Single gene dynamics under controlled mating

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Abstract

We seek models for the genotype evolution of agricultural animals, animals involved in primary production processes. Classical models for genotype evolution have tended to be very simple in order that analytic methods may be employed in their study. Unfortunately these models fail to describe processes in artificially controlled populations including agricultural livestock. It is particularly important to describe such processes in order to make better use of the massive genotyping data becoming available.

We describe an approach to stochastically modeling the dynamics of a biallelic polymorphism herds under conditions of controlled mating and restriction of herds size from above. The system of stochastic differential equations that we propose is based on jump diffusion processes to provide an effective platform for Monte Carlo simulation. Our choice of this modeling framework foreshadows the use of semi-analytic tools to complement simulation. Another reason for adopting the framework is its flexibility in modeling different population management systems.

A feature of the model is the division of the population into a main herd comprised of animals involved in the production process and a replacement herd of animals not currently in the production process, typically juvenile

animals. This feature allows for exploring different strategies for adding replacement animals to the main herd without altering the part of the model concerned with the dynamics of the main herd.

A discrete-time version of the model has been developed which reflects the typical practice of New Zealand dairy herd management.

Our Monte Carlo simulation has demonstrated that an isolated deme whose size is bounded above (by imposition of a fixed size control requirement) demonstrate size stabilization at a level less than the control limit, it is looks like partial extinction, the effect being well known in classic models. Another interesting feature of the model with a size control rule is its sensitivity to a form of a control. We have found that even change a rule to different moment of choice of animal substitution (from replacement herd to a main one) results in observable variation in herds' temporal characteristics. We demonstrate several simulation results under the condition of Mendelian inheritance and its corresponding rule of summation. We also propose a variant of the model taking into account animal inflows and outflows providing exchange through an external market. For future work we consider the cooperative development of an open source platform for such modeling and for in silico experiments utilizing real genotyping data from the New Zealand dairy cow population.

Introduction

The two seminal papers of G. Hardy [1] and W. Weinberg [2] on the steady state distribution of alleles were based on the Mendelian law of genetics. The Mendelian law and these papers are the corner stones of practical genetics and strongly influenced later development in the field.

One of the main results, called Hardy-Weinberg equilibrium, states that in a population satisfying certain conditions the observed frequencies of possible genotypes AA, AB, BB in some locus of interest are p^2 , 2pq, q^2 , where p and q=1-p are the proportions of the alleles A and B at the locus. In reality, the conditions needed to ensure Hardy-Weinberg equilibrium often fail to be met. For example in the case of New Zealand dairy cows, the national herd has about 4×10^6 cows distributed in about 1.1×10^4 herds. There were just over 3700 bulls used for insemination in 2013-2014 season with under 100 top bulls used to mate 80% of the whole national herd. Except by chance the genotype frequencies in whole population are far from

Hardy-Weinberg proportions at any locus and the proportions vary by herd, region, and loci. Table 1 compares the conditions needed to establish Hardy-Weinberg equilibrium with the production situation in the dairy industry in New Zealand and, we suspect, many other countries.

In reality such steady-state results are not of central interest for animal breeding decisions as the intent is to change the properties of the production herd in a favored direction. Before considering a more realistic model for such controlled breeding we will set the scene by mentioning some classical dynamic models in genetics.

One of the most influential such models was a genetic evolution model proposed by S. Wright [3] and R. Fisher [4]. In this model, for a fixed size total population and binary alleles (A, B), the discrete time dynamics of relative frequencies of different types of individual is considered under the neutrality (equal fitness) and Markov assumptions. This allows a stochastic dynamic flow with rather good analytical properties. The model has the same probability structure that would result if each of the N individuals of the $n+1^{st}$ generation picked their parents at random, though of course this cannot literally happen. A prominent phenomenon of the neutral Wright-Fisher model without mutation is a "fixation" that is the extinction of all types but one at a finite but random time.

The further development of the Fisher approach has been in ways of weakening the assumptions used. The two most evident ones are to introduce more types of alleles [5] and to consider a variable resampling rate (floating total population size) [6,7]. More sophisticated approaches are to introduce a more complicated distribution law (say, a Poissonian one) for a number of offspring of an individual [5], to take into account mutation and/or selection [8], to introduce a random process for mortality of individuals [9], or to work with diffusion-like models [10]. Good introductions to some of these general topics can be found in [11, 12] and the first chapter of [5].

These models are relatively simple in that analytical results for variables of interest, or asymptotic expansions for them, may be derived within them (see for example [13]). But to make the obtaining of analytical results a goal inevitably leads to a focus on mathematical tractability in the setting up of the model. This in turn encourages the avoidance of the complexities of real life problems, resulting in an oversimplified model.

An important point is that classical models typically assume *infinitely* large population size while investigating the dynamics of allele frequencies. While these models have powerful asymptotic analysis techniques available

to them they are not relevant to the situation of a typical farm running a herd of only a few hundred cows. So instead we will concentrate on accounting for the effects of a finite, stochastically driven, herd size.

While in this paper we concentrate on cows on a particular farm it is important to note that these farm herds are strongly connected by the fact mentioned above that a few tens of top bulls fertilize millions of New Zealand cows. This focus on a small number of male animals is in further contrast to the situation envisioned by the classical population models.

Another difficulty with the quest for analytic solutions is that often they are available only for the evolution of mean values of variables of interest and not for other properties of their distributions such as variance and shape, whose knowledge will be required in real industry applications. Thus it is necessary to put analytic methods to the side and develop realistic stochastic models allowing Monte-Carlo simulation of all required distributions.

The chief tool available to the dairy industry for improvement of the genetic merit of the herd is the ability, via artificial insemination, to choose the parents of the next generation. So our concern is chiefly with genotype dynamics under *controlled mating*, often termed *artificial breeding* in the dairy industry. Genomic methods are becoming important in sire selection now that statistical genomic prediction methods are available [14]. Hand in hand with this animal evaluation technology vast genotyping data sets are increasingly available.

The model we develop in this paper is a rather general one in sense of being capable of a range of adjustments. For example other species could be considered, as might more sophisticated rules of genotype sum possibly addressing genotype dependent (genomic) selection, or other departures from the equal fitness assumption. Our model simulates the dynamics of alleles at a single locus in each animal of a herd under controlled mating.

The model, in the discrete form given below, incorporates some features typical for New Zealand seasonal dairy herd management practice. This allows the model to be useful for estimating the time necessary to reduce the proportion of unwanted genomic variants in the population to an acceptably low value. Also it could be used to estimate the time to introduce some desirable genomic variant, for example one that influenced milk composition in a beneficial way.

There are a growing number of genomic discoveries published concerning the importance of some particular single variants [15], [16], [17]. It is obvious the number of known deleterious genes will increase as knowledge is gained and more is understood about common diseases. Every sire selected for AI carries some deleterious genes. The model developed may help in risk analysis by running different scenarios to optimize AI strategy in sense of performance merit vs deleterious gene carrying.

Methods

Firstly we introduce a general stochastic model for genotype evolution in an isolated herd subjected to a maximum herd size. Secondly we present a discrete-time version of this model as well as a generalization which allows a limited inflow of animals from an external source such as the market. The discrete model is then used in few simulations to illustrate its use, obtaining some interesting results. Finally we outline directions for possible further development.

Let us consider a herd as effectively comprising two sub-herds: the main (production) herd and a replacement herd. The main herd consists of adult animals providing the productive output of a herd e.g. cows in milk. The replacement herd includes mostly young animals from birth up to just before going into production. It can also include some (typically small) number of adult animals, each expected to be suitable when required to join the main herd as a replacement.

We will (for example in equations 2 below) use subscripts i and j to refer to individual members of each herd but these numbers will refer to a formal position in a herd, much as do the numbers on the shirts of football players in a team. We will use functions of the form $f_i(t)$ to refer to properties of the animal in position i of the herd as a function of time, t. If a maximum herd size is imposed, a new animal can only be introduced as a replacement for a removed animal or if the herd size is below the limit. In the latter case it will take the first unoccupied position. If animal i is replaced at time t_* this will typically cause a discontinuity or 'jump' in the function $f_i(t)$ at $t = t_*$.

The presence of animal replacements means the stochastic processes in our model will have jumps. Such processes have found much application in financial modeling. It has been found that the best way to formulate these processes is to use the integral form of stochastic differential equations using stochastic Ito integration ([18, 19]). Jumps usually arise in financial modeling as the result of a real-world event changing the value of a stock. The jumps in our model will not be of this kind. An analog of our type of

model in Finance might be where a portfolio of stocks corresponds to a herd of animals and a jump is caused by replacing one stock in the portfolio by a new stock.

Our model makes a number of assumptions about the main and replacement herds and some parameters of animal movements in and out of the herd.

List of assumptions for continuous time model

- 1. The number of cows in the main herd is initialised to N_0 at the initial time $t_0 = 0$ and never exceeds this value subsequently. The corresponding dynamical variable is N(t).
- 2. The number of cows in the replacement herd is initialised to M_0 at the initial time $t_0 = 0$ and never exceeds this value subsequently. The corresponding dynamical variable is M(t).
- 3. At initial time $t_0 = 0$, the age of cows in the main herd is generated by a customized random number generator.
- 4. The genotype of a progeny follows from that of its parents via a summation rule. In this article we consider the Mendelian only case expressed by equation 1.
- 5. The departure of an animal from the main herd is subject to a Poisson process with a rate parameter λ_D . This allows uniform accounting for different causes of animal departure (animal fate).
- 6. The departure of an animal from the replacement herd is also subject to a Poisson process with another rate parameter λ_d .
- 7. The animal movements between sub-herds and departures happen annually (once a year) and are simulated by the following scheme. Using assumptions 1 to 6 simulate this year's set of animals to depart. Then fill vacancies thus created in the main herd by random choice (variable ξ) from members of the replacement herd that have reached the age of t_{min} years to maintain predefined size. If this turns to be impossible due to lack of heifers of proper age in the replacement herd, then replace as many as possible, the main herd now taking a smaller size.

- 8. The replacement strategy in the replacement herd is annual (once a year) addition of newborn calves to maintain predefined size M. If it turns to be impossible due to lack of newborn calves, the replacement herd remains with this smaller size.
- 9. One bull, or team of bulls, of known genotype sires the whole herd. A new generation appears every year.
- 10. There is no in-flow of animals from outside.

Assumptions 5 and 6 are for simplicity and may later be replaced by other descriptions of these animal departure processes more closely reflecting actual herd management practice.

Assumption 7 somewhat departs from the common practice, which is to have some flow of animals from outside (say, from the market) but we leave this for a subsequent publication considering the modeling of multiple herds. There is some discussion of market influence below; see *Herd with a limited inflow of animals*.

The parameters λ_D, λ_d are chosen by estimating the mean of animal's life time in the main and replacement herds respectively either on common practice or detailed analysis of the survival curve. In New Zealand practice actual mortality as a cause of departure from either herd would be rare but poor condition might cause a decision to remove an animal from either herd

Variants of the model with different strategy, distribution and parameter settings are possible but are outside the scope of this article.

Rule of single genotype sum

We represent the genotype of an animal in the locus of interest as a number from $\{-1,0,1\}$. Where -1 and 1 stand for homozygous and 0 for heterozygous genotypes correspondingly.

The mode of inheritance at a single locus assumed to be Mendelian leading to the following rule of summation (where P gives the probability of each outcome):

$$(-1)\dot{+}(-1) = -1, P = 1$$

$$0\dot{+}(-1) = \begin{cases} -1 & P = 0.5 \\ 0 & P = 0.5 \end{cases}$$

$$1\dot{+}(-1) = 0, P = 1$$

$$0\dot{+}0 = \begin{cases} -1, P = 0.25 \\ 0, P = 0.5 \\ 1, P = 0.25 \end{cases}$$

$$1\dot{+}0 = \begin{cases} 0, P = 0.5 \\ 1, P = 0.5 \\ 1, P = 0.5 \end{cases}$$

$$1\dot{+}1 = 1, P = 1$$

$$(1)$$

Here $\dot{+}$ is a commutative infix operation giving a random value of a 'child' genotype as a random function of two variables of corresponding parental genotypes.

Continuous time model: integral form

Our goal in this article has been to introduce a very general model with the flexibility to represent a variety of types of managed animal populations. To express such a model in the language of Stochastic Differential Equations and so have access to that body of theory we need to represent time in a continuous manner. Models with continuous time can show closeness to the observable herd dynamics but require some modification to assumptions 6 and 7 in the list of model assumptions given above regarding the random jump time for the departure processes.

We will use the index j for the above-mentioned formal position in a main herd and the index i for the same in the replacement one. To develop our stochastic model of two interacting herds we state two elementary evolution processes for every index. The first is the process of the changing genotype value in a position (j or i), designated as $D_j(t)$ or $d_i(t)$. The second is the process of the changing animal age in a position, designated as A_j and a_i . These processes are responsible for decisions on position characteristics such as whether or not to replace an animal. The control on animal departure from the herds will be based on additional independent processes P_{D_j} and P_{d_i} in such a way that changes of $D_j(t)$ and (or) $d_i(t)$ occur precisely at the time moment of a jump of the appropriate Poisson process P.

Accounting for this and based on the previous discussion, we can write down a system of stochastic equations describing temporal evolution of ensemble of cows in main and replacement herds in the following form

$$D_{j}(t) = D_{j}(0) + \int_{0}^{t} (-D_{j}(s-) + d_{\xi_{j}}(s-)) dP_{Dj}(s + A_{j}(0))$$

$$d_{i}(t) = d_{i}(0) + \int_{0}^{t} (-d_{i}(s-) + f(D_{\eta_{i}}(s-), S_{\zeta_{i}})) dP_{d_{i}}(s + a_{i}(0))$$

$$A_{j}(t) = A_{j}(0) + t - \int_{0}^{t} (A_{j}(s-) - a_{\xi_{j}}(s-)) dP_{Dj}(s + A_{j}(0))$$

$$a_{i}(t) = a_{i}(0) + t - \int_{0}^{t} a_{i}(s-) dP_{d_{i}}(s + a_{i}(0))$$

$$(2)$$

where $t \in [0, T]$, and the other quantities in equation (2) are defined as follows

- D_j is the value of the allele for a formal j-th cow in the main herd;
- P_{D_j} is the Poisson process with a parameter λ_D defining the elimination rate for a cow in the main herd:
- A_j is the age of the j-th cow of the main herd;
- d_i the value of the allele for a formal *i*-th cow of the replacement herd;
- P_{d_i} is the Poisson process with a parameter λ_d defining the elimination rate for a cow in the replacement herd;
- a_i is the age of the *i*-th cow of the replacement herd;
- $f(\cdot,\cdot)$ is the female calf's genotype as a stochastic function of the parental genotypes. Here $f(\cdot,\cdot)$ is usually given by the rule of summation, equation 1, but other rules are possible.
- η is a random variable corresponding to the random choice of a cow from the main herd to be used as a dam for the replacement herd and which subsequently gives birth to a female animal.
- $\{S_k\}$ is a set of values of alleles for sires;

• ζ is a rule for choosing the sire; it can be a random variable or a determined sequence.

We explain the correctness of the system (2) for a position j in the main herd as follows. A jump of the Poisson process for the first equation occurs at a moment s. Due to the definition of the Ito integral the new value of the locus is formed by arithmetic summation with terms $-D_j(s-)+d_{\xi}(s-)$. The first term zeros the current position value and the second one establishes the new value (with a random choice ξ). Based on the same Poisson process jump the third equation in (2) reflects the change at position j of the age variable A_j , taking into account that age should be increased if there is no jump (term t in this equation). In a similar way we deal with replacement herd except for the fact that the new genotype value at the locus is defined by the summation rule (1). The connection of the replacement herd with a main one is fulfilled via the term $D_{\eta}(s-)$ as an argument in function f defined above.

At a given stage of the model construction we assume that all variables and processes are mutually independent, for example that the loss of a cow from the main herd is not affected by losses in the replacement herd. Integrals are in Ito's sense, see for example [20], p. 84.

The definition of integrals over a Poisson process can be done by taking into account the fact that $P(t) = \tilde{P}(t) + \lambda t$, where P(t) is the Poisson process with a parameter λ , and $\tilde{P}(t)$ is a martingale corresponding to P(t) known as the *compensated Poisson process*.

An important point to be mentioned is that the proposed model is a rigorously defined system of stochastic differential equations in integral form. One possible alternative approach to the modeling would be to proceed as is done in Evolutionary Game Theory [21] where one defines a stochastic dynamical flow by set of local "game rules", an approach which is also suitable for Monte-Carlo simulation of system evolution. Formulation in the form of stochastic differential equations also allows Monte-Carlo simulation but does not restrict itself to this. For example approximate methods of the so-called weak type [22, 23] exist which allow (admittedly in a rather difficult way) direct estimates of functionals constructed on solutions of stochastic differential equations, such as the functionals for mean and variance of variables of interest. These direct estimates do not require exhaustive Monte-Carlo simulation to ensure proper statistic quality of simulation results.

Leaving this possibility for future work, we turn to discrete-time methods.

So now let us reformulate the model in the discrete form suitable for Monte-Carlo simulation.

The model in discrete form

Digital computers operate in a discrete world and so for simulation purposes, it is convenient to work with a model in discrete time. Note also that we would commonly lack precise information on the timing of events in a herd but may have this information on a monthly or annual basis. We discretize the above model at a sequence of fixed time steps $0 = \tau_0 < \tau_1 < \ldots < \tau_L = T$

We suppose that in each of the L intervals $(\tau_{l-1}, \tau_l]$ the probability of more than one Poisson process jump (control action) within the interval is negligible, or alternatively that multiple jumps can be replaced by a single jump of value equal to the sum of the individual jumps.

Then we arrive at the following discrete system of model equations:

$$D_{j}(t) = D_{j}(0) + \sum_{l=1}^{L} (-D_{j}(\tau_{l-1}) + d_{\xi}(\tau_{l-1})) \operatorname{sign}[\mathcal{P}(\lambda_{D}A_{j}(\tau_{l-1}))] I_{[0,t)}(\tau_{l})$$

$$d_{i}(t) = d_{i}(0) + \sum_{l=1}^{L} (-d_{i}(\tau_{l-1}) + f(D_{\eta}(\tau_{l-1}), S_{\zeta})) \operatorname{sign}[\mathcal{P}(\lambda_{d}a_{i}(\tau_{l-1}))] I_{[0,t)}(\tau_{l})$$

$$A_{j}(t) = A_{j}(0) + \sum_{l=1}^{L} (1 + (a_{\xi}(\tau_{l-1}) - A_{j}(\tau_{l-1})) \operatorname{sign}[\mathcal{P}(\lambda_{D}A_{j}(\tau_{l-1}))]) I_{[0,t)}(\tau_{l})$$

$$a_{i}(t) = a_{i}(0) + \sum_{l=1}^{L} (1 - a_{i}(\tau_{l-1}) \operatorname{sign}[\mathcal{P}(\lambda_{d}a_{i}(\tau_{l-1}))]) I_{[0,t)}(\tau_{l}).$$

$$(3)$$

In the system of equations (3), the $\mathcal{P}(\kappa)$ are all independent Poisson random values with rate parameters

Herd with a limited inflow of animals

The model described in the previous section for a medium herd size can demonstrate a long period of animal deficit due to an "extinction effect" which has been mentioned in the literature and which is observable in our simulation study. (see the discussion of Figure 4 below). Such a situation seems not to be a typical one as a farmer tends to fill the gap by animal purchase.

To account for such herd size control polices, we will modify the model in the following way. We assume that a purchased animal is placed into the replacement herd first. Such a simple assumption, nevertheless allows us to incorporate a market inflow by reformulating the meaning of the η

variable in equation (3) only. Namely, a a zero value of this variable now will correspond to the *event of a male animal birth* whereas for born female the variable value is still the index of the dam in the main herd. Then we can rewrite the equations for the replacement herd in the following simple form

$$d_{i}(t) = d_{i}(0) + \sum_{l=1}^{L} \left(-d_{i}(\tau_{l-1}) + \operatorname{sign}(\eta) f(D_{\eta}(\tau_{l-1}), S_{\zeta}) + (1 - \operatorname{sign}(\eta)) D_{M} \right) \operatorname{sign}[P_{d}(\lambda_{d} a_{i}(\tau_{l-1}))] I_{[0,t)}(\tau_{l})$$

$$a_{i}(t) = a_{i}(0) + \sum_{l=1}^{L} \left(1 + \left((1 - \operatorname{sign}(\eta)) a_{M} - \operatorname{sign}(\eta) a_{i}(\tau_{l-1}) \right) \operatorname{sign}[P_{d}(\lambda_{d} a_{i}(\tau_{l-1}))] \right) I_{[0,t)}(\tau_{l}). \tag{4}$$

where D_M is the random variable defining the distribution of the modeled allele in animals from the market, a_M is the random variable for the cows age distribution at the market.

As one can see from the equations (4), when $\eta = 0$ (male is born) the sign-function gives a non-zero contribution into terms with index M and the last can be interpreted as incorporation of animal from market into the replacement herd. When $\eta > 0$, the factor $(1 - \text{sign}(\eta))$ zeros the market contribution, restoring the original system (3).

One additional technical advantage of the last proposed model is that now the size of the replacement herd is constant, which simplifies working with the system, especially for the goals of numerical simulation.

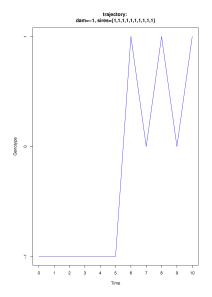
Simulation of genotype dynamics

In order to account for genomic selection models in animal breeding we now show some simulation results under the rule of genotype sum and controlled mating. We continue using the -1,0,1 coding. In each example we begin with a dam of genotype -1 (homozygous with allele to be eliminated), the dam and her resulting progenies are then inseminated by a sequence of sires of known genotypes. We choose the time points for the discretization with a constant one year spacing, that is we set $\tau_l - \tau_{l-1} = 1$ (year), $l = 0, 1, \ldots, L$. At the initial time τ_0 it is also assumed that the distribution of alleles in the

replacement herd is the same as in the main one. This leads, as we see later, to a two-year lag in switching dependence.

First, we consider the dynamics for unconditional switch of genotype into state 1 (homozygous with allele to be introduced). We achieve the goal by the sequence of sires, where all sires have genotype 1.

In Figure 1 we demonstrate two realizations of single trajectory in this case. It is worth mentioning that every plot shows the dependence of gene index in a particular, say the j-th, slot in the array of animals in the herd. Then in Figures 1a,b only jumps can be definitely interpreted as animal change, whereas horizontal lines could correspond, in principle, replacement at any time step an animal by another one with the same genotype. We stress that single trajectories (Figure 1) and bundles of trajectories (Figure 2) for the transition of an SNP from one state into another may differ quite markedly from the mean (Figure 4(a)).



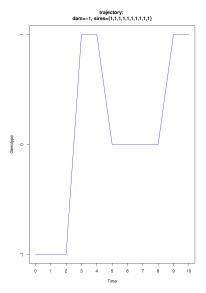


Figure 1: Two randomly chosen genotype trajectories. The dependent variable is a genotype value at the fixed index slot of the array of main herd, see in text for details.

Next, in Figure 2, we plot a bundle of 100 trajectories with jittering so that the probability of each route may be inferred from the plot. The density

of lines allows visual estimation of the number of animals in particular states -1,0,1.

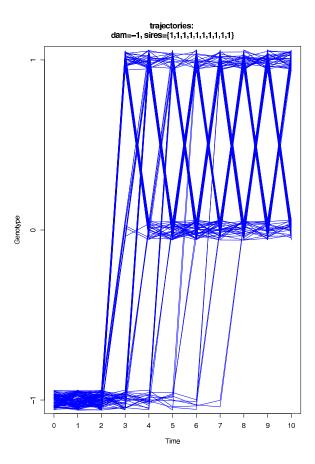


Figure 2: Bundle of 100 genotype trajectories.

Finally, in Figure 3, we illustrate the effect when one of the sires has the genotype -1 and again consider 100 individual trajectories. As one can see from this plot, a single fault (using a sire with g=-1), can seriously slow down the transition period. It needs to be pointed out that in Figures 2 and 3 the near vanishing of genotype -1 at the end of the simulation period does not mean that it has been eliminated from the whole of the herd.

Now we turn to the statistical characteristics of ensembles of simulated herds. In Figure 4 we show the temporal evolution of mean (a) and variance (b) for the case of 1000 herds, each simulation starting from a "herd" of 200

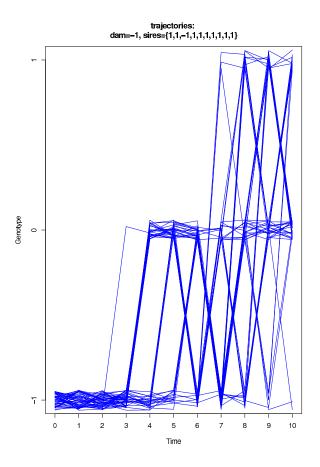
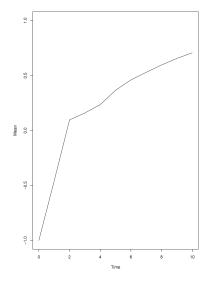


Figure 3: Bundle of 50 genotype trajectories, one bull in sequence (third one) with g = -1.

homozygous dams in the main herd (all initial genotypes are -1) and then developing independently.

An important feature discovered in this simulation is that the herd size evolves in time in direction of stabilization at a level which is less than what was chosen as a upper bound in simulation. The appropriate plot for herd size mean value is shown in Figure 5. It looks like some sort of "partial extinction" and can be explained as follows. Any positive fluctuation in number of female born at definite time step is cut by application of the rule of the upper bound control policy of assumptions 1 and 2.

In contrast to this, rare strong negative fluctuations in number of females



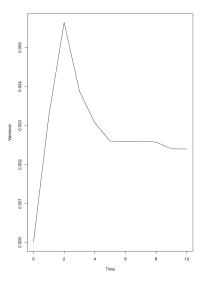


Figure 4: Mean (left) and variance of mean (right) of genotype value for 1000 herds, every main herd size is 200, replacement herd size is 100 at initial time, $\lambda_D = 0.114, \lambda_d = 0.25$.

born, which produce deficit of cows in the replacement herd seriously influence subsequent dynamics and lead to a period of slow herd size restoration. Averaging over herds does not improve the results, as this would include more and more rare but strong fluctuations.

As we see from the last plot, the dynamics of the replacement herd strongly influence on those of the main herd. In accord with this, the presented results on main herd should be considered as demonstrating only tendencies, because we did not seek to investigate the influence of replacement herd management nor try to optimize it somehow.

As we have already mentioned the at first sight an unpleasant "extinction effect" can be eliminated by animal inflow from the market in a way been discussed above. But much more profitable seems to be the following point of view, namely that "partial extinction" is a key ingredient in faster switch to a given allele. In fact, the Poisson process constant λ_D for the main herd is directly linked with "partial extinction" level as one can see from the following plots in Figures 6, 7, 8, 9, 10 where we demonstrate the rate of the

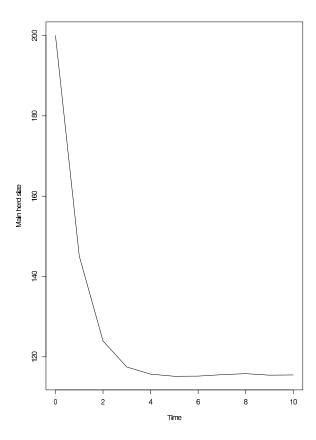


Figure 5: The dependence of the mean main herd size upon time. All parameters are the same as in Figure 4.

switch from a definite sign (it was chosen as -) of the allele into opposite sign depended on values of λ_D . Values λ_D and colors sequence (red, cyan, green, blue, black) corresponds to probability equals 0.8 for a cow to live in herd up to 4, 6, 8, 10, 12 years correspondingly, it was used averaging over 10000 herds in this simulations.

One of the interesting feature of the model is the sensitivity to a fine detail of the transition of animal from replacement herd to a main one. We consider two variants, in the first one we fill the main herd up to a limit size first from the replacement herd, then make a random choice of a way for rest animals in replacement hers to leave the herd. In the second variant, we make a random choice of leave/rest and then specify the variant of leave (if success). It turns out that at intermediate time these two slightly different procedure

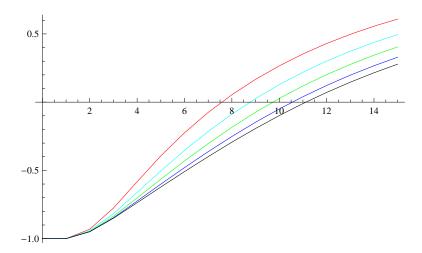


Figure 6: Mean genotype value time evolution for 10000 herds, every main herd size is 400, replacement herd size is 200 at initial time. Colors sequence corresponds to different values of the mean life constant in the main herd, see details in text.

give observably different behaviour, as demonstrated in Figure 11 for mean values, variances Figure 12 and mean size of the main herd Figure 13. For gene index dynamics both curves are very near, variances differ slightly but the mean herd size is influence strongly by the control scheme. The last leads to conclusion that it is necessary to be very accurate when formulating any control scheme for such a dynamical system, schemes seems to be very near at first glance could produce significantly different results.

Discussion

To summarize, we have constructed a system of stochastic differential equation that can model temporal evolution of biallelic polymorphism in a deme under conditions of controlled mating. The model incorporates peculiarities typical for New Zealand dairy herd management such as herd split into main and replacement herds, typical lifetime distribution, size control for main herd and rule of inflow from the replacement into main herd. Currently the model is implemented in R but an open source C++ version is under development [24].

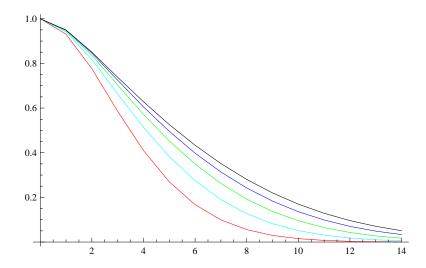


Figure 7: Mean displayed allele frequency time evolution for 10000 herds, every main herd size is 400, replacement herd size is 200 at initial time. Colors sequence corresponds to different values of the mean life constant in the main herd, see details in text.

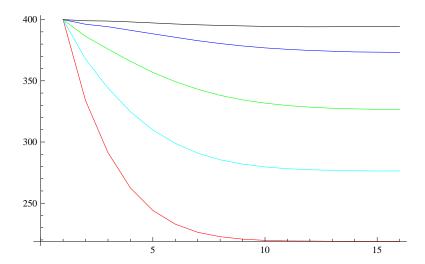


Figure 8: Mean main herd size time evolution for 10000 herds, every main herd size is 400, replacement herd size is 200 at initial time. Colors sequence corresponds to different values of the mean life constant in the main herd, see details in text.

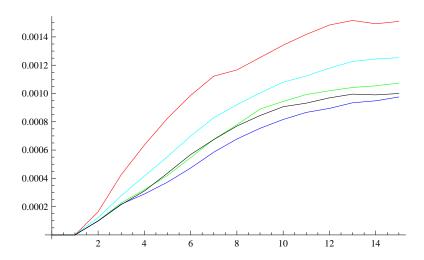


Figure 9: Variance of mean (right) of genotype value evolution for 10000 herds, every main herd size is 400, replacement herd size is 200 at initial time. Colors sequence corresponds to different values of the mean life constant in the main herd, see details in text.

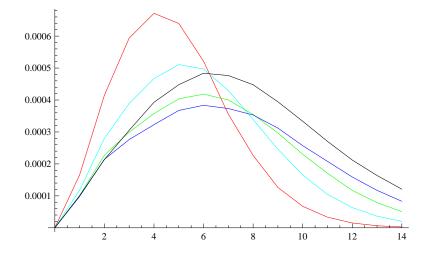


Figure 10: Variance of the displaced allele frequency for 10000 herds, every main herd size is 400, replacement herd size is 200 at initial time. Colors sequence corresponds to different values of the mean life constant in the main herd, see details in text.

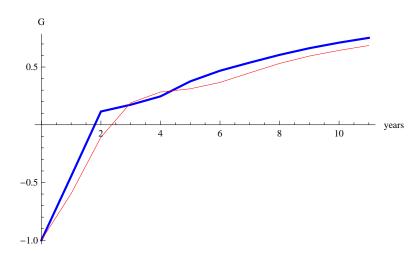


Figure 11: The comparison of the mean main herd gene index upon time dependencies for two models. Thin red line is for model 1, thick-blue line is for model 2. All parameters are the same as in Figure 4.

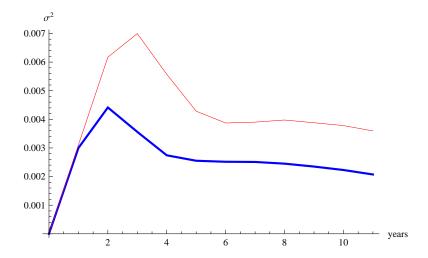


Figure 12: The comparison of the mean main herd gene index variance upon time dependencies for two models. Thin red line is for model 1, thick-blue line is for model 2. All parameters are the same as in Figure 4.

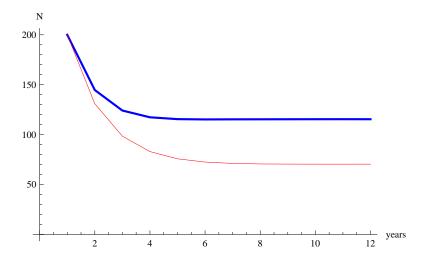


Figure 13: The comparison of the mean main herd size upon time dependencies for two models. Thin red line is for model 1, thick-blue line is for model 2. All parameters are the same as in Figure 4.

Simulations have demonstrated that when a maximum herd size is imposed local fluctuations of new born animals will strongly influence the system dynamics and lead to observable diminishing of the herd size (partial extinction). To suppress this feature, which is not observed in real farm situations, the model has been further adjusted to allow for an external inflow of animals from the market. Another important conclusion one can make is that the investigation of replacement herd management policy could be of great importance for reaching optimization goals.

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Table 1: Hardy-Weinberg Conditions and the New Zealand Dairy
Herd

11010	
Ideal Population	Production industry
Large homogeneous population	Heterogeneous Herds and Regions
Random mating	Controlled mating
No mutation	Mutations happen
No selection	Selection exists
No migration	Export/import of genes