THE ROLE OF COMPUTER SIMULATION AND LABORATORY ANIMALS IN THE DESIGN OF BREEDING PROGRAMS[1]

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SUMMARY

The potential application of systems analysis to animal breeding program design is reviewed and discussed. The quantitative nature of animal breeding facilitates computer modeling. Since breeding program design involves the integration of several sub-systems, modeling seems a practical alternative and complement to experimentation to address the complex questions and potential interactions involved. The relative merits of computer modeling and laboratory animal modeling are discussed with value seen for both. Some areas suggested as being worthy of such approaches are 1) definition of bio-economic objective, 2) interactions between genetic characteristics and management, 3) costs versus returns for complex selection schemes, 4) interactions between crossbreeding and selection response, 5) interactions between selection and expansion, 6) implications of enhanced reproduction. Examples of computer simulation studies and potential laboratory animal studies to address some of these questions and problems are presented. Considerable synergism is seen for experimentation in animal species of agricultural importance, computer simulation, and laboratory animal modeling, with interplay between them, for numerous questions of animal breeding program design.

INTRODUCTION

Harris, Stewart, and Arboleda (1984) presented a strategy for the design of animal breeding programs. They arranged the design questions into an organized nine-step structure, to be developed in sequential order

1. Describe the production system(s),
2. Formulate the objective - both simplified and comprehensive - of the system,
3. Choose a breeding system and breeds,
4. Estimate selection parameters and economic weights,
5. Design an animal evaluation system,
6. Develop selection criteria,
7. Design matings for selected animals,
8. Design a system for expansion,
9. Compare alternative combined programs.

The last step was included to allow for potential situations where there might be an interaction between the earlier steps that allows another possible

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combinations to be superior to the combination which would have been decided on sequentially. For example, some animal evaluation systems (Step 5) might allow greater reproduction for expansion (Step 8) so that the combined program is more effective in disseminating genetic improvement to the production system than what might have been chosen at Step 5. Such possible interactions seem to require Step 9 (Compare alternative combined programs) and will be addressed in this paper. It will be proposed that ''systems analysis'' studies are needed to answer several such questions. The present paper will focus upon the unanswered questions and may neglect some partial answers.

SYSTEMS ANALYSIS

Webster's Ninth New Collegiate Dictionary (1983) gives the definition

> Systems analysis n. (ca. 1956): the act, process, or profession of studying an activity (as a procedure, a business, or a physiological function) typically by mathematical means in order to define its goals or purposes and to discover operations and procedures for accomplishing them most efficiently.

Consideration of this definition suggests that animal geneticists were doing systems analysis much before 1956, but with present-day computers and with more complete knowledge (in quantitative form) of genetics, statistics, management systems, etc., our capabilities for doing systems analysis have matured. However, systems analysis by computer simulation requires a comprehensive, detailed mathematical description of components of the system and their interrelationships. For analysis purposes, the system needs to be ''closed.'' Defining ''boundaries'' for models of real-world systems that, in reality, are not completely closed can be troublesome. There are numerous possible applications of systems analysis or modeling in various disciplines and combinations of disciplines involved in animal production systems. In this paper, we will focus upon those concerned with the design of animal breeding programs.

Integration of Sub-systems

As pointed out by Harris et al. (1984), the design of animal breeding programs involves the integration of several sub-systems

(1) a multi-trait animal evaluation system in the nucleus herds
(2) a multi-trait and, probably, multi-stage selection procedure within the nucleus herds
(3) a mating system for reproducing nucleus herds
(4) a pure- or cross-breeding system
(5) an expansion system for disseminating genetic improvement from the nucleus herds to commercial production herds
(6) production system(s).

The primary concern is how effectively the first four sub-systems, (1) to (4), modify favorably the efficiency of the sixth, the production system(s), through the fifth, the expansion system. The production system(s) are the procedures involving herds or flocks of animals for converting inputs of feed, labor and facilities into outputs of animal products. Thus, the first four sub-systems provide the alternative ''controls'' on the production system that modify the efficiency of the system. In addition to genetic changes in the levels of performance, possible changes would be modifications of the details of the production system(s), e.g., change in the age or weight at slaughter.

The interplay between these sub-systems permit possible interactions that might allow some combined system to be superior to a comprehensive system arrived at by the first eight sequential steps. Furthermore, some of the eight steps require a detailed analysis of that sub-system. Thus, design of animal breeding programs is an appropriate field for application of systems analysis.

PAST DEVELOPMENTS IN BREEDING PROGRAM DESIGN

In experiments too numerous to review, with domestic livestock of agricultural importance and with laboratory species, the effects of selection have been studied, both with selection experiments and indirect parameter estimation procedures. These are consistent with the theory that short-term direct and correlated responses to selection can be described mathematically through quantities describing intensity of selection ($\bar{i}$), accuracy of selection (r_{GI}), genetic variability (σ_G) and generation interval (t). Allowing for different selection in the two sexes (m and f), the primary equation for describing the response to selection is with the objective of maximizing this

$$\frac{\Delta G}{t} = \frac{(\bar{i}_m r_{GIm} + \bar{i}_f r_{GIf}) \sigma_G}{t_m + t_f}$$

rate. In addition, procedures have been developed for obtaining optimum linear and quadratic indexes (I) for improving linear and quadratic objectives (G) (Wilton, Evans, and Van Vleck, 1968).

The consequences of cross-breeding have extensively been studied in all classes of livestock in conjunction with the development of statistical and genetic models to describe the elements of cross-breeding effects.

Even though exceptions may be cited, we shall note five general limitations we foresee to the ability to design breeding programs based upon the knowledge inferred by the above cursory review:

1. selection theory primarily addresses short-term response for purebred performance;
2. selection and cross-breeding have nearly always been studied separately, even though most breeding programs involve both;
3. choosing schemes that maximize $\Delta G/t$ for selection response does not consider the relative costs of alternative selection schemes;
4. most tools for breeding program design are specific to a single target environment but many breeding situations involve multiple target environments (production system); and
5. our understanding is meager about the interplay and possible interactions between the sub-systems.

In short, most easy questions have been answered, but there are numerous complex questions remaining.

ALTERNATIVE APPROACHES TO UNANSWERED QUESTIONS

There are three general alternative approaches for studying large, complex systems - experimentation, computer modeling, and laboratory animal modeling. Experimentation with food and fiber animal species is the approach of choice for answering most research questions about these species. However, experimentation is limited by constraints of time and resources. For large animals and for complex systems, these constraints are especially limiting. Several alternatives involving large numbers of animals cannot very easily be compared experimentally with replication. At most, experiments can only be for overly simple systems or for components of systems. Computer modeling has the potential for integrating results from such experiments to study larger, more complex systems, but is limited by the ability to describe the system and its components mathematically. In most cases, experimentation can and should be used to enhance the capacity of describing systems or components mathematically. Laboratory animal modeling is usually not limited by time and resources to the degree that large animal work is, because the species chosen for modeling (rats, mice, Coturnix quail) are much smaller in body size (less costly) and have shorter reproductive cycles than the livestock species they model. For very general questions of genetics, Drosophila and Tribolium have been used as pilot organisms. These species have the ultimate advantage in being small and highly reproductive. There does not seem to be a good biological model in a laboratory species for the specific questions concerning ruminants.

Replicated experimentation with the class of livestock of interest is preferred. But for many of the comprehensive questions of breeding program design which concern a large segment of a national industry, that is not practical. In such cases, there is a definite potential for computer modeling to describe and link components of systems and compare alternatives, but this is only possible if the knowledge of the components resulting from previous research and experimentation can be quantified and presented in a mathematical form. Fortunately, this latter condition is well satisfied for many of the components of quantitative genetics and animal breeding if empirical models of statistical relationships between traits of concern are satisfactory. However, this condition is not fully satisfied for numerous physiological details of animal performance, especially when mechanistic models are desired.

When experimentation in large animals is impractical and the ability to mathematically describe the details is limited, laboratory animal modeling potentially fills an intermediate niche. For example, when the details of the genetic mechanisms including gene frequencies, gene action, recombination effects, mutations, etc. are of concern, the mouse may be a better model for swine than is any of the computer models for such details. Since validity of results depend on adequacy of the model, the choice between computer models and laboratory animal models depends on which seems to produce the more accurate modeling for the research questions being asked. This choice shifts depending on the question being asked. The laboratory animal model would be preferable if it includes some similarities in biological details, such as genetic mechanisms, that cannot be included in the computer model at this point in time. The risk is that there are some dissimilarities between the model species and the species of interest, such as physiological functionings, that might distort the results. However, that is also a risk of computer modeling and can even be a limitation of experimentation when trying to generalize from the results for specific populations. In many cases, the known dissimilarities can be accounted for either in the design or interpretation of the experiment or simulation.

For the above reasons, we see a need for all three tools in a balanced program of systems analysis of breeding programs. Experimentation on large animals provide knowledge of the fundamental aspects of the system. Computer modeling offers the opportunity to integrate the detailed knowledge together. Laboratory animal modeling offers the chance to verify and demonstrate some aspects of the computer model that cannot be studied directly on the species of interest. And there needs to be considerable feedback and interplay between each of these three approaches and the others.

SYSTEMS QUESTIONS IN BREEDING PROGRAM DESIGN

We shall now review a few examples where the alternatives of computer and (or) laboratory animal modeling seems needed to answer questions of breeding program design that are difficult to evaluate completely through experimentation because the amount of time or number of animals necessary would be prohibitive.

Definition of Bio-Economic Objectives

Step 2A of Harris et al. (1984) involves developing mathematical descriptions of input-output relationships (economic) for production units of parents and their lifetime offspring in a form to reflect value of genetic differences in biological traits with a preference for these descriptions to be in the form of a linear or quadratic function. A more comprehensive systems model (Step 2B) from selection herds through to production herds needs to be formulated to include more complex aspects of the integrated system. In addition, there may be a mixture of production systems that need to be described. These considerations, described in the earlier paper, can be considered as systems analysis. Examples of this application are Cartwright (1970) for beef cattle, Tess, Bennett, and Dickerson (1983a, b, and c) for swine and Akbar, Harris and Arboleda (1986) for broiler poultry.

Potential Interactions Between Genetic Characteristics and Management. Genotype by environment interactions have long been of interest to animal breeders. Of particular interest are the interactions of either breed or cross differences or selection changes with the environmental differences controllable by management-nutrition, facilities scheduling, etc. Even though such interactions are known to exist, most genetic change by selection is directed to a specific environment (the test environment) and most management alternatives are researched for a specific genetic population (the population used for the experiment). There is a potential for genetic changes that allow management changes for a synergistic utilization of such interactions. For example, the trend to leaner swine has resulted not only in leaner market swine, but has facilitated marketing at heavier weights without over-fatness and associated declines in feed conversion. Systems analysis could lead to the discovery of other appropriate synergistic genetic changes with controllable management changes.

Returns versus Costs. In selection programs, it is often true that more elaborate schemes will lead to greater $\Delta G/t$, but these more elaborate schemes are usually more costly. The choice of the program with the greatest $\Delta G/t$ is not a satisfactory decision criteria for such alternatives. An example is the potential greater response to schemes involving feed consumption data recording (see Arboleda, Harris and Nordskog, 1976a and b). Both costs and returns need to be evaluated. But the value of the resulting genetic return is usually manifested in the production system after expansion and crossbreeding. Thus, a full evaluation needs to involve modeling the total system (the comprehensive objective of Step 2B) from selection through to the production system(s). Figure 1 shows a hypothetical, but, possible scatter diagram of alternative selection schemes expressed in terms of returns to the total system versus costs of the selection system. The diminishing returns curve draws the boundary of the schemes along the border where returns are at a maximum relative to other schemes for that cost. This raises the question - where is the optimum on such a diminishing returns curve? Many times the greatest return on investment (ROI) occurs for the simplest of schemes. This is represented by the greatest slope at the left-most portion of the curve. But this is not likely the optimum scheme. It seems that the optimum scheme is well along the curve where the recognized value of the response is greater than the recognized costs of achieving that response just enough to yield an acceptable ROI. Further to the right, the value of the recognized additional response would not be greater than the additional costs enough to yield an acceptable ROI. A key word in this conclusion is ''recognized.'' In complex, fragmented industries such as livestock production, the value of increased performance is not always fully recognized and rewarded in the market place.

Potential Interactions Between Sub-systems: Crossing. In Table 1, the relative merits and disadvantages of several alternative schemes are compared. These points are understood by most geneticists. The difficulty is in how to weight the alternative merits and disadvantages to arrive at a decision. In Step 3 of Harris et al. (1984), it was suggested that the performance of the cross was the primary criterion. When there is an appreciable amount of paternal, maternal, and progeny heterosis (general and(or) specific), this is likely to be in the direction of four-way crosses, unless the increased performance of the complex cross is offset by the costs coming from the complexity of producing the cross or in the lower performance of the purebreds necessary to produce the cross. In large animals, with low reproductive rate, the lower performance of the large number of immediate ancestors needed to produce the superior performing crossbred animals can offset the performance advantage. If there are not enough different breeds with adequate performance to support the cross, the compromise might have to be in the direction of simpler crosses and even to purebreeding. For example, in dairy cattle, purebreeding with Holsteins seems to be preferred even with evidence of heterosis (Touchberry, 1970). Gregory et al. (1982) discusses the potential of composites for partially exploiting heterosis when species have low reproductive rate and specific crosses are difficult to produce. However, the total question is so complex that systems analysis and computer modeling (Step 2B - comprehensive objective) and laboratory animal experimentation seems necessary to fully describe the alternative systems and to incorporate all the factors for arriving at a complete answer.

Potential Interaction Between Sub-systems: Selection and Expansion. Intense selection (to the degree that the reproductive rate allows it) is the choice to maximize response to selection. However, expansion from a larger number may produce more improved descendants in the production system. In Harris et al. (1984), it was suggested that the mass of improved stocks times the magnitude of genetic improvement is the appropriate decision criterion. Since magnitude is related to the standardized selection differential (z/b of the unit normal curve with $b = n/N$ for N = number evaluated and n = number selected), and mass is related to n (number selected) then mass x magnitude is proportional to $n \times z/b = n \times z \times N/n = N \times z$, which is maximum at $b = .5$ for a constant N. The answer is more complex when the proportion seected differs in the two sexes. Adding questions of scheduling of reproduction both for expansion and for reproduction of the nucleus herd can lead to more complex

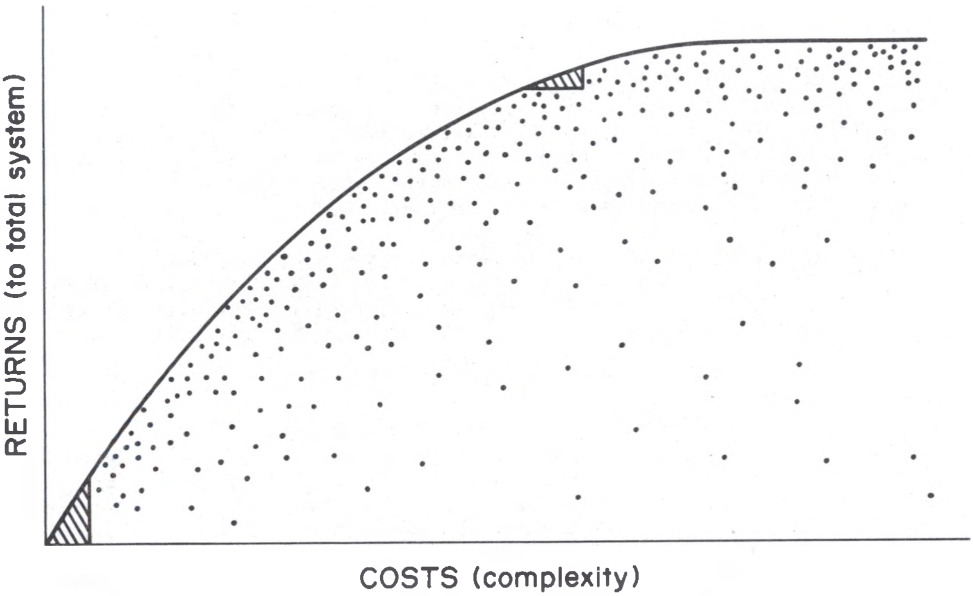

Figure 1. Returns versus costs for alternative selection schemes

Table 1. Comparison of advantages and disadvantages for alternative schemes.

Type of cross	Utilization of complementarity	Utilization of heterosis	Utilization of breed differences	Simplicity of producing
D purebred	none	none	greatest	simplest
C-D terminal	yes	progeny		
B x C-D terminal	yes	maternal and progeny		
B C D rotation	none	partial maternal, partial progeny		
B x C D rota-terminal	yes	progeny and partial maternal		
A-B x C-D terminal	yes	paternal, maternal and progeny	least	complex
Composite of A, B, C, and D	none	heterosis retention?	least	simplest after synthesized

design questions that require a form of systems analysis to compare alternatives.

Impact of Enhanced Reproduction Techniques of Biotechnology. New techniques and potential techniques of enhanced reproduction (embryo transfer, embryo splitting, etc.) enlarge the alternatives available to designers of breeding programs, especially in Step 8 (expansion) and in Step 5 (evaluation). The implications of these alternatives are complex enough to require systems analysis to facilitate comparisons (e.g. Van Vleck, 1981).

Long-Term Implications. An area in which considerable computer modeling has already been done to compare alternatives is the interplay between breeding population size, selection, inbreeding and reduction in genetic variability (see Gill, 1965a, b, c,; Qureshi, 1968; Qureshi et al., 1968; Harris, 1982).

ALTERNATIVE APPROACHES

Of the examples cited above of systems questions relating to design of breeding programs, which requires experimentation? Which requires computer modeling? And which laboratory animal modeling? Experimentation is needed for quantifying many of the details but computer modeling is appropriate and seems necessary for integrating the fragmented details together. Laboratory animal modeling seems necessary to verify and demonstrate numerous aspects of the computer models that cannot be investigated experimentally with large animals.

EXAMPLE: COMPUTER SIMULATION STUDY

Harris, Akbar, and Arboleda (1985) presented a preliminary report on a computer simulation program to model three-way cross broiler selection schemes. The program is specific for three-way crossbreeding schemes, but allows numerous alternatives concerning single-stage, two-stage, and three-stage selection for a variety of selection criteria. The possible selection points are (1) at end of broiler stage (e.g., 7 weeks), (2) at housing for laying test (e.g., 22 weeks), and (3) at end of laying tests of alternative lengths. In addition to studying alternative selection criteria at alternative selection points, the program allows alternatives of scheduling reproduction to produce grand-parents (expansion) and, thus, allows study of possible interaction between the selection intensities in conjunction with the number of hatches of the selected breeders and the expansion system. The modeling program is dynamic, deterministic and discrete-event oriented and is programmed through the SLAM (Simulation Language for Alternative Modeling) software (Pritsker and Pegden (1979). The system modeled includes foundation (selection) flocks, grandparent (expansion) flocks, parent (crossbreeding) flocks and broiler production flocks. In other words, all the sub-systems of comprehensive breeding and production systems described earlier in this paper are included in the model. The primary basis for comparing alternatives is the expected discounted profit from a fixed amount of investment over a specified length of time (say, twenty years). Economic inputs (costs) to the system are hatching, feed, labor and facilities for each type of flock, and processing costs. Outputs (income) are derived from cut-up broilers (breast-thigh-leg and remaining parts), roasters and hens.

Among the alternatives for selection criteria which may be evaluated are whether or not feed consumption data is worthwhile, whether or not sib or progeny carcass data is worthwhile, whether or not a laying test is advantageous for strains contributing to the parent female, etc.

This program contains over 4200 Fortran statements arranged in 66 user subroutines and functions and 14 SLAM or FORTRAN subroutines or functions. But this complexity seemed necessary to fully explore the possible complexities of the design of broiler breeding programs for which comparison by experimentation is not likely.

Similar computer simulation programs can be developed for studying breeding program design in other classes of livestock. However, those programs probably need to be expanded to consider alternative crossbreeding schemes such as rotational or rota-terminal systems in contrast to three- or four-way cross terminal systems, especially for modeling alternatives for swine.

EXAMPLE: LABORATORY SPECIES STUDY

Newman, Harris, and Doolittle (1985a, b, c, and d) have used mice as a pilot organism to study the effects of crossbreeding upon a comprehensive bio-economic objective including lifetime reproduction of the parent stock. The bio-economic objective was developed to simulate the appropriate objective for lean pork production from swine. Studying all 27 purebred and crossbred schemes possible from three strains up to and including three-way crosses with alternative reproduction-growth termination alternatives, the most efficient system was found to involve strain P♂ by strain S♀ crossbred females backcrossed to strain P males, with strain P males mated to the reciprocal cross strain S♂ by strain P♀ crossbred females being a close second. Even with appreciable progeny heterosis, the breed differences in favor of strain P relative to a third strain J for male reproduction traits and for leanness led to this backcross surpassing the three-way crosses in efficiency of producing dried lean muscle tissue (protein). Optimum production for the best cross (PxP-S) involved slaughter at 42 days of age with reproduction continuing through eight litters unless a 40-day interval between litters or 10 months of cohabitation occurred first.

Data collection for a study to evaluate alternative early-in-life evaluation systems and selection criteria in each of the three positions in the PxP-S cross is nearing completion with the objective being efficiency of protein production involving lifetime (8 litters) reproduction.

These strains and the information from these studies could provide the basis for a study of the possible interaction between crossbreeding systems and selection procedures within the component strains. In such a study, four alternative systems for producing parent females could be (1) P♂ x S♀, (2) both of the reciprocal crosses, P♂ x S♀ and S♂ x P♀, (3) the products of a rotational crossing system of P and S, and (4) a composite population derived from P and S. For all of these, the terminal cross would be the P♂ on the appropriate female. In addition, a rotational system involving P and S with P being used twice for each use of S, could be evaluated. As appropriate, three selection criteria could be developed and used for improving the strains and composites - (1) a post-weaning criterion involving only growth rate, feed conversion and carcass composition, (2) a maternal criterion involving age at first conception, litter size, preweaning, litter survival, litter weaning weights and rebreeding interval, and (3) a general purpose criteria involving all traits. The appropriate populations and selection criteria seem to be

	Type of Selection			
Population	Randomly Selected Control (C)	General (G)	Maternal (M)	Post-weaning (P)
P	X	X	X	X
S	X	X	X	
P-S composite	X	X	X	

Following selection for an appropriate number of generations, several alternative crossbreeding and selection combinations could be compared. The most interesting combinations seem to be (with subscripts to denote selection procedure)

$P_P \times P_M - S_M$

$P_P \times P_G - S_G$

$P_G \times P_G - S_G$

$P_P \times P_G - S_M$

$P_C \times P_M - S_M$

$P_C \times P_G - S_G$

$P_P \times P_C - S_C$

$P_C \times P_C - S_C$

$(\text{P-S Comp.})_C$

$P_C \times (\text{P-S Comp.})_C$

$P_P \times S_M - P_M$

$P_P \times S_G - P_G$

$P_G \times S_G - P_G$

$P_P \times S_G \rightleftarrows P_G$ rota-terminal

$P_P \times (\text{P-S Comp.})_M$

$P_P \times (\text{P-S Comp.})_G$

$P_P \times (\text{P-S Comp.})_C$

$$\begin{tikzcd} S_G \arrow[r] & P_G \arrow[r] & P_G \arrow[ll, bend left] \end{tikzcd}$$ rotation

Additional combinations might be evaluated, if time and space allow. Contrasts of particular interest in such a study would be

1. selection response in composites relative to those in components strains,
2. merit of potential greater selection response in composites relative to the loss of heterosis in composites,
3. merit of specialized selection for terminal cross relative to generalized selection for composite or rotational systems,
4. relative efficiencies of terminal systems to rota-terminal and to rotational systems following appropriate selection for each.

Even though the above represents a sizable study, it seems feasible in mice but practically impossible to do with replication in swine, although the implications of the results are pertinent to current practices of swine breeding. Although decisions for swine might not be conclusive from a mouse study, the pilot study with mice could narrow the alternatives for final evaluation with swine.

SEARCH FOR LESS DETAILED MODELS

In breeding program design, as with numerous other applications of systems analysis, to fully evaluate the potential complexities of the system, fairly detailed models seem necessary. However, through these studies, there needs to be a search for less detailed ''working'' models that adequately describe the system for decision making. These less detailed models can involve more simple approximations or empirical formulae or deletion of unimportant aspects of the more complex full model. In the context of the present paper, many of the complex issues raised seem to fall into Step 9 - (Compare alternative combined programs). It would be well if, after further study, the first eight steps could be found adequate or appropriately modified to incorporate and accommodate the cited concerns into a systematic approach to the design of animal breeding programs.

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