Optimum family size in progeny testing and the theory of games

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Abstract

In this paper, the optimum family size in a progeny test with limited testing facilities was determined for a scheme where several commercial companies were competing. Companies which determined family size in order to maximize the expected proportion of sires that will be selected from its stock were considered as competitive. On the other hand, companies that determined family size in order to maximize the expected genetic progress were considered as altruist. Using the theory of games, it was shown that competitive companies obtain better commercial results than altruist companies. When competing against competitive companies, altruist companies obtained worse commercial results than they expected. When all companies were competitive, the commercial results equalled those when all were altruist, but the total genetic progress decreased. A numerical procedure is described to calculate the family size to optimize the commercial results. The result of this algorithm showed that this commercial equilibrium depends only on the heritability and the ratio between the total testing facilities of the population and the number of sires required for the market. This commercial equilibrium did not depend on the number of companies or the size of each company. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Animal breeding; Progeny test; Family size; Theory of games; Nash equilibrium

1. Introduction

Animal breeding plans are usually based on selecting by truncation the animals to be used as sires and dams in the next generation. Parents are selected by using their predicted additive genetic

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criterion to optimize the programs (Foulley et al., 1983), the optimum number of progeny per sire is usually analyzed in terms of the expected genetic response.

When several commercial companies design their progeny tests, they will have to increase the genetic merit of their breeding stocks in order to be competitive. Nevertheless, the objective of commercial companies is to increase the proportion of the market that they can have in terms of selected AI sires or selected animals. Usually, the relationship between the genetic merit of the breeding stock and the proportion of the market is difficult to analyze (Hill, 1971). Although the companies will try to increase the genetic merit of their stocks to be competitive, they will design their breeding plans in order to increase their benefits and not to increase the genetic progress explicitly.

The genetic progress is expected to be optimum when companies try to optimize it explicitly. Nevertheless, when companies are competitive the genetic progress will be an indirect effect of the competition. The intuition that guided our search is that the genetic progress obtained as an indirect result of the competition will be smaller than the optimum. The theory of games (von Neumann and Morgenstern, 1944) provides a formal approach to the analysis of the optimal decision of the companies, or players, in cases where their interests are interdependent.

The objective of this paper is to investigate, using the theory of games, the impact of this competitive behavior. We will compare the genetic progress obtained in a scheme whose companies try to increase their proportion of the market with another scheme whose companies try to increase the genetic merit of their stocks. We will also analyze how to calculate the optimal decision of each company in order to maximize the number of parents selected from its stock.

In this paper, we propose a simple game that will try to catch the essentials of the competition between companies. We analyze the simplest case of the game, where only two companies are competing as a duopoly and we generalize the game to include several companies. Finally, we analyze the effect of the heritability and the amount of testing facilities on the result of the game.

2. Methods

In this section we propose a game where a given number of companies (the players) design simultaneously progeny tests for new artificial insemination (AI) sires. Although Ashtiani and James (1993) have shown that considering different strains can modify the optimum number of progeny per sire, we will assume that animals coming from different company stocks are sampled from the same population.

2.1. The rules and the notation

Each company has a fixed amount of testing facilities, that is, a fixed number of progeny that can be measured. Hence, the number of sires that each company can test depends on the number of progeny used to test each sire, and we will call the number of progeny per sire family size. All companies know the heritability \( h^2 \), the number of tested AI sires demanded for the market and the amount of testing facilities of the opponents. The game will be played for only one generation.

Companies can use their own family size and afterwards the market will choose the sires with the best selection index within the whole set of tested sires. The objective of each company is to maximize the number of selected sires coming from its stock.

We will use the following notation: \( T \) will be the total amount of testing facilities, \( N \) will be the number of tested sires which the market will require after the testing period and \( n \) will be the family size used for testing the sires. Corresponding to this notation, \( T_i \) will be the amount of testing facilities of the \( i \)th company, \( n_i \) will be the family size that the \( i \)th company uses for testing its sires, \( S_i = T_i/n_i \) will be the number of sires tested for the \( i \)th company and \( p_i = N_i/S_i \) is the proportion of sires selected from those tested.

Fortunately, the analysis of this game under the theory of games point of view is simple. For that reason we do not include an introduction about the theory of games here. From here on, we will outline definitions and explanations to illustrate the analysis where necessary. A general introduction about the theory of games can be found in Rasmusen (1994).
The game proposed here is a \( n \)-person zero-sum game, that is, if a company increases its proportion of the market, the proportion taken by other companies will decrease by the same amount. In games of this kind, there is no reason for coalition, and the only criterion for the \( i \)th company to optimize its strategy \( n_i \) is to maximize \( N_i \) or \( p_i = N_i/S_i \).

Depending on the family size used by each company, the expected number of sires selected from each company stock can be predicted.

### 2.2. Game payoffs

Each possible set of strategies \( n_i \) for all the players corresponds to a set of payoffs. A payoff is a number that determines the winner of the game.

When playing this game, the companies will try to maximize the expected number of sires selected from their stocks. So, in this case, a company will consider itself as the winner of the game when the proportion of selected sires which come from its stock is bigger than the proportion its testing facilities are of the total. For that reason, we define the payoffs as a set of numbers derived from \( N_i \):

\[
P_i = N_i - \frac{NT_i}{T_i}
\]

The payoffs can be determined after each company has decided the strategy \( n_i \). When the payoff of a company is zero, its expected proportion of the selected animals is equal to its proportion of the testing facilities, \( N_i/N = T_i/T \). A positive payoff for the \( i \)th company means that the proportion of selected sires coming from its stock is bigger than its proportion of the testing facilities. We show in this section how to calculate the whole set of payoffs from the whole set of strategies.

Setting the additive genetic variance equal to 1, the stock of the \( i \)th company corresponds to \( S_i \) sires whose predicted additive values (\( \bar{a} \)) are realized samplings from a normal distribution with null expectation and variance equal to

\[
\sigma_a^2 = \frac{0.25n_i h^2}{1 + 0.25(n_i - 1)h^2}
\]

Calculating the payoffs for each company requires the determination of the expected number of selected sires coming from each company stock, \( N_i = p_i S_i \). Order statistics for the whole set of normal distributions are not available, but given the distribution of the selection indexes, the truncation point that satisfies \( N - \sum p_i S_i = 0 \) can be obtained by using the bisection algorithm (Burden and Faires, 1985). This algorithm evaluates the candidate points and, by successive bracketing, approaches the truncation point \( k \) which satisfies \( N - \sum p_i^{(k)} S_i = 0 \). \( p_i^{(k)} \) is the proportion of sires selected from the \( i \)th company and the candidate truncation point \( k \). After the common truncation point was calculated, to obtain the expected number of sires selected from each company stock and the payoffs for each company is straightforward from \( N_i = p_i S_i \).

Note that each company can calculate its payoff only if it knows the strategies of the opponent companies, but the other players will hide their strategies like in a gambling card game. To optimize its own strategy, each company should guess which would be the strategies of the opponents. Further, to play rationally the game, each company will assume that the other companies will also choose their strategies rationally.

### 3. Results: the analysis of the game

#### 3.1. Result of the game involving two companies: the duopoly

To illustrate the procedure that a company should follow to decide its strategy, we present in this section the result of the game in a case with two companies. As an example, suppose that the testing facilities of the company 1 are 1000 spaces, the testing facilities of company 2 are 500 spaces and the heritability is 0.25. They compete in a market that will select 10 sires on the basis of the predicted breeding value. Company 1 expects two thirds (1000/1500) of the selected sires to come from its stock, and company 2 expects one third (500/1500).

In this game, both companies will calculate all possible pairs of strategies in order to decide its optimum family size. Table 1 presents a set of pairs of pure strategies, from 2 to 16 progeny per sire for
Table 1
Payoff matrix for company 1 in the duopoly game; payoffs for company 2 are equivalent but opposite in sign. Strategies of company 1 are presented in columns and strategies of company 2 are presented in rows.

<table>
<thead>
<tr>
<th>$n_1$</th>
<th>$n_2$</th>
<th>$n_3$</th>
<th>$n_4$</th>
<th>$n_5$</th>
<th>$n_6$</th>
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<td>1.980</td>
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<td>4</td>
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<td>0</td>
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</tr>
<tr>
<td>8</td>
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<td>-0.128</td>
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<td>-0.016</td>
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<td>10</td>
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<td>0</td>
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<tr>
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<td>-0.990</td>
<td>-0.049</td>
<td>0.253</td>
<td>0.333</td>
<td>0.312</td>
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</table>

*The column and row presented in italic font correspond to the best payoffs for company 1 and company 2, respectively.

The opposing interests of the two companies have an equilibrium point that corresponds to the row and column presented in bold in Table 1. In this table, the fourth column corresponds to eight progeny per sire and it contains the best payoffs for company 1, and the fourth row corresponds also to eight progeny per sire and it contains the best payoffs for company 2.

Fig. 1 shows the surface of the values presented in Table 1, with the strategies ranging 2 to 20. It can be shown that the opposing interests of the two companies have an equilibrium point that corresponds to the row and column presented in bold in Table 1. In this table, the fourth column corresponds to eight progeny per sire and it contains the best payoffs for company 1, and the fourth row corresponds also to eight progeny per sire and it contains the best payoffs for company 2.

Both companies can use the approximation of Robertson (1957) or numerical procedures to calculate that 14 progeny per sire maximizes the genetic progress with $T=1500$, $N=10$ and $h^2=0.25$.

$$n = 0.56 \left( \frac{T}{Nh^2} \right)^{0.5} = 13.7$$

So, both companies should decide to test their sires using 8 daughters per sire (the commercial optimum) or 14 daughters per sire (the genetic optimum). Table 2 presents the relevant information that both companies will have available to decide just between these two strategies. From Table 2, if company 1 guesses that company 2 will choose 8, its payoff is better if it choose 8 (0 over -0.237). In the same way, if it guesses that company 2 will choose 14, its payoff is still better (0.209 over 0) by choosing 8. Hence, company 1 will choose to test each sire with eight progeny, whatever the strategy of company 2. The same argument holds for company 2 to choose 8 progeny per sire. Hence, the equilibrium point is unique and stable. Both companies have the same payoffs at (8,8) as at (14,14).
but they will choose 8 to prevent the competitive behavior of the opponent giving it an advantage.

In the theory of games framework, this kind of stable optimum is called the Nash equilibrium (Nash, 1951). A set of pure strategies is a Nash equilibrium if no player can increase its payoff by a unilateral change in his strategy. The Nash equilibrium for games whose strategies have to be optimized within a range of numerical values is usually called the equilibrium of Cournot–Nash (Binmore, 1992). In general, this equilibrium does not have to be unique, but Fig. 1 shows a saddle form and the Nash equilibrium is unique for this game.

So, the result of the game is that both companies will simultaneously set their family sizes below the genetic optimum and no company will win the game, but the genetic progress will decrease from 1.242 to 1.201. Under the assumptions made for this game, big companies do not win over small companies nor vice versa, but companies that use the theory of games will win over altruist companies that use the expected genetic progress as criterion.

If only one of the companies decides unilaterally to be competitive, Table 2 shows that company 2 will increase its expected number of successful sires from 3.33 to 3.57 (7%), and company 1 will increase its results from 6.66 to 6.88 (3%). That is, the small company will be more interested than the big company to be competitive. In these circumstances, it can be noticed that a previous agreement between companies to be simultaneously altruist is difficult, as in any other zero-sum game.

3.2. Result of the game involving more than two companies

The game involving two companies was analyzed by setting several pairs of strategies and looking at the payoff surface (Fig. 1). If more than two companies are playing the game, the number of possible sets of strategies grows dramatically and the multidimensional table of payoffs is difficult to represent. For that reason, each company uses numerical procedures to obtain the Nash equilibrium.

The algorithm starts from an arbitrary set of strategies, and each company successively calculates its optimum considering fixed the strategies of the opponents. After several rounds of iteration, the algorithm reaches the equilibrium and the set of strategies is a Nash equilibrium. Although not presented in this paper, we corroborated the uniqueness of the Nash equilibrium by setting different sets of starting strategies. Each company considers fixed the strategies of the opponents as fixed just as an algorithmic artifact to reach the Nash equilibrium.

Usually, each company maximizes its payoffs by differentiating its univariate payoffs function considering the strategies of the other companies fixed. In this case, this function of payoffs is difficult to differentiate and we used a successive bracketing algorithm (Press et al., 1986) to find the maximum. This algorithm requires only several evaluations of the payoff function to find its maximum.

We considered an example with \( N=10 \) and \( h^2 = 0.25 \). The players were five companies whose testing facilities were 700, 400, 200, 100 and 100, respectively. As in the duopoly game, all companies have to decide the optimum strategy and they have to predict the optimum strategies of the opponents.

Starting strategies were arbitrarily set as 5 progeny per sire for all companies. We show in case 1 of Table 3 the result of the algorithm that converged in 2 rounds of iteration. The 3rd round was calculated to verify that results do not change and hence that the set of strategies reached is the Nash equilibrium.

The algorithm presented in case 1 of Table 3 can be interpreted as follows. First, all players can calculate that company 1 will choose \( n_1 = 8.299 \) as the optimum strategy using the successive bracketing algorithm on its payoff function and considering that the fixed strategies of the other companies were \( n_2 = 5, n_3 = 5, n_4 = 5 \) and \( n_5 = 5 \). Afterwards, all players know that company 2 will guess the strategy of company 1 and it will choose \( n_2 = 8.461 \) as the optimum strategy considering \( n_1 = 8.299, n_3 = 5, n_4 = 5 \) and \( n_5 = 5 \). Following this successive set of optimizations where each company can predict the behavior of the other companies, the algorithm reaches the Nash equilibrium. Note that the family size was not forced to be an integer number, as in the duopoly game.

Table 3 also shows four other cases with different number of companies and different testing facilities. All cases studied considered \( T=1500 \). From this table, we can conclude that the commercial optimum is equivalent for all the companies and does not
Table 3
Results and convergence of the algorithm reaching the Nash equilibrium in several cases with 2, 3, 4 or 5 companies and several testing facility structures

<table>
<thead>
<tr>
<th>Case</th>
<th>$T_1$</th>
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<th>$T_4$</th>
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<td>8.461</td>
<td>8.551</td>
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<td>8.647</td>
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*Heritability was 0.25 and the number of sires selected by truncation was 10. $T_i$ are the testing facilities of each company and $n_i$ is the strategy of each company.*

depend on the number of companies involved in the game. Moreover, it does not depend on the proportion of testing facilities of each company. In fact, it depends only on the ratio $T/N$ and the heritability. In the next section, we will investigate the relationship between the heritability, the ratio $T/N$, the commercial optimum and the genetic optimum.

3.3. Effect of the heritability coefficient and the ratio $T/N$ on the commercial equilibrium

We calculated both the genetic optimum and the Nash equilibrium for case 1 presented in Table 3 for a range of heritabilities. These results, which are shown in Fig. 2, demonstrate that the commercial optimum family size is always smaller than that for the genetic optimum, especially for small heritabilities. Fig. 3 shows the expected genetic progress when the five companies determine the family size in order to maximize the genetic progress explicitly and the expected genetic progress when the five companies determine the family size at the commercial equilibrium. The expected genetic progress obtained for 5 competitive companies is around 3% smaller than for five cooperative or altruist companies, under all values of the heritability.

Figs. 4 and 5 show the effects of the changes of the ratio $T/N$ on the family size and the expected genetic progress. With $N$ fixed at 10 sires to be selected, the ratio $T/N$ ranged from 20 to 500 and heritability was 0.20. These figures show that the family size determined in order to cooperate is also larger than the family size to compete, whatever the ratio $T/N$. All cases show that competition produces a decrease in the expected genetic progress.

4. Discussion

Despite the simplifying assumptions made, the game analyzed in this paper shows in general that optimizing the genetic progress does not produce the optimum commercial results. The game does not mimic exactly the real behavior of the market. It assumes that the number of sires selected for the market and the benefits have an exact linear relationship, without considering that selected animals have different commercial value depending on their selection indexes. Nevertheless, the benefits usually depend on the quality of the selected sires. It also does not consider the effect of different amount of information about the genetic value of the sires before the progeny test.

Both in the duopoly and the oligopoly cases, the
Fig. 2. Genetic optimum and commercial equilibrium for a range of heritabilities.

Fig. 3. Genetic progress obtained for the five companies when they use the commercial equilibrium or the genetic optimum for a range of heritabilities.
Fig. 4. Genetic optimum and commercial equilibrium or a range of ratios between the amount of testing facilities and the number of sires demanded by the market.

The game was only analyzed for one generation and the company stocks have the same mean breeding values. That is an important limitation of the game, because in a game involving several generations, a company can decide to optimize the genetic progress of its stock at the first generation, even decreasing its proportion of the market, in order to get an advantage for future generations. The reader will notice that analyzing multiple generation games is non-trivial because we should analyze complex generation dependent strategies like ‘be always competitive’, ‘be altruist while the others are also altruist, and be competitive otherwise’, ‘be altruist or competitive at random to be unpredictable’, ‘betray the mutual agreements from time to time’, etc. Sometimes, these long-term games are analyzed by simulating them repeatedly by using human role players, whose experience can help us to analyze the strategies and their approximate payoffs.

Another assumption made in order to simplify the game was to use a progeny test that ignores the relationships coming from the females. At present, AI sires are evaluated by assuming animal models, which consider all relationships. In this case, the accuracy of the sire evaluation is related both with the number of progeny and the mating strategy in the whole population.

Strategies have been restricted to pure strategies, that is, strategies where a company uses the same family size to test all its sires. For practical purposes, where the game is not so simple, analyzing strategies with a different number of progeny per sire may be very relevant in cases with previous information or cases where the testing period have to be done in several stages.

Even accepting these limitations, the result of the game suggests that the commercial strategy in practice should be testing more animals to achieve better commercial results. Nevertheless, companies usually do not like to reduce the accuracy of selection indexes of their animals because farmers usually will choose the sires not only because of their selection indexes but the accuracy also prefer high accuracy.

All cases presented show that the commercial equilibrium depends only on the heritability and the ratio $T/N$. This means that a company should...
concentrate its effort on the determination of the heritability, the number of total testing facilities available in the population and the number of sires required for the market. The last two numbers depend on the population size, the number of years that the sires are kept in the AI station, the percentage of animals that farmers will use to test new sires, etc.

During the game, there is no reason for two companies to cooperate when playing against other companies, because the size of each company does not affect the commercial equilibrium or its payoff.

A company that uses the theory of games to determine its family size will increase its proportion of selected AI sires when it is competing with other companies that determine their strategies in order to maximize the genetic progress. As we concluded from Table 2, the improving effect of the theory of games is bigger for small companies than for big companies. Furthermore, the theory of games will produce an extra benefit for small companies because when they use smaller family sizes, they will test more sires, and the sampling variance of their commercial results will decrease to a larger extent than for large companies.

Results presented in this paper suggest that a reduction in the number of progeny per sire will increase the number of sires selected from a company stock. In this case, the proportion of selected sires will decrease because both the accuracy and the variance of the expected breeding values will decrease. Thus, the better commercial results can be explained because of the rise in the number of tested sires. In this context, the commercial equilibrium is the strategy where the proportion of selected sires multiplied by the number of tested sires reach its maximum.

The main result of this paper can be considered as a paradox because companies that determined the family size in order to maximize the genetic average of their selected sires loose the game. Although the average of the breeding values of the sires selected from competitive companies will be smaller than the average of the altruist ones, they win the proposed
game because their objective is to maximize explicitly the number of sires beyond the truncation point.

References
