Estimation of economic values for traits of dairy sheep: I. Model development

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ABSTRACT

A bioeconomic model was developed to estimate effects of change in production and functional traits on profit of dairy or dual-purpose milked sheep under alternative management systems. The flock structure was described in terms of animal categories and probabilities of transitions among them, and a Markov chain approach was used to calculate the stationary state of the resultant ewe flock. The model included both deterministic and stochastic components. Performance for most traits was simulated as the population average, but variation in several traits was taken into account. Management options included lambing intervals, mating system, and culling strategy for ewes, weaning and marketing strategy for progeny, and feeding system. The present value of profit computed as the difference between total revenues and total costs per ewe per year, both discounted to the birth date of the animals, was used as the criterion for economic efficiency of the production system in the stationary state. Economic values (change in system profit per unit change in the trait) of up to 35 milk production, growth, carcass, wool, and functional traits may be estimated.

Key words: dairy sheep, bioeconomic model, economic value

INTRODUCTION

Sheep constitute the second most numerous livestock species in the world (FAO, 2001). Various reproductive management systems can be observed on sheep farms, ranging from annual lambing to light or hormonally induced multiple lambing periods per year, or both, to lambing throughout the year with aseasonal breeds.

In dairy sheep, production systems vary from very intensive through semi-intensive to extensive. Among other factors, they differ in the weaning strategy and management of ewes and may be related to the climatic and regional conditions of each country. Flexible

bioeconomic flock models would therefore be useful to evaluate the economic efficiency of different production systems and to examine consequences on economic efficiency of changing financial, management, and biological inputs. The economic effects of changes in biological characteristics (economic values of production and functional traits) are also needed to establish economically rational breeding programs for different sheep breeds and production systems (Simm et al., 1987; Cottle, 1990).

Generally, sheep farms must be competitive with other livestock species. One way to increase the income of the sheep farmer is through genetic improvement achieved by participation in a breeding program.

Earlier studies on the economic effect of genetic changes in sheep traits were mostly oriented to meat and wool breeds (Ponzoni, 1988; Cottle, 1990). These investigators applied a simple profit function at the farm level for the calculation of economic values for wool, fattening, and reproductive traits. In recent years, complex bioeconomic models have been applied, allowing the incorporation of different types of farms and intensive as well as extensive production systems (Conington et al., 2004; Jones et al., 2004).

Only milk production traits were taken into account in most previous breeding programs in dairy sheep (Smulders et al., 2007). However, functional traits have now become important for efficient breeding schemes in the dairy sheep industries, due to increased costs of production relative to milk prices and consumer demand for safe, quality food and attention to animal welfare (Barillet, 2007). Few recent studies deal with the estimation of economic values for functional traits as well as for milk production in dairy sheep (Legarra et al., 2007a,b; Fuerst-Waltl and Baumung, 2009). The calculations of Legarra et al. (2007a,b) were based on economic and technical data obtained directly on sheep farms, whereas Fuerst-Waltl and Baumung (2009) used a deterministic simulation model adapted from dairy cattle.

The objective of the present paper was to develop a flexible model and a computer program to estimate effects of change in production and functional traits on profit of dairy or dual-purpose milked sheep under

Received June 2, 2008.

Accepted January 16, 2009.

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Figure 1. Example of management events in chronological order and reproductive status of ewes in the dairy flock with 1 lambing per year.

alternative management systems. In the companion paper (Wolfová et al., 2009), the application of the model for calculation of economic values for milk, growth, carcass, wool, and functional traits in dairy sheep are presented.

MATERIALS AND METHODS

A wide range of production systems for dairy sheep are modeled using a deterministic approach (based on trait means only) with some stochastic elements (based on the distribution of the traits). The bioeconomic model includes the calculation of the stationary state of the ewe flock; the calculation of profit as a complex function of many biological, economic, and management parameters; and the calculation of economic weights for up to 35 traits. The model was implemented on a computer (Wolf et al., 2008), and the resulting program written in C language runs under Linux or Windows (Microsoft Corp., Redmond, WA).

Structure of the Flock

Reproductive Cycle. A reproductive cycle is defined as the time period between 2 adjacent lambing dates. All management events in the flock and all revenues and costs are expressed per reproductive cycle and per ewe entering that cycle. The economic efficiency of a production system and the economic values of the traits considered in the model are then expressed per ewe present in the flock at the time of lambing and per year.

A reproductive cycle is described by the following events: date of lambing, date upon which lambs are weaned, date of the end of the artificial rearing period (optional), date of drying off of ewes, and starting and ending date of the breeding (mating) period, all dates being expressed as flock averages. Because the

management system and feed (pasture) availability often depend on seasons of the year, starting dates of seasons (e.g., summer and winter seasons in temperate climates, dry or wet seasons in the tropics) are further important parameters. In the model, all dates are assigned chronologically starting with January 1 of the yr 0. An example of the time sequence of events in a reproductive cycle in the temperate environment in the northern hemisphere is given in Figure 1. A maximum number of 4 seasonal variants for each feeding ration are allowed. Lambing can occur at any date with the consequence that all following events must occur later in the same year or in the subsequent year. A representation of the flock composition, as described in the following paragraphs, is shown in Figure 2.

Structure of the Ewe Flock. A female is called a ewe after its first lambing. The structure of the ewe flock is determined by the length of the productive life of individual categories of ewes (i.e., by the ability not to be culled for low milk production or health problems, the ability to conceive successfully during the breeding season, or by the decision of the farmer to keep a barren ewe until the next breeding season).

Five stages of ewes are identified in all but the last reproductive cycle: (1) ewes that died, (2) ewes that were culled for health problems or low milk production, (3) ewes that were culled for failure to conceive, (4) barren ewes that entered the next reproductive cycle but did not lamb, and (5) pregnant ewes that entered the next reproductive cycle and did lamb. In the last reproductive cycle, the last 2 stages are absent, and the third stage is represented by ewes culled for age after their last lactation. Ewe categories are then defined as a combination of 2 variables: the sequential number of the reproductive cycle and the stage of the ewe within that cycle.

The probabilities of transitions between the categories form the so-called transition matrix $\mathbf{T}_E$, the form

Figure 2. Flock composition.

of which is equal to the matrix given in Wolfová et al. (2005). The structure of the ewe flock in its stationary state (a constant number of ewes) is derived using Markov chains. The procedure is similar to that described by Reinsch and Dempfle (1998). Let $\mathbf{T}_E$ be the transition matrix with element $t_{ii'}$ being the probability that a ewe changes in a given time interval Δt from category i to category i' . Assume further that $\mathbf{c}^{[t]}$ is the row vector with elements $c_i^{[t]}$ of the probability that a ewe belongs to category i at time t . Then the same vector at time $t + \Delta t$, $\mathbf{c}^{[t+\Delta t]}$, is calculated as:

$$\mathbf{c}^{[t+\Delta t]} = \mathbf{c}^{[t]} \mathbf{T}_E.$$

When $t \rightarrow \infty$, the Markov chain reaches its stationary state so that the difference $\mathbf{c}^{[t+\Delta t]} - \mathbf{c}^{[t]}$ approximates a vector with all elements being zero. The stationary

value of this vector will be written as $\mathbf{c}$. The elements of vector $\mathbf{c}$ are the relative frequencies of the individual categories of ewes in the stationary state. The relative frequencies of the ewes belonging to the individual reproductive cycles are calculated by summing all elements of vector $\mathbf{c}$ for the given reproductive cycle.

Structure of the Ram Population. Rams used in the flock for natural mating enter the flock at the start of the breeding season and stay in the flock until they die, are sold, or culled. Stages of rams within each but the last breeding cycle (time period between 2 subsequent breeding seasons) are as follows: (1) rams that died, (2) rams that were sold as breeding animals, (3) rams that were culled for health problems, and (4) rams that entered the next breeding cycle. In the last breeding cycle, the fourth stage is missing. The stationary structure of rams is calculated in the same manner

as for ewes using the transition matrix **T_R**. Transition probabilities vary depending upon breed and production system.

The total number of rams in a flock is calculated from the ewe:ram ratio and from the proportion of ewes mated by AI versus by natural service in the flock. Rams may be the same breed as the ewes (for production of replacement daughters) or another breed (for production of crossbred market lambs). The numbers of rams in both groups are calculated from the proportion of crossbred matings in the flock. Therefore, progeny can be either purebred or crossbred.

Structure of Progeny. The structure of purebred and crossbred progeny born per reproductive cycle at the stationary state of the ewe flock is determined mainly by 2 factors: replacement management and marketing strategy for surplus progeny. Both female and male progeny for replacement can be produced within the flock, purchased from outside, or a combination of both sources may be applied.

Progeny born in the flock are grouped in different categories. Each category is characterized by sex, specific management, revenues and costs, and by the length of the period the costs are assigned to the given category. A list of the possible categories is given in Table 1.

The number of weaned purebred female lambs needed for replacement depends on the replacement rate in the ewe flock, proportion of female breeding lambs that are purchased, survival and conception rate of female lambs, and mating strategy. The number of weaned purebred male lambs needed for replacement depends on the replacement rate of the rams in the flock and on the proportion of breeding males that are purchased rather than produced within the flock. The equations for calculation of the numbers of weaned female and male lambs needed for replacement is given in the appendix.

Surplus progeny can be sold for slaughter after weaning, after artificial rearing (when early weaning is applied) or after different finishing periods, or they can be sold as breeding animals. According to management and marketing options for progeny, up to 47 progeny categories are defined. Most of these categories exist both in purebred and crossbred progeny when crossbreeding is applied. Several of the categories are optional. All categories of fattened animals, for example, are defined only if there is fattening in the system.

Traits

Milk production traits, growth traits, carcass traits, wool traits, and functional traits are considered in the model.

Table 1. Definition of progeny categories¹

Group of animals	Sex ²	Time interval for calculating costs
Stillborn lambs and lambs died within 24 h of birth	M, F	0
Lambs died before weaning ³	M, F	(Weaning ³ date – lambing date)/2
Lambs died during fattening	M, F, C	Half of the appropriate fattening period
Lambs died during rearing of breeding animals	M, F, C	Half of the appropriate rearing period
Lambs from birth until weaning	M, F	Weaning date – lambing date
Lambs in artificial rearing	M, F	Date at the end of artificial rearing – weaning date
Lambs sold at weaning or after artificial rearing for slaughter	M, F	0
Lambs fattened to fixed age or weight (up to 5 limits of age or weight are possible)	M, F, C	Slaughter age – weaning ³ age
Breeding lambs sold without being mated before their first or second breeding period after weaning ³	M, F	Age of selling – weaning ³ age or age of selling – age at first breeding
Breeding females sold pregnant after the first, second, or third breeding season after their weaning ³	F	Days in pregnancy when the animals are sold
Breeding animals culled after the first, second, or third breeding season after their weaning ⁴	M, F	Length of the breeding season + days to culling after the breeding season
Breeding lambs from weaning ³ until the first breeding season	M, F	Date of starting breeding season – weaning date ³
Breeding lambs from first to second breeding season	M, F	Length of the reproductive cycle
Breeding lambs from second to third breeding season	F	Length of the reproductive cycle
Female lambs from conceiving after the first, second, and third breeding season to lambing	F	Lambing date – date of conceiving

¹A category is defined as a group of animals with a certain sex.
²M = male; F = female; C = castrate.
³If there is artificial rearing, replace “weaning age” by “age at the end of artificial rearing,” “weaning date” by “date at the end of artificial rearing,” etc.
⁴Female lambs culled for failure to conceive, male lambs culled for unsuitability for breeding.

Milk Production Traits. Milk yield during the milking period and fat and protein percentage (or fat and protein yield during the milking period as alternative traits) are the main milk production traits. In addition, SCS can be evaluated if milk price is influenced by the number of somatic cells.

The time course of milk production is modeled using the Wood function (Wood, 1967) in the form:

$$y(t) = a \times t^b \times e^{-c \times t},$$

where $y(t)$ is the milk yield (in kg) on day t of lactation and a , b , and c are parameters for the standard lactation curve, normally defined for a first-lactation ewe with 1 suckled lamb. The lactation curves of ewes during different lactations and with different numbers of suckled lambs are calculated by multiplying the above formula by corresponding adjustment factors specific for each lactation and number of suckled lambs.

Growth Traits. Birth weight, daily gain from birth until weaning or weaning weight, daily gain from weaning until the end of artificial rearing or weight at the end of artificial rearing (for early weaning only), daily gain in the finishing period of lambs, daily gain in rearing of breeding animals, and mature weight of ewes are considered in the model.

A general growth curve is not applied in the model because the growth pattern of the same breed can be very different under diverse conditions (lowland or highland farm, intensive or extensive feeding, early or traditional weaning, etc.). Growth is therefore described by a multiphase growth curve assuming linear functions for the individual phases. The first phase is from birth to weaning, which is followed by the phase from weaning to the end of artificial rearing if there is early weaning. For fattened animals, the phase to the end of lamb finishing follows, and for breeding animals, the growth rates until the first breeding season, from the first to the second, and from the second to the third breeding seasons are distinguished. For females, the period from conception to lambing is added. This approach is very flexible and allows describing the real growth pattern in any production system with high accuracy.

Until weaning (or the end of artificial rearing), growth rates are assumed to be specific for lambs of different sexes and from litters of different size. After weaning (or the end of artificial rearing), growth rate is differentiated only between sexes.

Carcass Traits. Carcass quality traits can be evaluated only if the pricing system for slaughtered and culled animals takes carcass quality into account, whether evaluated on live or slaughtered animals. Dressing percentage is evaluated only when marketing is on a carcass weight basis. Depending upon the pricing

system, the following traits can be evaluated: average quality class of lambs paid for live weight and sold for slaughter at weaning, at the end of artificial rearing or after the finishing period; average carcass quality class of lambs paid for carcass weight and sold for slaughter at weaning or at the end of artificial rearing; and average class for fleshiness and fat covering of lambs after the finishing period or of adult sheep based on the SEUROP carcass grading system. In this grading system, there are 6 classes for fleshiness (S, E, U, R, O, P), where S is the most valuable class and P is the least valuable. For the calculation of the economic value for fleshiness, numerical values 1 to 6 are inserted for S to P. For fat covering, 5 classes (1 to 5) are distinguished, class 1 being the most desirable.

Wool Traits. Fleece weight defined as amount of greasy wool per shearing is the only wool trait evaluated.

Functional Traits. Conception rate of female lambs, conception rate of ewes, average litter size (total number of lambs born) per ewe lambing, survival rate of lambs through 24 h after birth at the flock average litter size, survival rate from 24 h after birth until weaning or until the end of the artificial rearing period, and length of productive life of ewes belong to the complex of functional traits.

Economic Efficiency of the Production System

Present value of profit (i.e., the difference between total revenues and total costs discounted to the birth date of the animals and expressed per ewe per year at the stationary state of the ewe flock structure), increased by total subsidies per ewe per year (T_{sub}), is the criterion of economic efficiency of any modeled production system:

$$profit = \frac{365}{lengthrc} (\mathbf{rev}' - \mathbf{cost}') \mathbf{p} + T_{sub}, \quad [1]$$

where $\mathbf{rev}'$ and $\mathbf{cost}'$ are the row vectors of the sums of discounted revenues and costs, respectively, per animal, the elements of which are the revenues and costs for the individual categories of animals, $\mathbf{p}$ is the column vector of the numbers of animals per ewe and reproductive cycle in the individual categories, and $lengthrc$ is the length of the reproductive cycle in days.

The elements of vector $\mathbf{cost}'$ in equation [1] (i.e., the discounted costs for category i of animals $cost_i$), are calculated as follows:

$$cost_i = \sum_j q_{ij} cost_{ud_{ij}} = \sum_j (1+u)^{-t_{ij}/365} cost_{ud_{ij}}, \quad [2]$$

where $costud_{ij}$ is the undiscounted cost component j for category i of animals, q_{ij} is the discounting coefficient for $costud_{ij}$, u is the annual discount rate, and t_{ij} is the age of the animal at which the costs occur. The elements of vector $\mathbf{rev}'$ in equation [1] (i.e., the discounted revenues for category i of animals rev_i) are calculated in the same way as the discounted costs for category i replacing $cost_i$ by rev_i and $costud_{ij}$ by $revud_{ij}$, the undiscounted component j of revenues for category i of animals, in equation [2].

Revenues. Revenues in a dairy sheep production system come from sales of milk or cheese, or both; weaned or finished, or both, lambs sold; breeding animals; culled sheep; wool; raw or tanned, or both, skin; and manure. Revenues from milk depend on the average milk price, which can be a function of fat and protein content, and of SCC. Therefore, the concrete form of this function depends on the milk pricing system. A normal distribution is assumed for fat and protein content or SCS, or both, when calculating the average milk price from these variables. Milk can be partially or fully processed for cheese. Revenues for cheese and cheese whey are then included in the revenues for the corresponding categories of ewes. Revenues for slaughtered and culled animals can be calculated on the basis of live or carcass weight taking or not taking conformation of animals or carcass quality (fleshiness and fat covering, meat color) into account.

Costs. Costs are calculated for feeding, housing, health care, labor, shearing, tanning of skins, marketing, breeding, milking, cheese production, and purchasing breeding animals. All remaining costs are accounted for as fixed costs per animal of each category per day.

Feeding costs are calculated on the basis of daily net energy, protein (optionally), and water requirements of animals of all categories, from the price for feed with given DM, net energy, and protein content, and from the price of water and minerals. The equations for the calculation of net energy and protein requirement for maintenance, growth, pregnancy, wool, and milk production of all sheep categories were taken from ARC (1980), AFRC (1995), and Kica (2005). If the protein content of feed is unknown, the feed requirement can be calculated on the basis of net energy only. Water requirements are assumed to depend on DMI and temperature (Infascelli et al., 2005).

In the model, up to 5 rations can be differentiated for ewes: (1) lactating ewe with no or with one lamb, (2) lactating ewe with 2 or more lambs, (3) ewe during flushing, (4) ewe that is barren or in early pregnancy, and (5) ewe in advanced pregnancy. Two feeding rations are possible for rams, during or outside the breeding season. For lambs, the following rations can be defined: for the period until weaning, during artificial rearing,

during the rearing period of breeding lambs, for flushing of female breeding lambs, for female lambs in later pregnancy, and for finishing of female and male lambs or castrates. For each ration, seasonal variants are possible.

Housing costs are those for bedding material. Costs for health care include general veterinary costs that are expressed per animal, cost for removing and rendering dead animals, and costs for drenching against ecto- and endoparasites. Labor costs include only general labor costs and the part of labor costs for milking that are independent of milk yield.

Shearing costs are included if shearing is done by contract workers. For sold animals, marketing costs can be included, which may cover costs for transport, advertising, or auction costs for selling breeding animals. Breeding costs are included only if AI is done in addition to natural mating or if females are mated outside of their natural fertile estrus and hormones are needed for estrous induction. Costs for milking are computed by multiplying the amount of milk produced during the milking period by the costs per kilogram of milk, which include only costs depending on milk yield (e.g., costs for milking facilities, energy for milk cooling, part of the labor costs for milking). If cheese is processed on-farm, costs for producing cheese are added, which include costs for the cheese room, facilities, labor, and energy.

Fixed costs include depreciation expense, energy, repairs, insurance, and overhead costs. Though these costs are called fixed in the model, their sum is variable in each system according to the number of animals in each category and the length of the time periods the animals are kept. Thus, an alternative use of saved production factors (e.g., a shorter fattening phase because of increased growth rate) is possible and the costs normally called fixed are assumed to be variable in the long-run perspective. On the other hand, increasing the survival rate in fattening would require more fattening places and would result in higher total fixed costs.

Calculation of Marginal Economic Values of Traits

The marginal economic value of trait l (ev_l) is defined as the partial derivative of the profit function [1] with respect to that trait:

$$ev_l = \left. \frac{\partial profit}{\partial TV_l} \right|_{TV_l = TV_{l_{av}}}$$

where TV_l is the value of the given trait and $TV_{l_{av}}$ is the trait mean in the population. Because the model is very

complex, the derivative can only be calculated numerically as a difference quotient. In traits with continuous variation, the trait mean is increased and decreased by 0.5% of its value. Let us write TV_l^h and TV_l^l for the increased and decreased value of trait l , respectively, and $profit_h$ and $profit_l$ for the profit calculated from the increased or decreased value, respectively, of trait l . Then the economic value of the trait is approximated by

$$ev_l = \frac{profit_h - profit_l}{TV_l^h - TV_l^l}. \quad [3]$$

For categorical traits (e.g., litter size, average class for fleshiness and fat covering), a method based on an underlying normal distribution, which was proposed and described in detail in Wolfová et al. (1995), was used. The frequencies in the individual classes (e.g., the frequencies of singles, twins, and triplets) are input parameters. From these frequencies, an average value (e.g., average litter size) is calculated. Furthermore, on the basis of the original frequencies, thresholds between classes in the standardized normal distribution (with mean 0 and SD 1) are calculated. Then the underlying normal distribution is shifted to the left and to the right, each time by 0.05. The resulting new frequencies of the individual classes (e.g., of different litter sizes) are used to calculate new average values of the trait and the corresponding new profit, both for increasing and decreasing the trait; these values are inserted into equation [3] to calculate the economic value of the trait.

To calculate the economic value for milk yield during the milking period, the daily milk production in the entire lactation is changed, keeping the form of the lactation curve constant. The resulting change in profit is then related to the change in the milk yield during the standardized milking period or to the change of average daily milk yield during the whole milking period. The economic values for fat and protein yield are calculated by changing the fat and protein percentages during the whole lactation but keeping the milk yield constant.

For calculating the economic value for a growth trait (e.g., gain or weight), its expression is considered to be the same trait in both sexes and that trait values between sexes differ by a multiplicative factor, which stays constant despite genetic improvement in the trait. The same principle is applied to the growth of lambs stemming from different-sized litters. The economic values for growth rate are calculated separately for each of the growth periods, keeping the growth rate in the previous and following periods constant. Economic values are then expressed per unit of the appropriate base growth trait. The base growth traits in the periods until weaning or until the end of artificial rearing are

those expressed in females born as singles. For later growth rates and for mature weight, the base traits are mostly those expressed in females without differentiation according to the litter size at their birth. For growth traits that are expressed both as daily gain in the given growth period and as weight at the end of this period, daily gain is considered to be the primary trait and weight is considered to be the derived trait in all calculations of economic values. For example, when calculating the economic value of birth weight, daily gain from birth until weaning is held constant; therefore, changes in birth weight will have an effect on weaning weight. This definition of growth traits means that if the breeding objective includes birth weight modeled in this way, it cannot also include further weights at a fixed age because it would cause double-counting. Instead, the breeding objective must include live weight gains for the periods after birth as further growth traits.

When calculating the economic values for carcass quality traits and dressing percentage, only a change in the revenues from slaughtered animals is taken into account.

To calculate the economic value of fleece weight, the fleece weights of the individual categories are related to the fleece weight of adult rams; thus, intrabreed differences in fleece weight between sexes and age categories are assumed to show constant ratios. No direct costs are assumed to be associated with increasing fleece weight because there is no strong evidence to suggest there are significant increases in feed requirements with improved genetic potential for wool production at a constant BW (Conington et al., 2004). The costs of shearing are generally paid per animal and are not expected to change for additional fleece weight. Only the benefit in additional revenues from extra weight of fleece sold is therefore included in the economic value of fleece weight.

Litter size per ewe lambing is handled as a categorical trait and proportionally changed in all parities; the resulting change in profit is expressed per ewe with average litter size. The survival rate of lambs within each size of litter is held constant when changing the average litter size. The total losses of lambs at lambing and in rearing, however, change due to increased frequencies of higher litter sizes.

When calculating the economic weight for survival rate, this trait is changed by the same factor within each litter size. Although litter size at birth is held constant, litter size at weaning will be influenced by the change in survival rate having an effect on revenues and costs of several progeny categories.

Productive lifetime of ewes is defined as the time interval from entering the herd to death or culling. Alternatively, productive lifetime of a ewe can be expressed

as number of reproductive cycles entered. When calculating the economic value for productive lifetime, the proportions of ewes died and culled for health problems in each reproductive cycle are varied, keeping the proportion of ewes culled for low milk production constant. Then the new stationary state of the sheep flock and the new average lifetime of ewes are calculated.

All economic values are expressed per breeding ewe and per reproductive cycle, which is equal to a year in the described production system. An economic value calculated by the described model takes into account the number of expressions of the trait (i.e., number of animals of different animal categories bearing and expressing the trait) as well as the time when a trait influences revenues and costs. The time factor is considered in the economic value by discounting all costs and revenues to the birth date of the progeny of improved parents (Figure 3).

Because the described model handles sheep production systems applying purebreeding as well as terminal crossing, economic values may be calculated both for the breed of the flock and for the sires used for crossing in this system. Because the terminal sires do not produce any replacement, the traits of these sires, which would be expressed in female replacement only (e.g., milk production traits), will have zero economic values. The calculation of economic values for specialized crossing systems, as done by Wolfová et al. (2005) or Berry et al. (2006), was not included in the model yet because these systems are rarely used in specialized dairy sheep breeds.

RESULTS AND DISCUSSION

Various models have been used for the calculation of the effect of changes in traits on the economic efficiency of sheep production systems. They include simple profit functions (Ponzoni, 1988; Morais and Madalena, 2006) as well as more complicated bioeconomic models (Wang and Dickerson, 1991a; Kosgey et al., 2003; Conington et al., 2004). Most of them were developed for meat sheep. In recent years, the economic values for milk production as well as for growth and functional traits have been estimated for dairy sheep. Legarra et al. (2007a) used data evaluation and a simple profit function for the calculation of economic weights for milk yield, reproductive traits, and productive lifetime, whereas Fuerst-Waltl and Baumung (2009) applied a normative approach for evaluating dairy, fattening, and functional traits. This last procedure was also applied in our model.

Normative approaches allow modeling a broad variety of breeds and production systems within a wide range of management and marketing circumstances. Studies

in meat sheep and beef cattle showed that the same marginal economic values should not be applied to different breeds and production circumstances (Wang and Dickerson, 1991b; Phocas et al., 1998; Amer et al. 2001). Milk sheep are kept in intensive (in door) systems as well as in extensive conditions on hill pastures. For low-producing breeds, traditional weaning generally is practiced. A system with early weaning and artificial rearing or with joint suckling of lambs and extraction of milk for human consumption until weaning is common in high-producing breeds. Modeling the seasonality of feed availability and allowing lambing at different times throughout the year makes our model utilizable for temperate climatic zones as well as for the tropics. A further advantage of our model is that protein requirement in addition to net energy may be taken into account when calculating feed requirement, which allows a more accurate estimation of feeding costs.

Growth may be described by a nonlinear growth function over the whole lifetime (Conington et al., 2004; Fuerst-Waltl and Baumung, 2009) or by a multiphase growth curve assuming linear functions for individual phases, as was done in our model. Though the nonlinear growth function over the whole lifetime may be preferable from the biological point of view, this procedure can cause problems when calculating economic values. Changing the parameters in the curve will generally influence all growth traits, which may cause a double-counting of changes on economic values. Furthermore, it is not clear which parameters should be changed and in which ways to calculate the economic values for growth traits. Multiphase growth with linear functions for the individual phases, though being only an approximation of the real growth function, allows for directly changing the trait of interest, whereas remaining growth traits retain their original values.

Using the Wood function may be a relatively rough estimation of the milk production in some cases (especially when food resources are limited) and should be complemented by other methods in the model and computer program in future. Similar as for growth, a multi-phase curve may be used instead.

Using an underlying normal distribution in the calculation of the economic weights for litter size and further categorical traits is an approximation. In most situations, it should work with sufficient precision because the number of animals in the production system is usually high and only small changes in the frequencies are considered when calculating economic weights. Nevertheless, in some cases (litter size in prolific sheep breeds), the results may be biased and should be considered with caution. Different methods were used by Amer et al. (1999) and Conington et al. (2004). The method of Amer et al. (1999) is based on modeling the

Figure 3. Principle of discounting procedure and definition of the base unit for expression of economic values. All revenues and costs per animal of each progeny category are multiplied by the numbers of animals of this category per ewe and year and discounted to the birth date of progeny.

ovulation rate assuming an underlying normal distribution. Different than in our model, equal distances between thresholds were assumed. Conington et al. (2004) estimated the numbers of singles, twins, and triplets by equations that were derived by equating the mean and variance of litter size to their expectations.

Although the number of traits included in the model is large, the model in its current state is deficient for wool quality traits. According to Conington et al. (2004), there is no consistent trend in prices received across years for fleeces that differ in the degree of kemp and gray fibers. Importantly, the price premiums for improved quality are smaller than if the fleece was simply free from contamination. Hence, fleece weight was the only wool trait included in the model.

Fuerst-Waltl and Baumung (2006) also calculated economic values for conformation traits of sheep estimating the effects of conformation scores in some exterior traits on the auction prices of breeding stock. But the main economic effect of genetic improvement of traits is achieved in the commercial flock; therefore, the economic values should be estimated at this level. Conformation traits do not have a direct economic effect on revenues and costs in commercial farms and cannot therefore be evaluated by applying a profit function. However, many of them are correlated with economically important traits. For example, udder conformation traits in dairy sheep are correlated with milk production and culling for bad milkability (i.e., with productive lifetime of ewes). From that reason, these traits will be generally used as indicator traits in a selection index rather than as traits in the breeding objective.

The discounting procedure used in our model includes only 1 generation of progeny of selected parents. However, including more generations in a purebred production system will not change the relative economic importance of traits.

Together with the calculation of economic values of traits, the model also provides information on economic characteristics of dairy sheep production systems. It can be used to estimate the effect of changes in many input parameters on the economic efficiency of those systems and on the trait economic values themselves. Therefore, it can also be a useful tool for the optimization of mating, culling, and other management and marketing strategies in an enterprise. An application of the model is presented in a companion paper (Wolfová et al., 2009). The computer program written for the model in C language for Linux and Windows platforms including a detailed manual (Wolf et al., 2008) is freely available on request from the authors.

ACKNOWLEDGMENTS

We thank M. Margetín, E. Krupa, J. Daňo, M. Oravcová, and D. Peškovičová from the Slovak Agricultural Research Center Nitra, Slovakia, and M. Milerski from the Institute of Animal Science Prague Uhřetěves, Czech Republic, for their helpful comments. Special thanks are due to W. D. Hohenboken (Corvallis, OR) for editing the English of the paper. Furthermore, the technical assistance of P. Mrázková (Prague Uhřetěves) is acknowledged. The research project was supported by the Ministries of Agriculture of the Czech Republic (MZE0002701401) and of the Slovak Republic (2006 UO27/0910502/0910517) and by the program KON-TAKT (SK-CZ-0007-07/MEB 08082).

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APPENDIX

Calculation of the Number of Purebred Weaned Female Lambs Needed for Replacement

Weaned female lambs intended for breeding can be mated at less than 1 yr of age if they reach the minimal weight for breeding, which is expressed as a required proportion of the mature weight of ewes. The proportion of females reaching the minimal weight ($pmatFP_1$) is calculated assuming a normal distribution with known mean and standard deviation for weight of females at the start of their first breeding season after weaning. Females not conceiving in their first breeding season and all remaining females surviving to the next breeding season are mated in that subsequent breeding season. The maximum number of breeding seasons for female lambs is 3 in the model, but it can be restricted

to 2 through the decision to cull all nonpregnant female lambs after the second breeding season.

The fraction of weaned female lambs conceived ($prconFP_i$) and the fraction of weaned female lambs entering the flock ($pflockFP_i$) in breeding season i are given by the following equations:

$$prconFP_1 = surFP_1 \times pmatFP_1 \times conrateFP_1$$

$$pflockFP_1 = prconFP_1 \times surmlFP$$

$$prconFP_2 = [surFP_1 - prconFP_1 - surFP_1 \times pmatFP_1 \times (1 - conrateFP_1) \times (1 - pbarrFP_1)] \times surFP_2 \times conrateFP_2$$

$$pflockFP_2 = prconFP_2 \times surmlFP$$

$$prconFP_3 = (pmatFP_2 - prconFP_2) \times pbarrFP_2 \times surFP_3 \times conrateFP_3$$

$$pflockFP_3 = prconFP_3 \times surmlFP,$$

where $surFP_i$ is the survival rate to breeding season i , $conrateFP_i$ is the conception rate of female lambs in breeding season i , $surmlFP$ is the survival rate from mating to lambing, and $pbarrFP_i$ is the proportion of barren females kept from breeding season i to the next breeding season $i + 1$.

The total fraction of weaned female lambs that enter the flock as replacements ($PflockFP$) is then:

$$PflockFP = \sum_{i=1}^3 pflockFP_i.$$

The number of female weaned lambs that must be reared for flock replacement per ewe and reproductive cycle ($NflockFP$) depends on the replacement rate of ewes, which is given by the relative frequency of ewes in the first reproductive cycle (pE_1):

$$NflockFP = pE_1 / PflockFP.$$

If any female replacement lambs are to be purchased, $NflockFP$ is diminished by this number. All remaining female weaned lambs are surplus animals that can be sold for different purposes.

Calculation of the Number of Purebred Weaned Male Lambs Needed for Replacement

Weaned male lambs intended for breeding can be used for mating during the breeding season after their

weaning (under 1 yr of age) if they reach the minimal weight for breeding, which is expressed as the required proportion of the mature weight of rams. The proportion of males reaching the minimal weight (p_{matMP_1}) is calculated in the same way as for females. The remaining males are used for mating starting with the second breeding season after their weaning.

The fractions of weaned male lambs entering the flock in breeding season i ($p_{flockMP_i}$) are given by the following equations:

$$p_{flockMP_1} = surMP_1 \times (1 - cullMP_1) \times p_{matMP_1}$$

$$p_{flockMP_2} = [surMP_1 \times (1 - cullMP_1 - p_{matMP_1})] \\ \times surMP_2 \times (1 - cullMP_2),$$

where $surMP_i$ is the survival rate and $cullMP_i$ is the culling rate to breeding season i .

The total fraction of weaned male lambs entering the flock ($P_{flockMP}$) and the proportion of replacement rams that are young rams (younger than 1 yr, $p_{youngMP}$) are calculated as:

$$P_{flockMP} = \sum_{i=1}^2 p_{flockMP_i} \\ p_{youngMP} = pR_1 \times p_{flockMP_1} / P_{flockMP},$$

where pR_1 is the replacement rate of rams (the proportion of rams on the first breeding cycle).

To calculate the number of weaned male lambs needed for replacement per ewe and reproductive cycle ($N_{flockMP}$), the average ewe:ram ratio ($ratioR$) is calculated using the ewe:young ram ratio ($ratioYR$) and the ewe:old ram ratio ($ratioOR$). If there is crossbreeding in the system, the fraction of ewes mated to rams of their own breed ($ppurE$) is also needed. It depends on the proportion of ewes (pE_l) in reproductive cycle l ($l = 1, \dots, L$) and the proportions of crossbred matings in each reproductive cycle ($pcrossE_l$):

$$ratioR = p_{youngMP} \times ratioYR + (1 - p_{youngMP}) \times ratioOR \\ ppurE = \sum_{l=1}^{L-1} pE_l \times (1 - pcrossE_l) \\ N_{flockMP} = ppurE / ratioR.$$

If purebred male replacements will be purchased, $N_{flockMP}$ will be lowered by the number of purchased animals. All rams for crossbreeding are assumed to be purchased. All the remaining purebred male weaned lambs and all crossbred male weaned lambs (in case of crossbreeding) are surplus animals that can be sold for different purposes.