and allows for more accurate prediction of breeding values of young animals without own records. The animal model also permits correction for interactions among animals and some fixed effects.

The first practical application of an animal model was done for horses. Arnason (1983, 1984) applied a multitrait animal model to estimate breeding values for 10 traits in Icelandic Toelter horses. Since 1987, data from the Swedish Riding Quality test have been used to predict breeding values for conformation, gaits, and jumping performance using a multitrait animal model (Arnason, 1987; Hedebro-Velander *et al.*, 1989). In 1987, 2347 animals with records plus 2323 unrecorded animals were evaluated. Routine prediction of breeding values for German riding horses began in 1989 (Meinardus, 1988); 95,000 horses from dressage and 165,000 from jumping competitions have been evaluated (Bruns, 1990, personal communication). In France, genetic evaluations of jumping and trotting horses are computed regularly and published (Langlois, 1990, personal communication); 565,251 jumpers and 140,107 trotters have been evaluated. Chico *et al.* (1987, 1989) applied an animal model to evaluate 1330 thoroughbreds with own performance and 3815 animals without records in Spain. In 1989, a catalogue with breeding values for log of earnings and rank at finish was published for mares, stallions, and runners. Wilson *et al.* (1988) predicted breeding values for official finish time with a reduced animal model for the American Quarter Horse Association; 173,808, 151,164 and 70,875 animals were evaluated for performance in 320-, 366-, and 402-m races. The basis for animal model evaluation of trotters has been established in Belgium (Leroy *et al.*, 1988) and in Norway (Klemetsdal, 1988). Application of an animal model for the thoroughbred population also is planned in France, Germany (Preisinger, 1989, personal communication), and Sweden (Hedebro-Velander *et al.*, 1989).

Models for riding and jumping evaluations include effects of sex, year, place or region, and rider quality as fixed effects and animal and permanent environment as random effects. A random dam-by-herd interaction effect also is included in French evaluations. Models for racing performance account for sex, age, and type of race (distance, race track, weight carried) as fixed effects and animal and permanent environment as random effects.

SWINE BREEDING

The pyramidal structure of nucleus, multiplication, and commercial breeders is common to most countries' swine industry. Application of mixed model methods permits more flexibility in this breeding structure by allowing selection across herds (even of relatively small size) and, therefore, leads to a decentralization of the breeding structure (Webb and Bampton, 1988). Another benefit of the animal model in swine breeding is the improvement that could be realized for evaluations of traits of low heritability. Traits of increasing interest for the pig industry such as litter size and eating quality (Webb and Bampton, 1988) are evaluated more accurately if more pedigree information is included in the analysis.

Implementation of the animal model for estimating breeding values of pigs has to be adapted to characteristics of swine production systems. Currently, pedigree information sometimes is missing. Pigs have a much faster reproductive rate and shorter generation interval than horses, sheep, goats, and cattle. Because animals are promoted to parent status rapidly and evaluations must be run often, data collection and preparation must be done efficiently, and evaluations should be adapted to these circumstances by establishing special organizational and computing strategies.

Animal model evaluations for swine have not been implemented in many countries on a large scale. Across- and within-herd evaluation first was applied in 1984 in Ontario, Canada (Hudson and Kennedy, 1985) and was expanded to the whole country 1 year later (Kennedy, 1987). March 1987 evaluations included records on 604,191 pigs, and growth rate and backfat thickness were evaluated. In the United Kingdom, across- and within-herd evaluations were started for a pig breeding company in 1988 (Bampton, 1989, personal communication). Individual farms are linked by AI; dam lines are selected for litter size and lean growth rate and sire lines for lean growth, efficiency, and muscle distribution. Animal model evaluation systems for production and reproduction traits are being prepared by other swine breeding companies in the United Kingdom.

Several countries have or will initiate estimation of breeding values for performance in central test station using an animal model. In Denmark, a univariate animal model is run weekly for daily gain, feed efficiency, and percentage meat (Sorensen, 1989, personal communication). For feed efficiency, analysis is done on averages. Although litter size is not part of the breeding goal yet in Denmark, evaluations are calculated every 3 months for number of pigs born alive in dam lines using a repeatability animal model.

In all programs, an individual trait model is used because of the difficulty in insuring that all data are available at the different stages in the selection process rather than because of the increased computational needs for multitrait evaluation. Models for traits related to the fattening period include herd, year-season, sex, and parity of dam as fixed effects and animal as a random effect. Effects of litter have been included as either fixed or random, and problems on how to consider effect of litter size and litter environment on individual performance still remain.

BEEF CATTLE BREEDING

Beef cattle usually are raised under extensive conditions. As a consequence, herd environments differ greatly and maternal traits become especially important for economically efficient production. As in other species, recording performance of animals under a common environment has been undertaken in most countries to produce comparable genetic values. However, limitations of using central station performance to select for preweaning direct and maternal growth effects and reproductive traits are widely recognized (Morris and Carter, 1982). Application of an animal model allows a more efficient selection of animals for both growth and maternal traits. Multitrait BLUP evaluations also are especially suitable for beef cattle to reduce bias from selection at early stages and to provide evaluations for traits that are not measured in all animals, such as birth weight.

The limiting factor for implementation of an animal model in national evaluations for beef cattle populations is the low level of genetic links among herds. For extensive management conditions in which AI is not widespread, use of more complete models (such as animal models) combined with more accurate evaluation procedures (such as mixed model methodology) does not necessarily produce accurate and comparable evaluations unless a sufficiently high number of connections among herds exists (Parnell *et al.*, 1986). Links among herds are checked routinely for Canadian beef cattle evaluations (Chesnais and Song, 1988) and for American Simmental evaluations (Benyshek, 1987).

Several solutions have been applied in different countries to overcome lack of connected field data. A reduced animal model was implemented in the United States for Limousin and Brangus breeds in 1984 and for Horned Hereford, Gelbvieh, and Red Angus breeds in 1985 and 1986. Benyshek *et al.* (1988) estimated that 600,000 registered beef animals potentially could be evaluated each year. Of registered animals (12 breeds), 30% are AI sired (Koch *et al.*, 1986). This rapid evolution of the animal model has been possible because of the organization of beef cattle breeding in the United States. Field data recording, development of AI, and sire reference schemes were established early, which improved accuracy of genetic evaluations (Marlowe, 1982; Benyshek *et al.*, 1988). Canada started to provide multitrait animal model evaluations in 1988 (Chesnais and Song, 1988; Robinson and Chesnais, 1988). Across- and within-herd evaluations are computed for four breeds; approximately 44,000 animals are evaluated each year under the beef sire monitoring program (Robinson and Chesnais, 1988). In Australia, two evaluation systems (Breedplan and Group Breedplan) provide multitrait animal model evaluations within and across herds. Ten widely used reference sires are used as a fixed base relative to which all evaluations are made. A total of 443 herds were enrolled in Breedplan in 1987; average size of herds is 75 cows (Ponzoni, 1988). Animal model evaluations also are computed in New Zealand for a small portion of the Hereford population (Baker, 1990, personal communication). The basis for animal model implementation for beef cattle evaluations is being determined in France. New performance records are available annually for 130,000 Charolais and 50,000 Limousin cattle. For Limousins, this would result in estimating 600,000 breeding values for both direct and maternal effects (Renand, 1990, personal communication.)

Evaluation models are similar in all countries. A contemporary group consisting of animals of similar age, same breed and sex, similar management, and same birth year is included as a fixed effect. Additive genetic direct and maternal effects as well as a permanent environmental maternal effect are included as random factors (Benyshek *et al.*, 1988; Chesnais and Song, 1988; Robinson and Chesnais, 1988; Ponzoni, 1988; Baker, 1990, personal communication).

In most cases, a multitrait evaluation is computed. Weights at different ages or gain between two ages are evaluated in all cases. Calving ease also is considered in some U.S. evaluations and in Canadian evaluations. Including reproductive traits such as scrotal circumference, calving interval, and number of services is being considered for the future (Benyshek *et al.*, 1988; Ponzoni, 1988).

SHEEP AND GOAT BREEDING

Similar to beef cattle, use of animal model techniques for sheep and goats presents appealing advantages. Multiple objective selection in many sheep production systems, diversity of environments in which sheep are raised within the same breed and within the same country, and interest in traits with low heritability such as reproductive characteristics make an animal model especially appropriate.

Despite these advantages, mixed model methodology was not implemented for sheep evaluation until recently in several countries. One exception is the use of mixed model evaluation techniques in the Swedish sheep breeding program (Danell, 1982). Most reasons for this resulted from the fact that sheep populations are usually raised extensively (Rae and Anderson, 1982; Baker and Parrat, 1988). Under these conditions, recording performance and pedigree becomes difficult. Recording under less extensive conditions such as for dairy sheep and goats has been better developed (Croston *et al.*, 1980). Paternity identification still is missing in many cases because of multiple sire mating. Techniques to introduce multiple-sire mating information in animal model evaluations to improve prediction of progeny and dam breeding values have been developed by Henderson (1988).

Another constraint for implementing animal models for sheep is limited use of AI in sheep breeding. Techniques for handling frozen sheep semen are not developed fully, and use of AI under extensive conditions becomes impractical in many situations. To overcome this difficulty, several schemes for sire referencing have been developed (ram circles and cooperative nucleus schemes). Also, interest in discrete traits such as many reproductive characteristics and in combining discrete and continuous traits requires development and application of more complicated evaluation techniques.

The animal model has been implemented recently for sheep in some countries and is being developed in several other countries. In New Zealand, an animal model is used with data from three sheep breeds; a sire referencing scheme links flocks genetically through AI. About 1400 rams with 150,000 progeny are involved. Wool and weight traits are analyzed with a model that includes year-flock-sex, dam age, birth rearing rank, and birth date (within year-flock-sex effect) as fixed effects. Currently only breeding values for sires are provided to participants, but breeding values for ewes and progeny could be made available eventually (Johnson, 1990, personal communication). In Spain, an animal model has been used since 1988 for evaluation of Latxa dairy sheep. About 90,000 ewes and 63 AI rams were evaluated in 1989. The evaluation model includes flock by year, season, number of lambs born, and dam age as fixed effects. Permanent environmental and animal genetic effects are included as random effects (Gabiña, 1990, personal communication). Within-flock evaluation programs to produce multitrait animal model evaluations for meat sheep have been developed in Canada (Chesnais and Song, 1988).

Animal model evaluations for dairy goats have been implemented in the United States. Over 140,000 animals were evaluated for milk and fat in July 1988. About 70% of animals had protein evaluations as well. The evaluation model included fixed management group and random herd-sire, permanent environmental, animal, and residual effects (Wiggans, 1989).

Interest in BLUP techniques for sheep and goats likely will spread in the next few years (Elsen and Bibe, 1988; Ponzoni, 1988).

CONCLUSIONS

Animal models have been implemented in recent years for predicting breeding values across herds for horses, swine, beef, sheep, and goats. Use of animal model allows operational models to approximate ideal models more closely in regard to genetic effects and possible interactions between animal genetic and environmental effects. Resulting evaluations have provided new tools for selection and are causing changes in breeding schemes. Because all available performance and pedigree information is combined, predicted breeding values of animals of both sexes are comparable even though amounts of information and environments may differ. Therefore, more animals are used as breeding stock, and accuracy of evaluations for traits with low heritability, such as litter size in pigs and sheep, can be increased. Application of animal models has emphasized the importance of creating genetic links among herds and of accurately recording field data. Traditional pyramidal breeding structures can be relaxed, and a larger number of individuals can be considered as potential parents of the next generation.

Although interest in using animal models for both national and within-herd evaluations has been widespread, difficulties in computing evaluations for large populations has prevented its more extensive use. Additional challenges with animal model evaluations include definition of genetic and environmental factors and their interactions that may determine performance, especially for horse and swine breeding; estimation of accurate genetic parameters, particularly for multitrait and categorical data evaluations; preferential treatment; selection bias if records used to select individuals are not included in the analysis; and incomplete pedigree information.

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