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ANALYSES OF THE MAMMALIAN CONSUMER SUBMODEL OF ELM: 1973

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ABSTRACT

In order to explore several means of assessing the performance of the Mammalian Consumer Submodel of the Ecosystem model ELM, a series of manipulations was devised and implemented. In addition to a preliminary review of the submodel objectives with respect to those of the ELM model, three biologically verified alternatives and additions to basic functions in the submodel were chosen for study, tailored to fit within the framework of the submodel, and substituted into their respective positions. Responses of four species have been assessed over a two year simulation period with respect to animal weights, reproductive patterns, effects of metabolic changes, and density changes. In addition, the key parameter governing reproduction has been selected for evaluation with respect to the literature. Finally, survivorship curves were constructed to assess changes in population dynamics in response to submodel alteration. Discussion has centered on the biological mechanisms represented within the model which bring about the observed changes.

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CHAPTER I

INTRODUCTION

MODELS - DEFINITIONS AND TYPES

Models may be defined as representations of a system in a simplified form (Goodall, 1972). They may range in type from the static form, which represents only the structure of the system at a given point in time, to the dynamic form, which addresses the processes within the system in addition to its structure. Of these two forms, the latter may have more predictive value by having the capability of varying over time. The familiar box-and-arrow diagram, while considered a dynamic model in that it addresses processes, does not always represent quantitative relationships in time. Therefore, while the diagram itself cannot predict the future state of the system, it does contribute to the understanding of the relationships existent among the system components (Goodall, 1972).

It is the mathematical dynamic model which seeks to represent the processes as they operate within the system. By lending itself to computer simulation, this type of model is capable of dealing with predictions of large systems. As such, it is also capable of quantitative evaluation or validation (Goodall, 1972).

Dynamic models may be framed in a number of contexts, depending on the nature of the system under study, the type of information available about that system, and the result desired from the model. On the one hand, the model may be stochastic, dealing with probabilistic inputs and outputs, while on the other it may be deterministic, a given input always generating identical output (Garratt, 1974).

Models can vary greatly in the detail to which they attempt to reflect the system. This detail, or resolution level, can be increased either by increasing the number of attributes addressed or the number of processes included (Bledsoe, et al., 1969).

Many other designations of model type and design are possible, each dependent on the specific purposes for which it has been constructed.

PURPOSES OF MODELING

We may safely say that all models have as their purpose the "understanding" of the system. For ecosystem models this usually implies some degree of prediction (Goodall, 1972), principally intended to pinpoint specific areas of the system for additional research, or to suggest management decisions and strategies. The precise purpose varies with each individual model and must be clearly stated from the start.

MODEL-TESTING PROCEDURES

No standard procedure exists for evaluating large, complex models such as the ecosystem level model ELM (Anway, et al., 1972). A number of guidelines have been set, however, from which an evaluation approach can be designed which best suits the model in question. According to Forrester (1961):

> "The significance of a model depends on how well it serves its purpose. The significance of models should be judged by the importance of the objectives to which they are addressed and their ability to predict the results of system design changes. The defense of a model rests primarily on the individual defense of each detail of structure and policy, all confirmed when the total behavior of the model system shows the performance characteristics

associated with the real system. The ability of a model to predict the state of the real system at some specific future time is not a sound test of model usefulness."

Thus, a thorough approach to the evaluation of an ecosystem model should include a variety of tests, both quantitative and qualitative, which inspect both internal details and overall performance.

AN APPROACH TO EVALUATION OF COMPLEX ECOSYSTEM MODELS

1.) Review of Objectives

Because the validity of a model depends on how well it serves its purposes (Forrester, 1961), the first step in its assessment should be a review of the original objectives to determine whether they are useful, justifiable, feasible, and whether criteria for model acceptance are stated.

2.) Verification: the evaluation of the internal correctness of the model.

Several different approaches to this problem may be taken. Qualitative testing should include a review of the model design by re-assessing the assumptions, functions, variables, and parameters for their biological "correctness" with respect to literature values.

Statistical tests to compare the model output with observed data not used in the model development represent one means of assessment regarding the precision of overall model performance.

More detailed quantitative testing of the significance and correctness of the functional components can be done by comparing alterations in those components with the corresponding changes in output (Smith, 1970). This process, a form of sensitivity analysis, pinpoints functions or values within the model which are responsive to change. Such information provides knowledge regarding which sections of the model demand the most precise input. In addition, to the extent that the model actually represents the system under study, sensitivity to changes in input should correspond to the sensitivity of the real system. This affords some means of prediction in the form of 'What if" games (Wiens and Innis, 1973). In these games, chosen model components are systematically altered and the corresponding outputs analyzed with respect to the expected "real world" response. Such results may be assessed by either quantitative or qualitative means, depending on the nature of the output.

3.) Validation: the evaluation of output with respect to accepted standards or data not included in model construction.

Numerous statistical tests have been devised which are appropriate for a variety of validation questions. These can vary from the testing of the output values themselves to evaluating the shapes of output traces. Not all components within a model will lend themselves to objective valudation techniques. Some subjective, graphical approaches to this problem have been suggested (Naylor and Finger, 1967 in Garratt, 1974).

Forrester disagrees with the attitude that validation of models can only be treated in quantitative terms, stating that this "hardly seems justified," considering that, although a model may be expressed in quantitative terms, not all the information used in its construction is necessarily received in that form. Thus, the validation of some aspects of the model might justifiably rest as heavily on the subjective judgement of the biologist as on the tests applied by the statistician. Viewed as a whole, the evaluation process for a large model must employ both approaches in order to be considered complete.

CHAPTER II

OBJECTIVES AND PROPOSED INVESTIGATIONS FOR THIS STUDY

OBJECTIVES

The purpose of this study is to explore means of qualitatively assessing the performance of the Mammalian Consumer Submodel with respect to its objectives and those of the total ecosystem model ELM. As such a model is designed and implemented, questions regarding the purposes for which it is being constructed, the logic involved, and the choices of functions and parameters may naturally present themselves. To address some of these questions, methods must be devised for determining the reliability of the internal mechanisms as reflected by change in output associated with submodel alterations.

PROPOSED INVESTIGATIONS

In an effort to survey a variety of qualitative biological approaches to assessing the performance of the submodel, the following investigations were carried out:

1.) Review of Objectives for ELM and Mammalian Consumer Submodel of ELM

2.) Analysis of Threshold Parameter Governing Reproduction
A parameter value has been assigned to determine whether reproduction will occur in the submodel. Applications of this value to biological situations found in the literature should reveal whether such a manipulation is justified.

3.) Substitution of Alternate Growth Function
It is of particular interest to determine the changes in output which accompany the substitution of equally

substantiated alternatives to biological functions included in the original submodel. As such a replacement essentially creates a second submodel based on a new functional relationship, changes in output will similarly be altered. These can be assessed for their biological realism with respect to accepted values. The new output will thus support or refute the accuracy within which the functional mechanisms of the original submodel are operating.

4.) Addition of Functions to Model Effects of Ambient Temperature on Animal Survival

The inclusion of functions modeling additional processes may serve as a means of determining whether the framework already developed in the submodel is adequate. Should such additions be accepted, while yielding biologically interpretable output, the realism of the original canonical framework is supported.

5.) Combined Alterations of Growth Function and Ambient Temperature Effect

Once the results of (3) and (4) are known, a test combining their effects may be run and analyzed by comparison to the individual tests as standards.

6.) Substitution of Alternate Parameter for Calculating Metabolic Weight

As above, the substitution of an alternate, equally acceptable parameter essentially creates another, similar submodel and another point from which output comparisons can be made.

7.) Construction and Evaluation of Survivorship Curves from Output
As a model is constructed, checks against literature reports and field data can be made to validate the results and guide the continuing process. Here, validation through the use of survivorship curves, a standard biological tool, is considered.

Comparisons of the output are based on whether the test output:

1.) Mimics the biological pattern expected
2.) Shows changes which can be explained on the basis of individual species characteristics.
3.) Shows changes in accordance with those expected from the nature of the new functions or parameters included.
4.) Remains within biologically acceptable boundaries determined from literature values.

Specifically, the following submodel responses will be observed:

1.) Pattern of weight gain
2.) Reproductive patterns
3.) Increases in metabolism for the young
4.) Animal densities and survival rates by cohort.

CHAPTER III

REVIEW OF OBJECTIVES FOR ELM AND MAMMALIAN CONSUMER SUBMODEL OF ELM

OBJECTIVES OF ELM

The ELM model developed at the US/IBP Grassland Biome contained as its original objectives the development of a total system model representing grasslands comprised of abiotic, producer, consumer, and decomposer submodels and was designed to be "all encompassing without being all inclusive" (Anway, et al., 1972). The model was intended to represent the various grassland sites within the Biome study. It is to be considered valid provided it can indicate the direction and order of magnitude of ecosystem response to perturbations, as well as the normal dynamics of the system traced as the flow of carbon through the various components.

OBJECTIVES OF THE MAMMALIAN CONSUMER SUBMODEL

In addition to these general objectives, the Mammalian Consumer Submodel has as a major subobjective the development of a canonical, or generalized, formulation simulating the dynamics of mammalian species, both inter- and intraseasonally (Anway, et al., 1972). The term canonical refers to the approach of applying a single functional framework to all mammalian groups, allowing for variation among those groups through species specific input parameters (Courant, et al., 1963).

DISCUSSION

As the objectives for the entire model bear directly on the Mammalian Consumer Submodel, they too, should be addressed here.

The objective of representing the "normal dynamics" of the system lends itself to both statistical analysis (Garratt, 1974) and to qualitative inspection by the biologist. This objective should be satisfactorily met before perturbations are imposed. The ability to "predict the direction and order of magnitude of responses to perturbations" is highly generalized but gives the evaluator some means of establishing the success or failure of overall model performance when stressed. The feasibility of this goal can be tested through application to other comparable sites. In a sense this constitutes a "stress" of the model, as it was originally developed using only Pawnee Site data. Such a goal is indeed a useful one, as it extends the possible utilization of the model beyond its original setting.

As a model which is designed to be "all encompassing without being all inclusive," ELM is based on a framework of generality, implying that results are to be judged, not a minute details, but on the overall characteristics.

An additional objective of the canonical consumer submodel is that of formulating a common functional framework for the grassland mammals. A number of canonical representations have been proposed and widely used in biology (Anway, 1974). Some of the better known ones are the various growth curves and calculations for metabolic weight, all of which can be, and often are, applied across species. Once the submodel is properly designed in accordance with this goal, the specification of parameters for each species is all that is necessary for the determination of its response. Such a goal has the advantages of efficiency, both in minimizing the data needed for including additional species and in saving computer time by minimizing the submodel framework. At the same time it provides the generalized overview of mammalian consumer processes required by the model as a whole.

CONCLUSION

The stated objectives for the ELM model have followed the guidelines set by Forrester (1961). The goals set have been found to be both useful to the Grasslands Biome program and feasible. Criteria have been set for the testing of the resultant model and its output. In addition, the goal of a canonical formulation for the Mammalian Submodel is found to be a feasible, efficient means of dealing with a variety of animals, rendering this objective useful for the submodel, itself, and essential for the ELM model as a whole.

CHAPTER IV

ANALYSIS OF THE THRESHOLD PARAMETER GOVERNING REPRODUCTION

The achievement of a steady state population size implies a balance in those processes governing birth, death, immigration, and emigration. A replacement rate in which each female ultimately replaces herself with one surviving female during her lifetime is necessary for maintaining such a balance (Slobodkin, 1961).

Among various biota numerous reproductive strategies have developed which operate within the framework of environmental change, achieving this end. For instance, among various animal groups such characteristics as fecundity, time and number of breeding seasons, age of sexual maturity, and number of young produced at any one time may vary widely. That species numbers do not change "permanently and strikingly at a much greater rate than existing evidence indicates" shows that, though there is great variation in reproductive patterns, the ultimate result tends toward this balanced reproductive rate (Slobodkin, 1961, pg. 46). Clearly, seeking a canonical representation of these various reproductive strategies is futile; however, the use of other tools supplied within the model seems justified in an effort to achieve the same end, though by different avenues.

Such tools, involving parameters common to all species and available for use in the consumer submodel, are animal age and the corresponding expected weight. These submodel values indicate the general state of health and level of maturity, operating ultimately as a means of maintaining a population steady state.

Thus, these factors have been utilized as an alternative means of representing general, underlying mechanisms, the remaining unique characteristics of any animal group being supplied as species specific input parameters.

As a means of numerically indicating this state of health/level of maturity, an age index was devised for the submodel and related to Brody's (1945) generalized growth curve. In developing this relationship, Brody fit growth data for a variety of plants, as well as animals, to a single curve, forcing them to coincide by adjusting the time axes. A function approximating this curve was developed and used as the basis for much of the framework in the mammalian consumer submodel (Anway, 1972). It is as follows:

$$W = MW(1 - e^{-9\ t/LS}) \tag{1}$$

where: W = Animal weight (kg carbon)

MW = Maximum expected adult weight (kg carbon)

t = Animal age (days)

LS = Expected life span (days)

As defined previously, such a representation is canonical, or generalized in application.

The Age Index represents the maximum expected adult weight attained for a given age and is calculated as:

$$AI = \frac{W}{MW}$$

The relationship between this index and the growth function (Eq. 1) is shown in Fig. 1. The index, in combination with weight considerations is used in controlling several biological mechanisms, two of which are the threshold and rate of reproduction. Should the combined index fall below a chosen value of 0.83, reproduction will not occur. Above this point, reproduction can occur, the reproductive rate being a function of

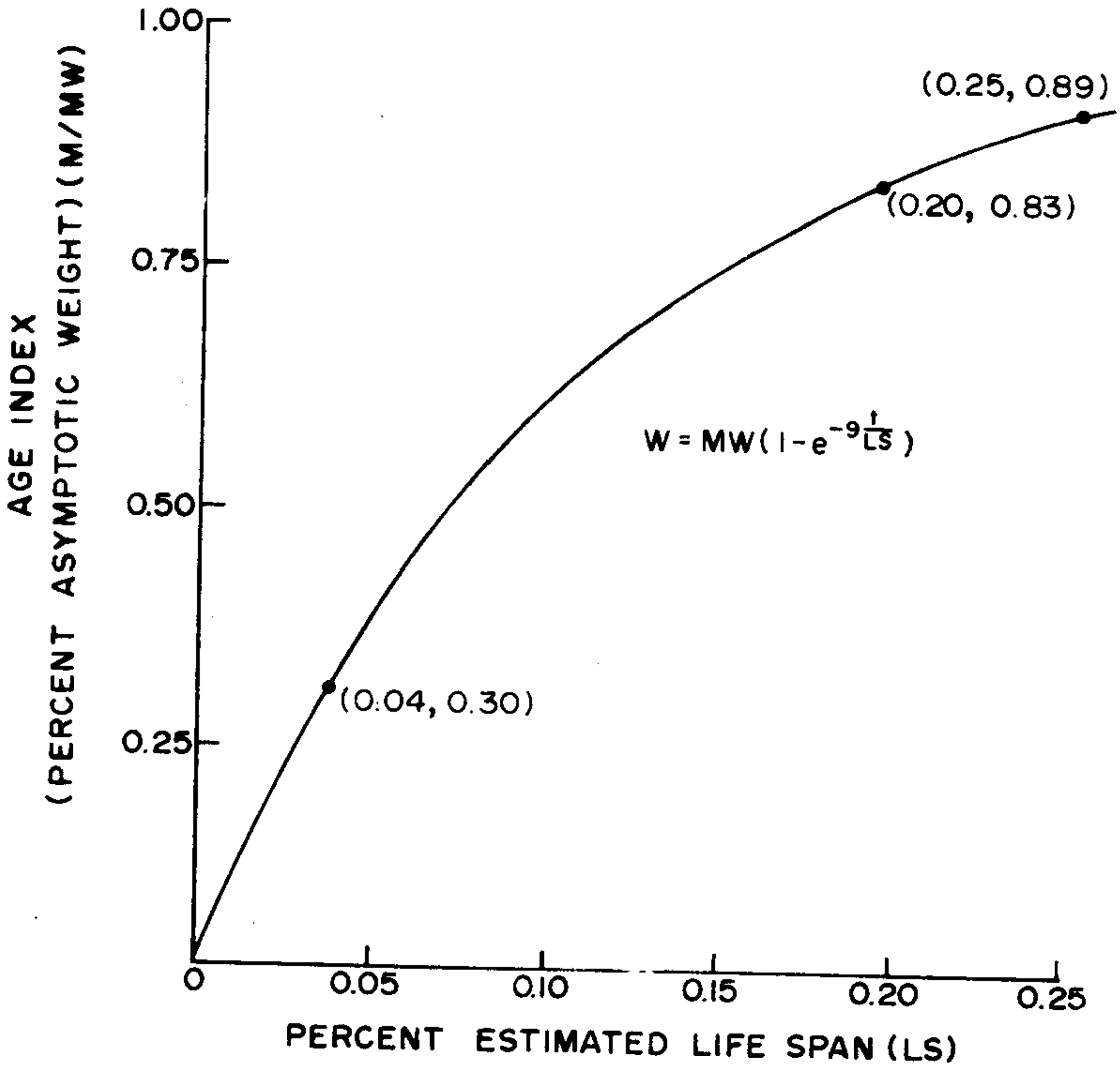

Fig. 1. Relationship Between Brody Approximation and Biological Index.

the combined index value. Thus, this value within the submodel represents a basic reproductive threshold. As it has no single, biological counterpart, it can neither be directly validated nor refuted. It does, however, appear to be a reasonable means of mimicking a natural phenomenon within the limits defined for the submodel, as evidenced by submodel output.

Ricklefs (1967) pointed out that, once growth curves of similar species have been made to correspond (i.e., rendered canonical) through adjustment of the time axes, various aspects of development may be compared across species, growth rate having been removed as a factor. Thus, it seems reasonable to use a calculation based on the generalized growth curve in deriving values for a reproductive threshold for use in the submodel. Indeed, Brody (1945) stated that the inflection point of his generalized growth curve represents the age of puberty. This occurs in the submodel context at 0.04 estimated life span, or a corresponding age index of 0.30 (Fig. 1). Submodel assumptions derived in a similar fashion place the minimum age of successful reproduction at 0.20 estimated life span, or an age index value of 0.83. In addition, the maximum age of first reproduction, assumed at 0.25 estimated life span, identifies an age index value of 0.89. First reproduction in the submodel will then occur at an Age Index value between these two indices.

HYPOTHESIS 1

The relationship between ages of expected first reproduction and the estimated life span as used in the submodel is supported by the literature.

METHOD OF TESTING

In an effort to align this concept more clearly with actual data, literature values for age of puberty, gestation period, and estimated life span were obtained for a number of species. These data were treated in the manner used in the model in an attempt to relate age at first reproduction to total life span. Since ages of puberty and reproduction are more reliably measured, they are utilized as the means of establishing the relationship to life span estimates for comparison with those given in the literature.

It should be realized that within the submodel the threshold for reproduction operates at the time of birth, rather than at mating. Therefore, the age of first reproduction has been estimated for each species (Table 1, Col. 4) as the age of puberty plus gestation period, corrected for season, if necessary.

RESULTS

The following calculations yield the results found in Table 1, Col. 6:

$$\frac{\text{Averaged Life Span Est. (Literature)}}{\text{Age at First Reproduction (Literature)}} = \text{LS Factor}$$

CONCLUSIONS

Hypothesis 1

The hypothesis so stated is rejected. As the variance in the estimated life spans found in the literature are so great, attempts to relate reproductive threshold with life span in this way result in no precise verification for the age equivalent utilized in the submodel (0.20 - 0.25). However, there is support for the theory that some

Table 1. Reproductive Data for Several Mammalian Species.
(Unless indicated, all data are taken from Altman, et al., 1962). Age at first reproduction (4) has been calculated as: Age at sexual maturity (1) and gestation period (3), corrected for breeding season (2) if necessary. From these and literature life span estimates (5), a factor representing age at first reproduction in terms of life span (6) is calculated.

Species	(1) Age at Sexual Maturity	(2) Breeding Season	(3) Gestation Period	(4) Age at First Reproduction	(5) Estimated Life Span From Literature	(6) Calculated Factor: (4)/(5)
Bison (*Bison bison*)	2.5 yrs	June-Sept	10 mo	3.5-4.0 yrs	18 yrs 15 yrs***	0.21-0.24
Moose (*Alces alces*)	1.5-2.5 yrs	Sept-Oct	8 mo	2.5-3.5 yrs	17.5 yrs* 19.0 yrs*	0.14-0.19
Elk (*Cervus canadensis*)	2.5 yrs*	Sept-Oct	8.5 mo	3.0-4.0 yrs	14.0 yrs*	0.21-0.29
Bighorn Sheep (*Ovis canadensis*)	2.5-3.0 yrs	Nov-Dec	6 mo	3.0-4.0 yrs	15.0 yrs* 7.5 yrs***	0.27-0.36
Antelope (*Antilocapridae*)	15-16 mo	Sept-Oct	8 mo	2.0 yrs	8.0 yrs* 14.0 yrs 7.5 yrs***	0.25
Mule deer (*Odocoileus hemionus*)	1.5*	Sept-Oct*	8 mo	2.5 yrs	16.0 yrs* 7.0 yrs**	0.22
White-tailed deer (*Odocoileus virgintanus*)	1.5**	Nov-Feb**	8 mo	2.5 yrs	16.0 yrs* 7.0 yrs** 10.0 yrs***	0.25
Coyote (*Canis latrans*)	2.0-2.5 yrs	Feb-Aug	1 mo	2.0-3.0 yrs	9.0 yrs*	0.22-0.33
Meadow vole (*Microtus pennsylvanicus*)	25 days**	All year	21 days	1.5 mo	2.0 yrs*	0.25
Deer mouse (*Peromyscus maniculatus*)	5-6 wks*	Feb-Nov*	21 days**	2.0 mo	2.0 yrs*	0.33
Snowshoe hare (*Lepus americanus*)	1 yr	Mar-Aug	1 mo	1.0-1.5 yrs	3.0 yrs* 3.0 yrs***	0.33-0.50
Desert Cottontail (*Sylvilagus audoboni*)	Year of Birth	Jan-Aug	1 mo	6.0-12.0 mo	2.0 yrs*	0.25-0.50

*(Burt, W. H. et al., 1964)
**(Leichleitner, R. R., 1969)
***(Palmer, R. S., 1954)

regularity in the timing of developmental processes is found across species in conjunction with a common growth curve (Brody, 1945; Ricklefs, 1967). The translation of these "equivalent ages" to biological indices does not alter this contention. Whether a single value can acceptably represent this stage in development for all mammalian species is open to question, the answer to such a question requiring the successful application of such a value to more species than has been attempted or accomplished to date. Thus, whereas the selected values operate accurately, as defined, for the species included in the submodel it appears from the literature that a broader region along the common growth curve may be more representative of a reproductive threshold when all mammalian species are addressed.

CHAPTER V

SUBSTITUTION OF ALTERNATE GROWTH FUNCTION

Several assumptions on which the submodel is based rest heavily on the submodel approximation to Brody's growth curve (Eq. 1) and utilize this function and the associated biological index in determining key values.

Submodel assumptions utilizing the derived growth function:

1.) Reproductive capability, while a function of age, is also related to the state of health of the animal, these qualities being represented in the submodel by the biological index value which is derived from the Brody growth curve.

2.) The number of young produced is related to parent age and state of health. As such, it too is controlled in the submodel by the biological index value.

3.) Young animals have higher metabolic rates, which increase their food needs. These rates are calculated in the submodel on the basis of the biological index.

4.) Death due to starvation or predation is calculated as a function of weight deviation from that predicted by the growth curve for a given age and is reflected as a biological index value. This value is intended to represent the vulnerability of the animal to these pressures.

The response of the submodel to the substitution of a second, also biologically verified growth representation, will likewise be based on each of these assumptions. Changes in outcome stemming from the substitution of this second function can only be examined through its effect on such relevant output as weight gain or loss, number of young produced, and population trends for each species. To assess the biological appropriateness of the original submodel with respect to this function, then, is to determine whether the altered submodel yields new output which are as expected and biologically reasonable and acceptable.

SELECTION AND PREPARATION OF GROWTH FUNCTION

Several steps are involved in the approach to the above question:

1.) An alternative growth function must be selected which is generally appropriate to mammalian species.

2.) The chosen function must be tailored to suit the particular specifications of the submodel. All components of the function (variables, parameters, constants) must be defined as are those of the submodel framework into which the function must fit.

3.) The substitution of the chosen function as an acceptable alternative must be justified by showing it to be either as good as, or better than the original function, fit to mammalian growth data.

4.) The response of the submodel to the substitution can be reviewed for its biological realism as represented by change or lack or change in output.

Selection of Alternate Growth Function

Selection of a comparable function to represent mammalian growth was done according to the procedure presented by Ricklefs (1967). This method is used for comparing three well-known growth functions: the logistic, and those of Gompertz and Von Bertalanffy.

In this method raw data are replaced by conversion factors which transform growth curves into straight lines whose slopes can be measured graphically and are proportional to the overall growth rate (Ricklefs, 1967). Briefly, this is accomplished by choosing each converted linear function to be a line tangent to a given growth function at its point of inflection. Thus, whereas each growth equation presents weight as a function of time ($W = f(t)$), the converted function ($C = g(W)$) presents the converted factors as a function of weight. This derived function can be chosen, as stated above, such that the function with respect to time ($C = h(t)$) is linear (see Fig. 2). The resultant sets of converted values derived for each of the three growth equations will thus correspond to given percentages of the asymptotic weight attained.

When this method is applied to raw data, the sets of converted values so derived will approximate straight lines defined above as the tangents to their respective growth functions at their points of inflection. As each growth equation describes a slightly different pattern, one of the derived functions will most closely describe a straight line. This can be measured graphically or by regression analysis in order to choose that growth equation most closely fit by the data.

Mammalian growth data for comparison were obtained for rats (Kleiber, et al., 1956), rabbits (Haskell, et al., 1947), goats (Brody, 1938), Jersey and Holstein cattle (Brody, 1945), the intention being to address a wide range of animal weights. When plotted (Fig. 3A), the converted data values for each species present a family of approximately straight lines whose slopes differ in proportion to their differing overall growth rates. Converted values for rats, Holsteins, and Jerseys were found by regression analysis to best fit Von Bertalanffy's equation, while those for rabbits and goats fit Von Bertalanffy's and Gompertz's equations equally well (Table 2). Thus, the Von Bertalanffy equation was selected as the best representative of mammalian growth pattern and,

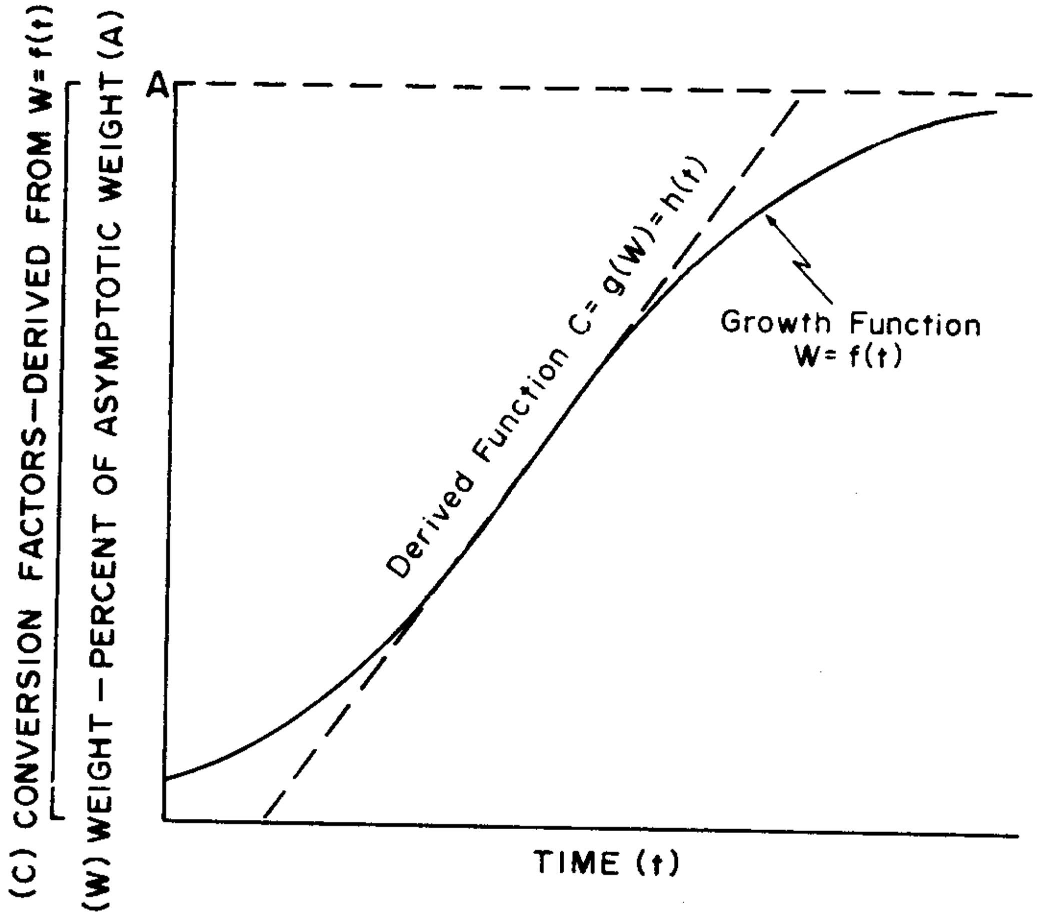

Fig. 2. Graphical Representation of Derivation of Conversion Factors (after Ricklefs, 1967).
Relationship between W (weight) and C converted weights derived by Ricklef's method is indicated. Percent asymptotic weight achieved and conversion factors are given in detail as tables in Ricklefs, 1967.

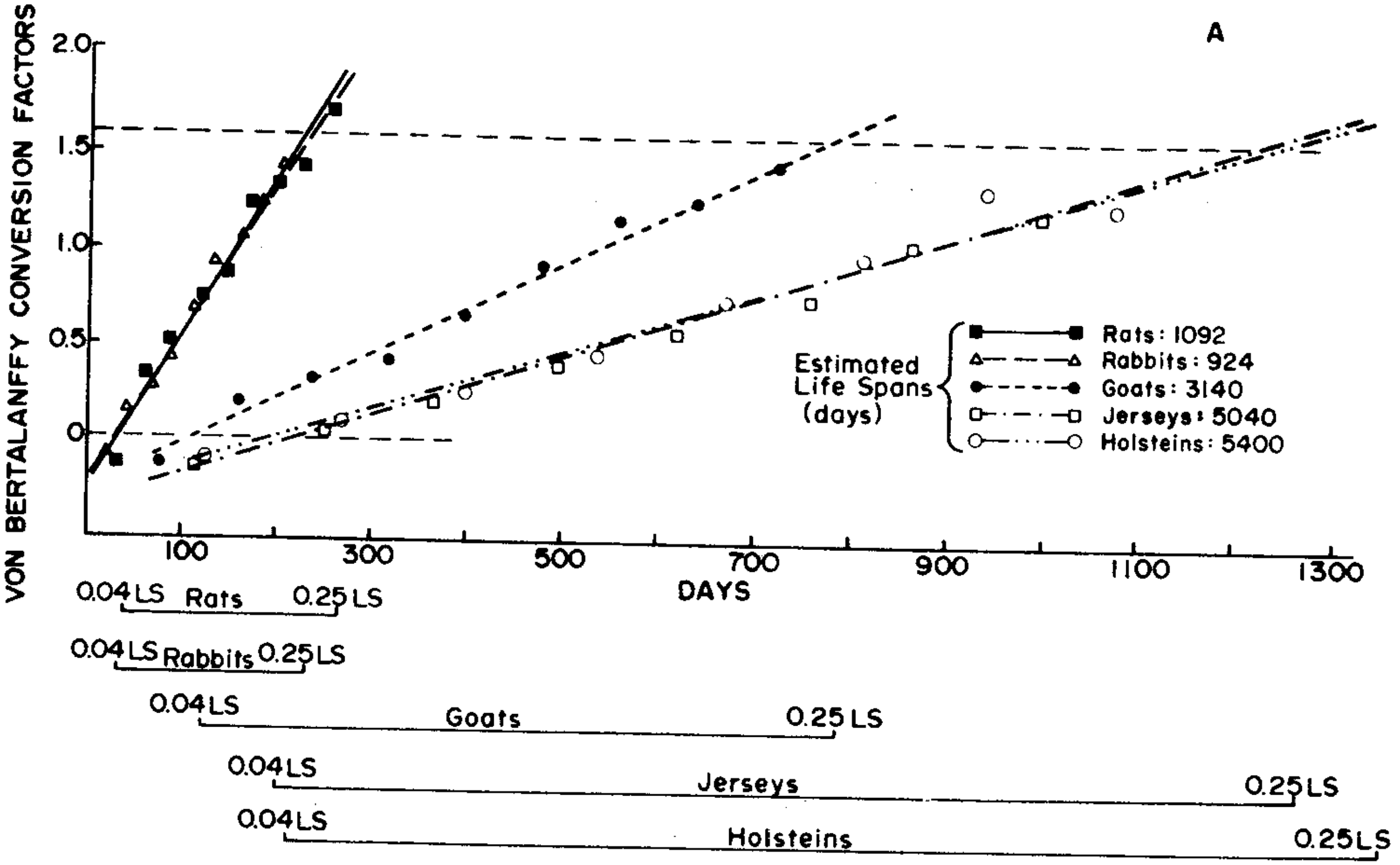

Fig. 3A. Data Converted from Von Bertalanffy Growth Curve Function.
Growth data for the given species have been converted and plotted. The point 0.04 * Life span and 0.25 * Life span are assumed (see text) to represent common stages in development for all mammalian species. As such, they correspond with common conversion factors. Adjustment of the time (x) axis such that these points coincide for all species renders the representation canonical. Thus, a single expression for mammalian growth rate (slope of the common line) is considered appropriate for all species (see Fig. 3B).

Table 2. Selection of Growth Curve Using Ricklefs' Methods.

Species	Growth Curve	Regression Equation Y = weight; X = age	r^2
Rats	Logistic	Y = 2.06X - 0.54	0.86
	Gompertz	Y = 2.22X - 0.35	0.95
	Von Bertalanffy	Y = 2.43X - 0.28	0.97*
Rabbits	Logistic	Y = 1.536X - 0.45	0.98
	Gompertz	Y = 1.785X - 0.34	0.99*
	Von Bertalanffy	Y = 1.996X - 0.30	0.99*
Goats	Logistic	Y = 1.338X - 0.40	0.90
	Gompertz	Y = 1.453X - 0.25	0.93*
	Von Bertalanffy	Y = 1.588X - 0.19	0.93*
Jerseys	Logistic	Y = 1.64X - 0.50	0.70
	Gompertz	Y = 1.74X - 0.39	0.99
	Von Bertalanffy	Y = 1.79X - 0.31	1.00*
Holsteins	Logistic	Y = 1.73X - 0.52	0.97
	Gompertz	Y = 1.82X - 0.37	0.99
	Von Bertalanffy	Y = 1.88X - 0.29	1.00*

* Indicates best fit to straight line, identifying selected equation.

as such, an appropriate candidate for substitution into the submodel for comparative testing.

Von Bertalanffy Equation (Ricklefs, 1967):

$$W = AW\ (1 - \frac{1}{3}e^{-Kt})^3 \qquad (2)$$

where: W = Animal weight (kg carbon)

AW = Average adult weight (kg carbon)

K = 9/4 * slope of plotted conversion factors

t = Animal age (days)

Tailoring the Equation to Submodel Specifications

In order to make comparisons, the time axes for the linear representations can be corrected such that the growth lines for each species are caused to coincide (Fig. 3B). Such a conversion is possible provided each species growth curve is fit by the same quation, as is the case here. Thus, all species are plotted in terms of their equivalent ages, and the percent of asymptotic weights achieved at any "equivalent age" also coincides. This representation is, then, a generalized equation for mammal growth derived from the data for the species mentioned above. As such, the growth representation can be considered canonical, different growth rates for different species no longer being a factor. Other aspects of development can now be considered comparable across species.

In order to substitute this function in the submodel, it must be related to Equation (1) through these common values:

1.) Use of the same life span estimate for each species as modeled. (Input parameter).

2.) Use of 0.25 life span as age of sexual maturity.

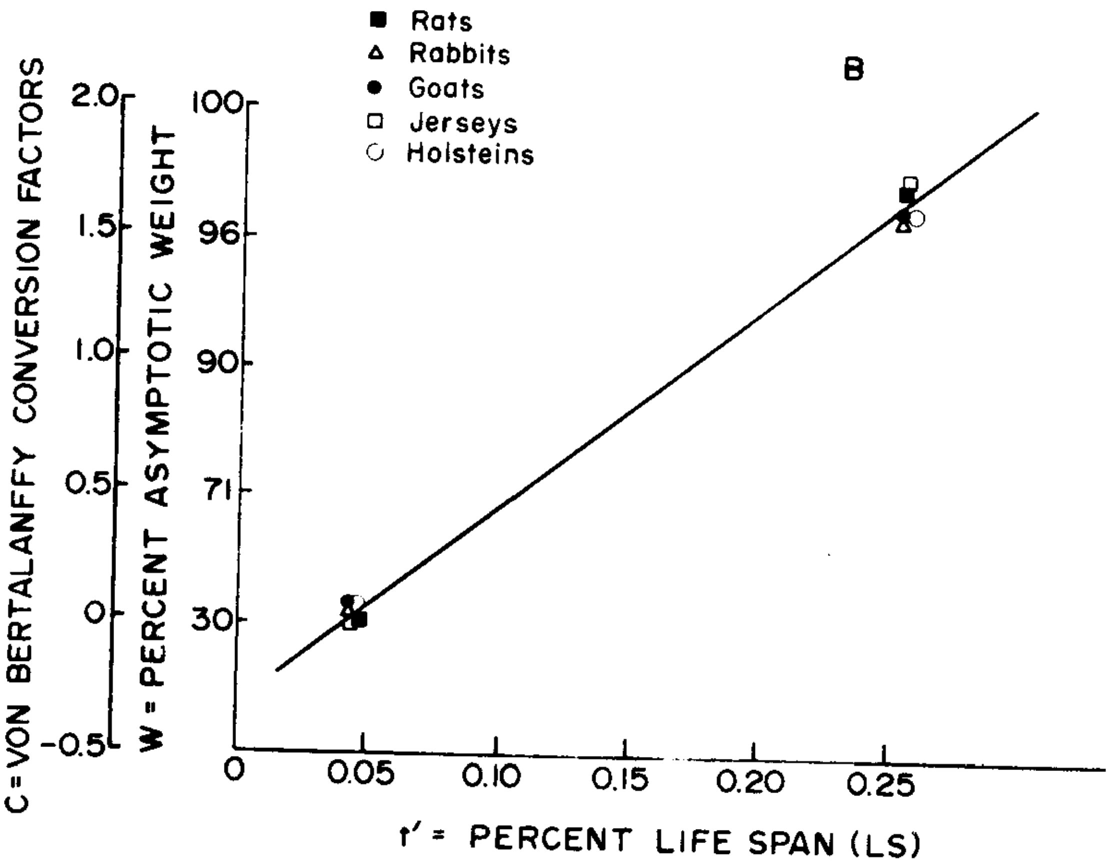

Fig. 3B. Converted Growth Curves Corrected for Growth Rate. For use in Von Bertalanffy's equation, the slope of this line is calculated as:

$$\text{Slope} = \Delta C/\Delta t'$$

$$= \frac{1.6 - 0}{(0.25 - 0.04)\text{LS}}$$

$$= \frac{1.6}{0.21 * \text{LS}}$$

Assuming the second of these to be a developmental stage occurring at the same quivalent age for all species under consideration necessitates the selection of a new age index threshold for reproduction corresponding to this equivalent age. When plotted over the original curve, the Von Bertalanffy curve is shown to identify 0.97 as this equivalent value (Fig. 4). This value of 97% adult weight achieved is also found to correspond to the Von Bertalanffy conversion factor of 1.6 reached by each animal at 0.25 life span in the plot of converted weights (Fig. 3B).

Equation (2) may now be generalized and related to Equation (1) by using the following calculations for K and t:

$$K = 9/4 * \text{slope of plotted conversion factors}$$

$$= 9/4 * \Delta c/(\Delta t * LS)$$

where LS = life span (species-specific input parameter)

$$= 9/4 * \frac{\text{con. factor at } 0.25\ LS - \text{con. factor at } 0.04\ LS}{0.25{*}LS - 0.04{*}LS}$$

$$t = \text{time} - 0.04\ LS$$

Thus, Von Bertalanffy's Equation (2) becomes:

$$W = AW\ (1 - \frac{1}{3}\, e^{-Kt})^3 \qquad (2)$$

$$W = AW \left[1 - \frac{1}{3}\, e^{-(\frac{9}{4})(\frac{1.6}{0.21\ LS})(t - 0.04\ LS)}\right]^3$$

$$W = AW \left[1 - \frac{1}{3}\, e^{-(\frac{14.4}{0.84\ LS})(t - 0.04\ LS)}\right]^3 \qquad (3)$$

This equation represents a generalized form of Von Bertalanffy's Equation (2) and is not appropriate for inclusion in the submodel as a substitute for the Brody approximation (Equation 1).

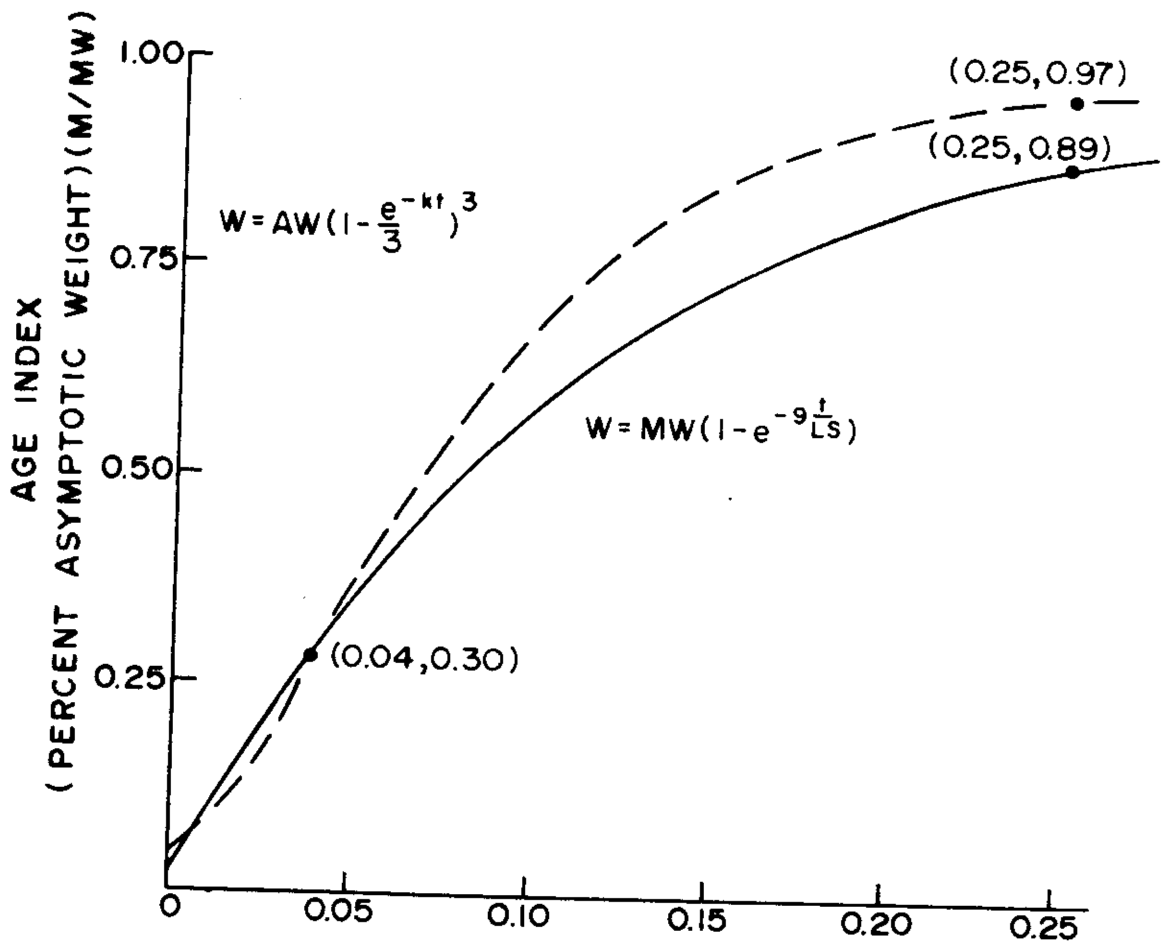

Fig. 4. Comparison of Two Growth Curves to Age Index.

Justification of Equation Against Data

Differences between the assumptions for the two equations regarding the maximum weight to be attained necessitates the adjustment of data values for the purpose of comparison to data. For Equation (1) the asymptote governing weight (MW) is an estimated maximum expected weight and, as such, will be achieved by few, if any, of the populations. Thus, the data values to which this curve is compared must be expressed in relation to this upper limit as the percent maximum weight (Fig. 5-A). Similarly, Equation (3) will be compared with the same data values adjusted with respect to the average expected adult weights (AW) and, as such, will be achieved by most members of the population (Fig. 5-B). Therefore, while each curve must be compared to the same data, the percent of asymptotic values have been scaled to remain within the context of each of the original formulations (Table 3).

Since a test of significance is not possible on such modified data, a sum of squares ratio will be used to compare Equations (1) and (3) with respect to the data. The data being received as averages per species per unit time, the sum of squares of the deviations is represented by:

$$\sum_{sp=1}^{5} \sum_{t=1}^{9} \left[f(t)_{(1),sp} - \bar{x}_{(1),sp,t} \right]^2 \quad \text{for Equation (1)}$$

$$\sum_{sp=1}^{5} \sum_{t=1}^{9} \left[f(t)_{(3),sp} - \bar{x}_{(3),sp,t} \right]^2 \quad \text{for Equation (3)}$$

Comparison of the two representations reveals their relative fits to the scaled data:

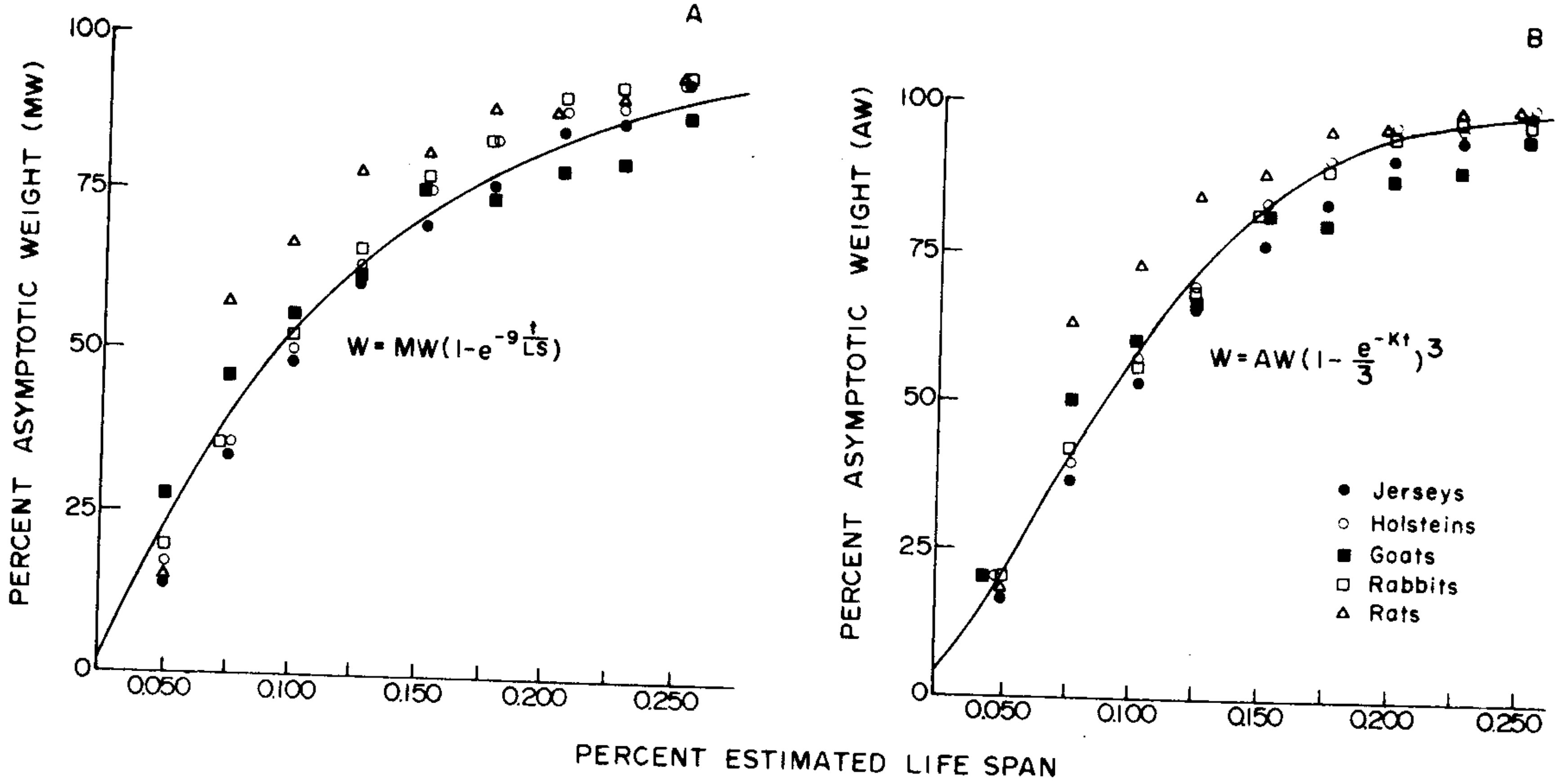

Fig. 5A. Comparison of Brody Approximation to Data.
Data are expressed in terms of maximum expected adult weight (MW).

Fig. 5B. Comparison of Von Bertalanffy Growth Curve to Data.
Data are expressed in terms of average adult weight (AW).

Table 3. Comparison of Calculated Weight Values with Raw Data.

t = % Age at Maturity	t = % Life Span	Brody Growth Curve % Asymptotic Weight (MW) at Time = t (Predicted by Equation (1))					Von Bertalanffy Growth Curve % Asymptotic Weight (AW) at Time = t (Predicted by Equation (3))				
		Rats	Rabbits	Goats	Jerseys	Holsteins	Rats	Rabbits	Goats	Jerseys	Holsteins
0.2	0.050LS	0.37	0.36	0.37	0.38	0.36	0.39	0.37	0.39	0.40	0.38
0.3	0.050LS	0.50	0.49	0.50	0.51	0.49	0.57	0.55	0.57	0.59	0.56
0.4	0.100LS	0.61	0.59	0.60	0.62	0.59	0.71	0.70	0.71	0.73	0.70
0.5	0.125LS	0.69	0.67	0.69	0.70	0.68	0.81	0.80	0.81	0.83	0.72
0.6	0.150LS	0.75	0.74	0.75	0.76	0.74	0.88	0.87	0.88	0.89	0.87
0.7	0.175LS	0.80	0.79	0.80	0.81	0.79	0.92	0.91	0.92	0.93	0.91
0.8	0.200LS	0.84	0.83	0.84	0.85	0.83	0.95	0.94	0.95	0.96	0.94
0.9	0.225LS	0.88	0.87	0.88	0.89	0.87	0.97	0.96	0.97	0.97	0.96
1.0	0.250LS	0.20	0.20	0.21	0.21	0.20	0.19	0.18	0.19	0.19	0.18
		$\bar{x}_2$ (Calculated from Raw Data)					$\bar{x}_3$ (Calculated from Raw Data)				
0.2	0.050LS	0.56	0.35	0.45	0.33	0.35	0.62	0.41	0.49	0.36	0.39
0.3	0.075LS	0.65	0.51	0.54	0.47	0.49	0.72	0.55	0.59	0.52	0.56
0.4	0.100LS	0.76	0.64	0.60	0.59	0.61	0.83	0.67	0.66	0.65	0.68
0.5	0.125LS	0.79	0.75	0.73	0.68	0.73	0.87	0.80	0.80	0.75	0.82
0.6	0.150LS	0.86	0.81	0.71	0.74	0.81	0.94	0.88	0.78	0.82	0.89
0.7	0.175LS	0.86	0.88	0.77	0.83	0.86	0.95	0.93	0.85	0.90	0.95
0.8	0.200LS	0.88	0.89	0.78	0.84	0.86	0.96	0.95	0.86	0.93	0.94
0.9	0.225LS	0.90	0.90	0.85	0.89	0.89	0.98	0.96	0.93	0.97	0.98
1.0	0.250LS	0.16	0.20	0.27	0.16	0.17	0.18	0.20	0.20	0.16	0.20

$$\frac{\sum_{sp=1}^{5}\sum_{t=1}^{9}\left[f(t)_{(1),sp} - \bar{x}_{(1),sp,t}\right]^2}{\sum_{sp=1}^{5}\sum_{t=1}^{9}\left[f(t)_{(3),sp} - \bar{x}_{(3),sp,t}\right]^2} \tag{4}$$

for: $\frac{SS_1}{SS_3} > 1$: Equation (3) provides the better fit

$\frac{SS_1}{SS_3} = 1$: Both fit equally well

$\frac{SS_1}{SS_3} < 1$: Equation (1) provides the better fit

For use in the model, Equation (3) should fit the data as well as, or better than, the original Equation (1). This will insure that according to the literature, the second submodel so formed is operating on at least as biologically acceptable a growth function.

Calculating Equation (4) from the data (Table 3) yields the following results:

$$\frac{SS_1}{SS_3} = \frac{0.1936}{0.1796} = 1.08$$

This result shows little (8%) difference between the two equations with respect to the data. Equation (3) is, therefore, acceptable as a substitute for Equation (1) and, as such, should alter the submodel structure in a biologically acceptable way.

HYPOTHESIS 2

Animal weight, as predicted by a biologically acceptable growth function, operates within the submodel to calculate the biological index, which then predicts "health status" and "maturity level" as used in Assumptions 1-4.

METHOD OF TESTING

The results of substituting the second growth function (Equation 3) will be compared to the control output (using Equation 1) on the basis of:

1.) Pattern of weight gain

2.) Reproductive patterns

3.) Calculated increase in metabolism for the young

4.) Animal densities

RESULTS

Pattern of Weight Gain

The early pattern of weight gain is shown (Fig. 6 through 9) to follow the general pattern of the Von Bertalanffy curve as compared with the Brody representation (see also Fig. 4). The young of each species are found to be consistently heavier at birth (compare Tables 1 and 3 in Appendix), show slower initial growth, exhibit a more rapid spurt when approaching adulthood, and achieve a higher final adult weight. This final weight is dictated by the growth curve asymptote and, thus, is within a defined, biologically acceptable range.

Eventually the curves tend to converge, as expected, the Brody growth curve tending toward the asymptote which represents the average adult weight for the alternative equation. This is most readily seen in the graphs for deer mice (Fig. 6-B, D) since a relatively short life span allows several groups to be followed throughout life. Once adult status is attained, all species demonstrate a regular drop in body weight as birth occurs, this drop being greater in the test case than in the control. This result is a reasonable finding, birth weight being greater in all cases. Recovery time for the parents is the same for both functions.

Reproductive Patterns

As animals in the test run tend to reach their reproductive thresholds earlier, births may potentially occur early enough to result in the appearance of additional generations. This is seen to occur in deer mice (Fig. 6-E, G, H, I) and in sheep (Fig. 9-F). Such results are within the range of biological reality, mice being capable of reproducing at minimum 23 day intervals in the breeding season, (Asdell, 1946) while sheep have the capability of reproducing the next spring following birth (Ensminger, 1970).

Theoretically, in the model representation, increased births could occur for all species; however, species-specific parameters limiting the numbers of reproductions per year and relating reproduction to environmental conditions have the ultimate control over this result. That the numbers of reproductions for coyotes remains at one verifies the operation of these limiting parameters for this species. As jackrabbits are potentially allowed three reproductions per season in the submodel, the environmental control parameter is operating to hold the number or reproductions at two per season (Fig. 7-C, E, F). Thus, the value of this parameter could be questioned.

Metabolic Increase for the Young

The rate of decline in animal densities for the newborn is shown (Fig. 10-C) to be slightly less pronounced at first, representing a small survival advantage for the very young associated with the test function. (Further discussion of survivorship appears in Chapter IX).

This is attributed to the calculation of a lower expected weight, and consequently, a reduced maintenance demand to achieve that weight. This is as predicted by Equation (3). Afterwards, the rate of decline follows the general pattern set by the control, although there is a slight increase in rate over the entire test period. This is attributed to a disadvantage imposed by a greater expected weight standard.

Animal Densities

When parent weights are elevated, the number of young produced, being a function of parent biological index, is similarly increased, the limit on this number being controlled by a species specific input parameter. As the total number of young produced is a function of parent numbers, as well as their biological indices, the densities observed in Fig. 10-C, E, F reflect the submodel response to these combined effects. In jackrabbits new groups of individuals are observed to be more numerous in association with higher parent weight in addition to higher parent numbers. In the second year, young produced by the original parent group are less numerous than the first offspring of the younger, relatively heavier populations.

In coyotes (Fig. 11) the drop in parent density at the time of birth appears to be abnormally abrupt in the control run (see Chapter IX for survival curves). Correspondingly, there is an increase in the death rate for their offspring as well, the young being dependent on their parents for food. In the test run, a similar, although slightly exaggerated pattern for deaths is seen as a result of the different weight standard. Thus, the density pattern for coyotes is following the general pattern set by rabbits of a diminished early decline; however, in the second year (Fig. 11-D) this pattern is masked by the excessive parental death rate, resulting in a greater decline for the young than would otherwise be expected. At other points in time, coyote density tends to decline at a steady rate. Therefore, the parameters used in calculating coyote death might be questioned; however, the relative performances of the two submodel runs appear to be similar, thus supporting the underlying functional framework.

In cases where parent density is reduced sufficiently, the numbers of offspring are low enough to result in the early disappearance of all members of that group (Fig. 7-E, 10-E). Therefore, while in all cases the net result of changing the weight standard appears to be a population increase, the population structure appears to be changing in favor of the young and their earlier offspring. These are reasonable results stemming from the altered weight standards imposed, which grant a slight survival advantage at the outset to the very young and a slight disadvantage thereafter.

CONCLUSIONS

Hypothesis 2

Animal weight, as predicted by a biologically acceptable growth function, operates within the submodel to calculate the biological index, which then predicts "health status" and "maturity level" as used in Assumption 1-4.

The hypothesis is accepted, as the alternative growth function, operating through the devised biological index has been found to model:

1.) reasonable patterns of weight gain and loss,

2.) expected changes in timing and success of reproduction, both generally and in specific cases, 3.) appropriate increases in numbers of young produced, and

4.) realistic changes in survival patterns for all ages.

The abnormal death rate for parent coyotes discussed above appears to be designed into the original submodel. As variations in densities associated with the test function follow expected changes upon this basic pattern, the parameters involved are open to question; however, the submodel framework is supported.

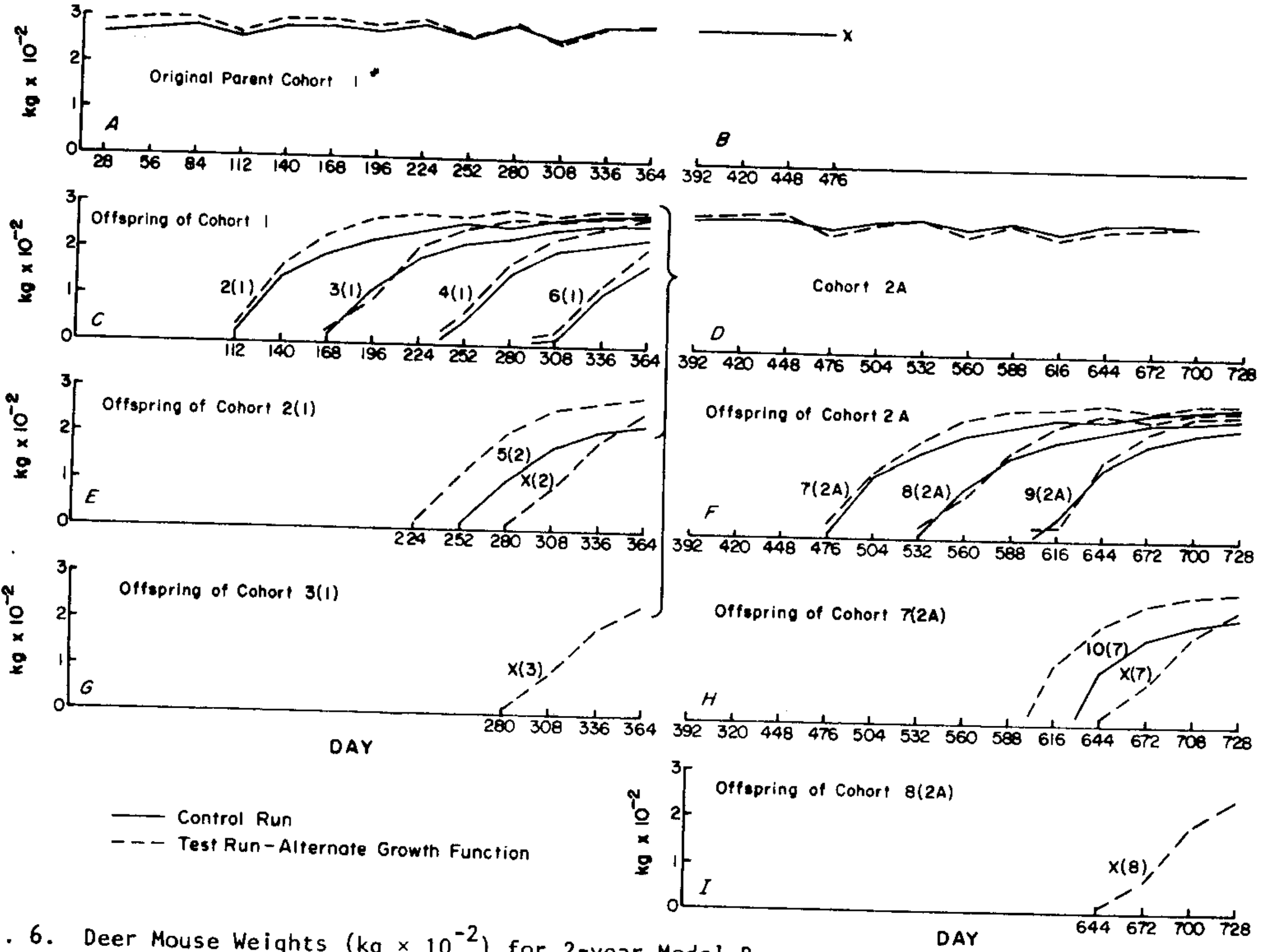

Fig. 6. Deer Mouse Weights (kg × 10^{-2}) for 2-year Model Run. The * indicates that each group is identified by a cohort number followed by the identification number for its parent group.

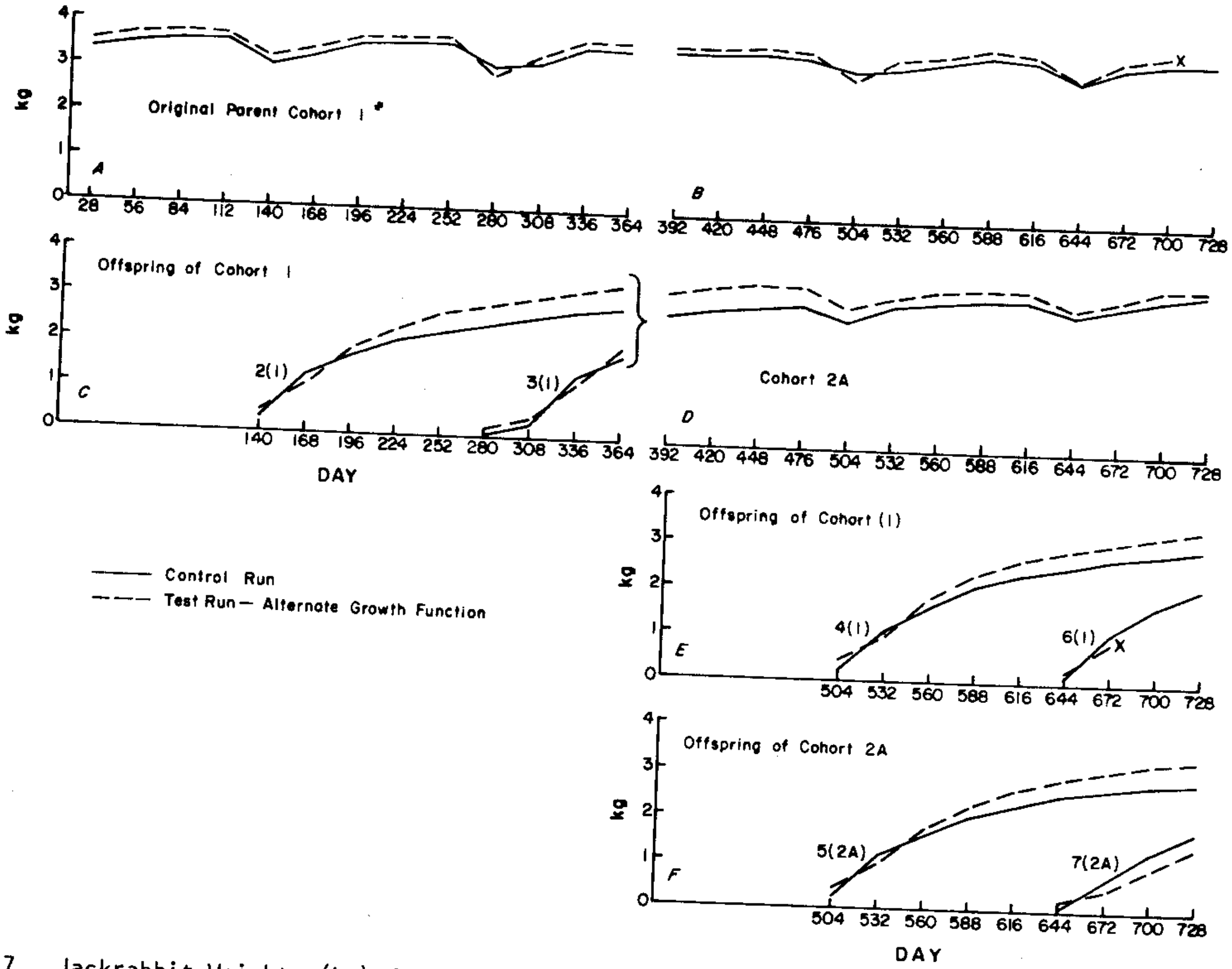

Fig. 7. Jackrabbit Weights (kg) for 2-year Model Run. See Fig. 6 for *.

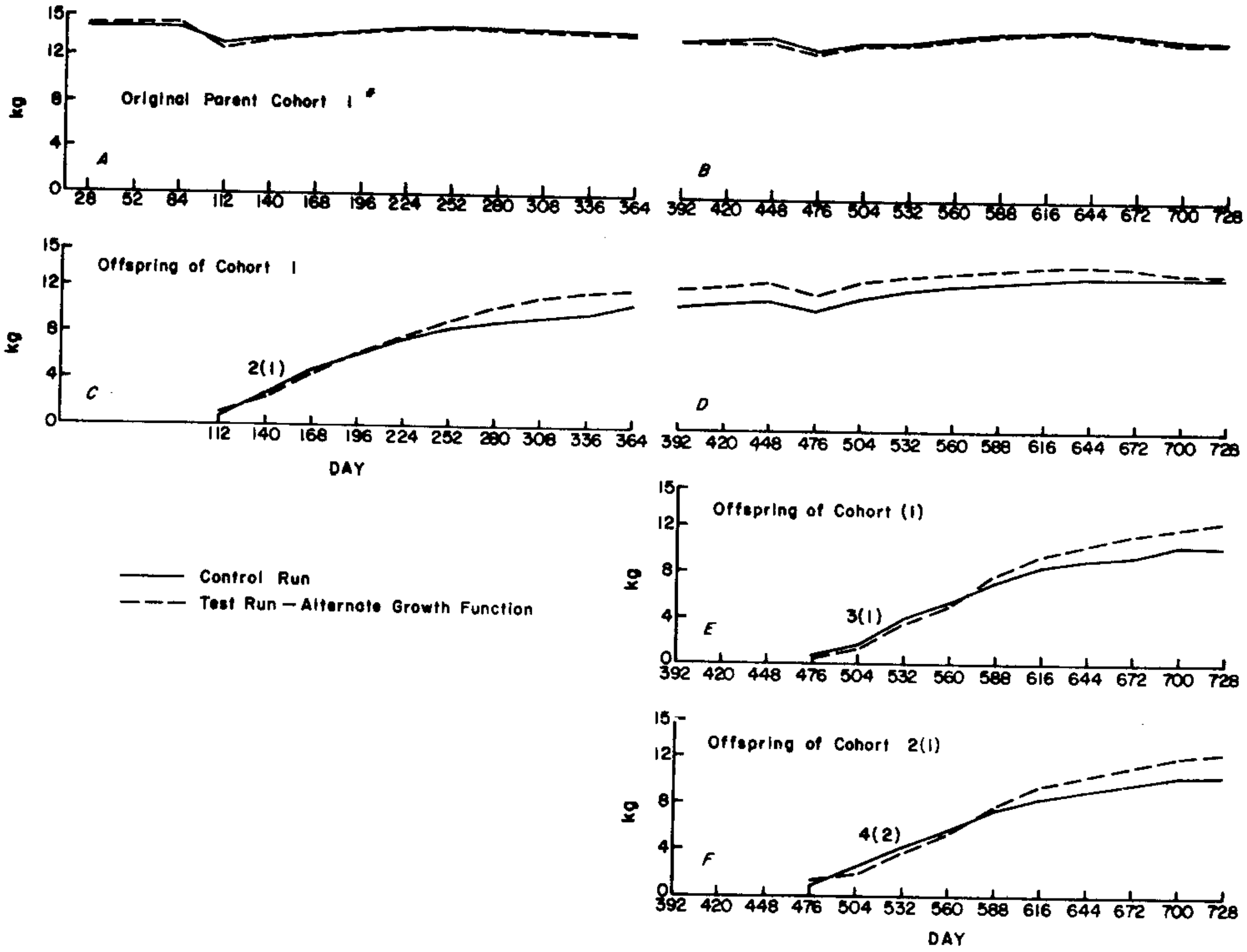

Fig. 8. Coyote Weights (kg) for 2-year Model Run. See Fig. 6 for *.

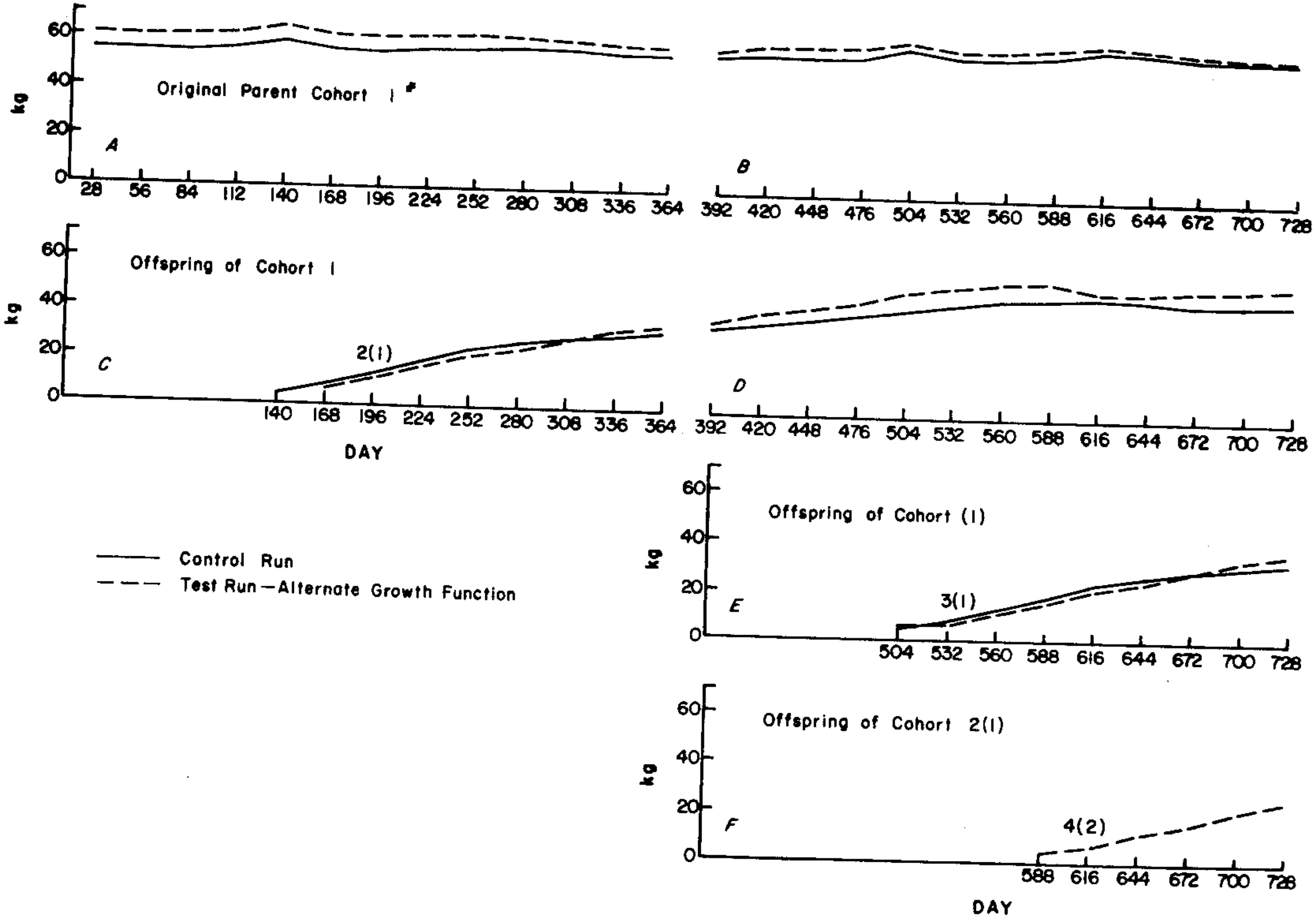

Fig. 9. Sheep Weights (kg) for 2-year Model Run. See Fig. 6 for *.

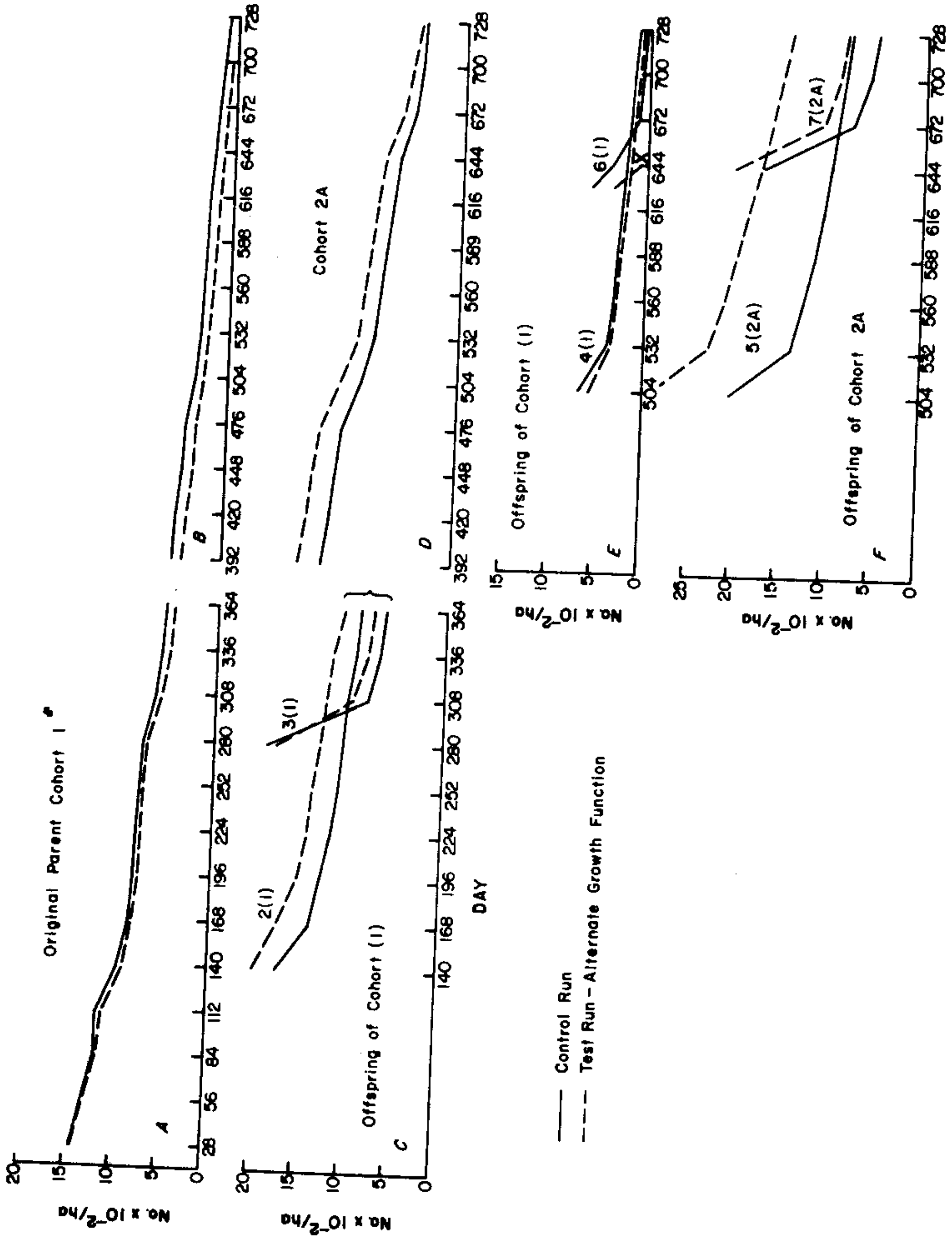

Fig. 10. Jackrabbit Densities (no. × 10^{-2}/ha) for 2-year Model Run. See Fig. 6 for *.

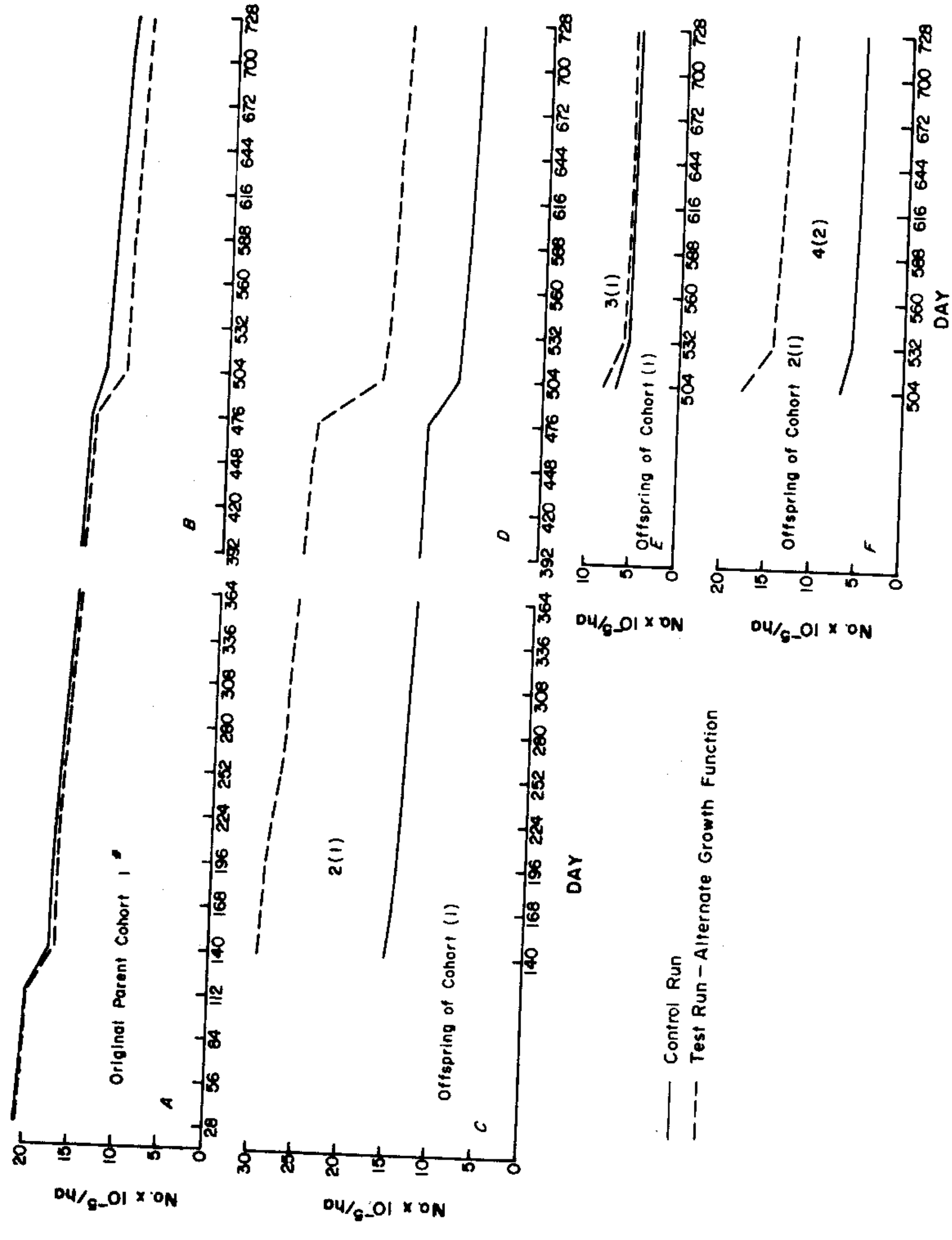

Fig. 11. Coyote Densities (no. × 10^{-5}/ha) for 2-year Model Run. See Fig. 6 for *.

CHAPTER VI

ADDITION OF FUNCTIONS TO MODEL EFFECTS OF AMBIENT TEMPERATURE ON ANIMAL SURVIVAL

To effectively meet the stated objective of representing the inter-seasonal dynamics of grassland mammals, consideration must be given to the effect of changes in ambient temperature on animal survival. In the present submodel, temperature reduction is compensated through increases in food demand in order to increase heat production. In its present form the submodel utilizes a single temperature threshold of 13°C to initiate this increased energy demand which is assumed to be uniform for all mammalian species. It has been demonstrated (Blaxter, 1967; Kleiber, 1961) that such things as body heat production, body surface area, and insulation capabilities, operate to produce differences in energy demand at reduced ambient temperatures. Such increases are also dependent on other variables more difficult to quantify. Of these, species behavior, such as the limitation of activity and microclimate selection, and physiological mechanisms such as vasoconstriction, are extremely influential in conserving heat. Since the processing of food in itself, produces heat and can provide some of the needed body warmth, the energy demand of the animal is further altered as feeding occurs. This in turn alters the food need that might be projected prior to feeding and imposes difficulties in modeling this phenomenon, since a single formulation is sought as a means of predicting increased food need.

It was decided that the varying effects of ambient temperature on the modeled species could be better represented by utilizing body weight, which is calculated in the submodel as the critical variable. Thus, this value will be used in determining the effect of ambient temperature on different sized members of each species.

That ambient temperature at which an animal must produce additional heat in order to maintain its normal body temperature is known as its lower critical temperature (Blaxter, 1967). Although there is some evidence that an increase in food intake is stimulated as the ambient temperature reaches this threshold, it has not been found to increase to the point of weight gain, or even necessarily to that of basic maintenance (D. E. Johnson, pers. comm.). It is probable, however, that with lowered temperatures sustained over an extended period of time, intake will be consistently increased such that an optimum weight can again be achieved. Should the animal be unable over time to reach this level, death will occur.

In an attempt to devise an approach for determing an acceptable critical temperature and ultimately the increase in food intake brought about by this threshold, the following equation is used (Blaxter, 1967):

$$T_c = T_b - \overbrace{\left(\frac{HP - HW - HE}{A}\right)}^{a} * \frac{1}{K} \qquad (5)$$

where: T_c = Critical ambient temperature (°C)

T_b = Body temperature (°C)

HP = Heat produced (kcal/day)

HW = Heat needed to warm food (kcal/day)

HE = Evaporative heat loss (kcal/day)

A = Body surface area (m^2)

1/K = Insulation (°C)(m^2)$(kcal)^{-1}$(day)

It is readily apparent that any increase in section (a) in this equation will lower the critical temperature and thus lower the energy requirements of the animal.

The value for heat production (HP) is taken to be $2(70W^{3/4})$, or the basic maintenance need of the fed animal (D. E. Johnson, pers. comm.). As energy calculations for the fed animal project needs lower than that of the fasting animal they should afford the better estimate of his situation over the ensuing day (Kleiber, 1961). For animals spending a substantial amount of time in the open, it is apparent that the smaller members of the species will be at a disadvantage at reduced ambient temperatures (Severinghaus, et al., 1969; Einarsen, 1969). Because their heat production:surface area ratio is lower, an increased rate of heat loss results and a need for additional heat replenishment is imposed. On the other hand, those species which avoid temperature stress by retreating into dens do not experience this disadvantage to the same degree.

By considering all mammalian species to have the same critical temperatures the present model does not consider differences in response to reduced ambient temperatures brought about by differences in body size.

METHOD

In an attempt to represent these biological responses more realistically, the following functions, patterned after Blaxter's formulation (Eq. 5) are introduced into the model:

$$T_c = 39°C - \left(\frac{140W^{3/4}}{0.1W^{2/3}} - 300\right) * 0.049 \qquad (6)$$

where: T_c = Critical ambient temperature (°C)

$0.1W^{2/3}$ = Body surface area (m^2) (Brody, 1945)

$2(70W^{3/4})$ = Basic maintenance need $(kcal)(day)^{-1}$ (D. E. Johnson)

300 = Evaporative heat loss $(kcal)(m^2)^{-1}(day)^{-1}$ (Blaxter, 1967)

0.049 = Insulation factor $(°C)(kcal)^{-1}(m^2)(day)$ (Blaxter, 1967)

The value HW has been deleted from Equation 6 for the following reasons:

1.) Nursing young will have no heat penalty to pay for the warming of food.

2.) Warming of food for foraging animals is minimal for dry feed (Blaxter, 1967). As this is the expected case for the adult diet at these ambient temperatures, the value is not included.

Calculation of the interactive effects of this derived critical temperature with a given ambient temperature (Fig. 12) is as follows:

$$\frac{HP - MM}{T_a - T_c} = HS$$

where: HP = Heat produced $(kcal)(m^2)^{-1}(day)^{-1}$

MM = Maintenance metabolism $(kcal)(m^2)^{-1}(day)^{-1}$

HS = Sensible heat loss $(kcal)(m^2)^{-1}(day)^{-1}(°C)^{-1}$

T_a = Ambient temperature (°C)

T_c = Critical ambient temperature (°C)

Thus:

$$HP = HS(T_a - T_c) + MM \qquad (7)$$

Finally, a heat factor is derived which is a multiple of the heat production needed under unstressed conditions (see Fig. 12). This factor

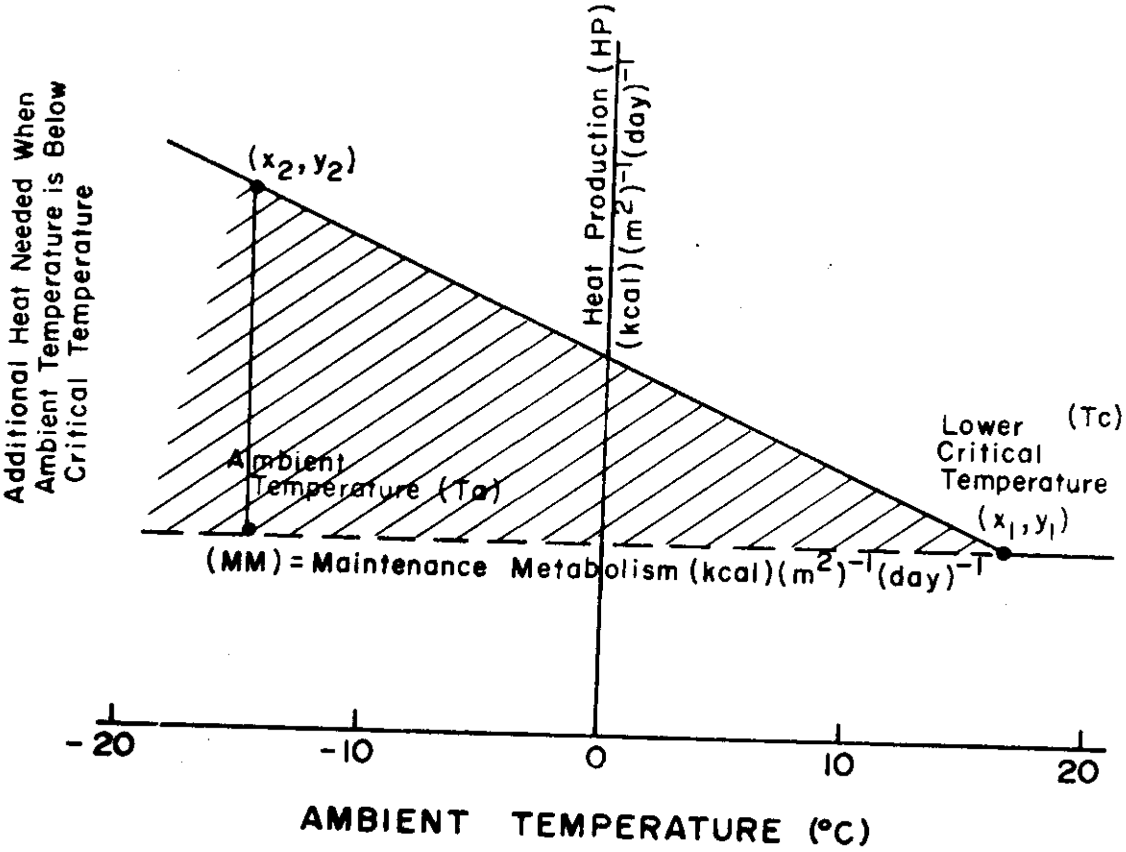

Fig. 12. Calculation of Heat Factor

where: $HP = HS(T_a - T_c) + MM$

Heat factor = HP/MM

$1 \leq \text{heat factor} \leq 2$

This factor is used to calculate additional heat needed in meeting metabolic demands at ambient temperatures below the animals calculated critical temperature.

is assumed to range from 1 (no effect) to an upper limit of 2 (double the heat production when no stress is applied, D. E. Johnson, pers. comm.)

$$\text{Heat factor} = HP/MM \tag{8}$$

$$1 \leq \text{Heat factor} \leq 2$$

Summarizing: The inclusion in the submodel of Equation (6) will result in the calculation of the critical ambient temperature for a given animal weight. Equation (7) will then determine the necessary heat for maintenance at the given ambient temperature. Finally, Equation (8) compares the heat production needed at the given temperature with the basic maintenance metabolism for the animal under consideration, producing a factor for increasing maintenance metabolism up to double that of the normal value.

In order to better represent those animals which remain in the open, and thus experience the more distinct differentiation of response associated with reduced temperatures, the value of W (weight) for each cohort will be used. For those animals which are expected to seek shelter, the average weight for the species will be used as W. In the submodel test, this treatment was applied to deer mice only.

HYPOTHESIS 3

The addition of size specific responses to reduced ambient temperatures will produce results which penalize the smaller members of each species and favor the larger members in the submodel.

METHOD OF TESTING

The results of adding the temperature functions (Equations 6-8) will be compared to the control output on the basis of:

1.) Pattern of weight gain
2.) Reproductive patterns
3.) Calculated increase in metabolism for the young
4.) Animal densities

RESULTS

Pattern of Weight Gain

The pattern of growth produced by the test run adheres closely to that of the control run, as the Brody approximation (Eq. 1) is once again operating (Fig. 13 through 16). However, for all species the early weights are shown to be slightly lower; this effect extending to adulthood, where weights tend to remain slightly under those expected. This response results from the altered metabolic demand placed on the animals, particularly the younger smaller members of the species by the stress at reduced temperatures. This makes it more difficult for them to attain their expected weights.

Among the other features affected by this change, the drop in parental weight which accompanies birth of the young still occurs (Fig. 14-A, B). However, recovery time in the test case is longer. This points out again that reduced weight is operating to produce a disadvantage through increased energy demand as proposed. Thus, a sudden drop in weight below that expected from Equation 1 penalizes the parent more severely than in the control run.

Reproductive Pattern

Births for all species are delayed (Fig. 13-C; 14-E; 15-C, E, F; 16-C, E), parent weight and the resultant biological index being lowered. This delay in reproductions results in the production of one less generation in the case of deer mice (Fig. 13-C). Corresponding delays for other species are apparently not sufficient to affect numbers of offspring.

Metabolic Increase for the Young

The increased metabolic demand imposed on the young by the test functions, operating with the higher metabolic demands calculated for them by the biological index, provides a disadvantage which decreases animal densities (Fig. 17, 18). Here a rapid decline in density of the young of all species is seen.

Animal Densities

While initial densities diminish quickly for all species, the remaining pattern generally follows that of the control run (Fig. 17-C, D, E, F; 18-C, E, F). Throughout adulthood, however, the rate of decline is slightly less, an apparent advantage being extended to heavier members of the species. This is seen in the tendency of the original parent population to decline at a slower rate in the test case, resulting in greater numbers of young born to this group (Compare Fig. 17-B, E; 17-D, F). However, the disadvantages imposed by the temperature functions override this initial effect quickly, resulting in an overall decline in animal numbers for the entire population of each species. As in the previous test, coyotes are demonstrated to have an exaggerated early death rate, this now being a result of both the elevated parental death rate mentioned before (Chapter V) and the added effects of the temperature functions (Fig. 18). In all cases, the net result of changing animal responses to reduced temperatures appears to be a decrease in the density of younger individuals accompanied by a longer retention of older members in the population.

CONCLUSIONS

Hypothesis 3

The addition of size specific responses to reduced ambient temperature will produce results which penalize the smaller members of each species and favor the larger members in the submodel.

The hypothesis is accepted, as the test functions do effectively differentiate between the population members according to weight, resulting in a disadvantage to the smaller, younger members of each species.

It is contended that such functions should be included in the submodel to represent the proper interseasonal dynamics of all species. To impose a single effect equally upon all members of all species is to ignore the known differences in vulnerability to temperature change attributed to different animal size (Blaxter, 1967; Einarsen 1969; Kleiber, 1961; Severinghaus, et al. 1969). Since the tools to address this effect are present or calculated within the existing submodel, it appears that an inclusion of this sort is needed.

The submodel accepts this additional complexity and provides output in keeping with that expected by the nature of the new functions. This supports the general framework and the operation of the original functional relationships.

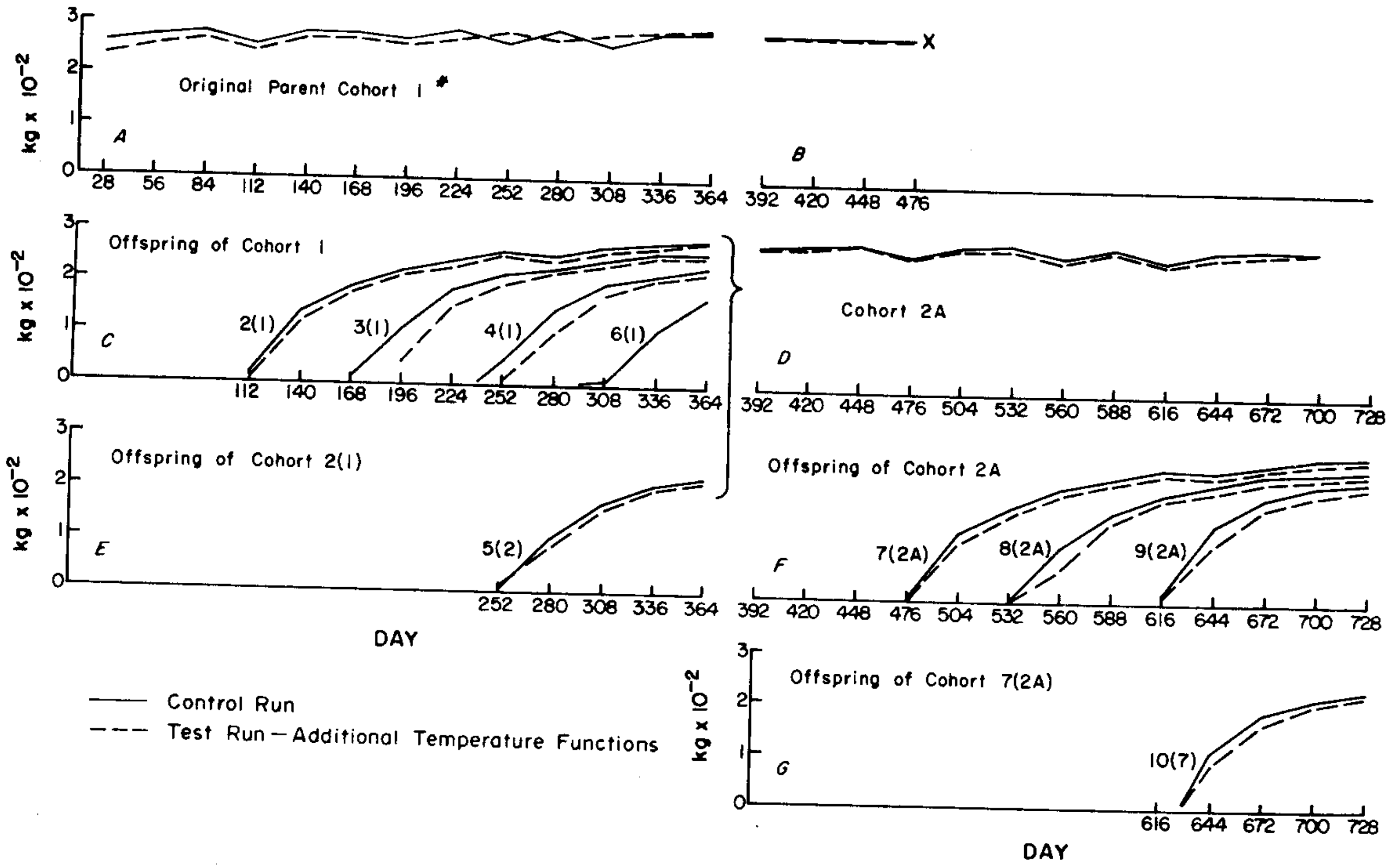

Fig. 13. Deer Mouse Weights (kg × 10^{-2}) for 2-year Model Run. See Fig. 6 for *.

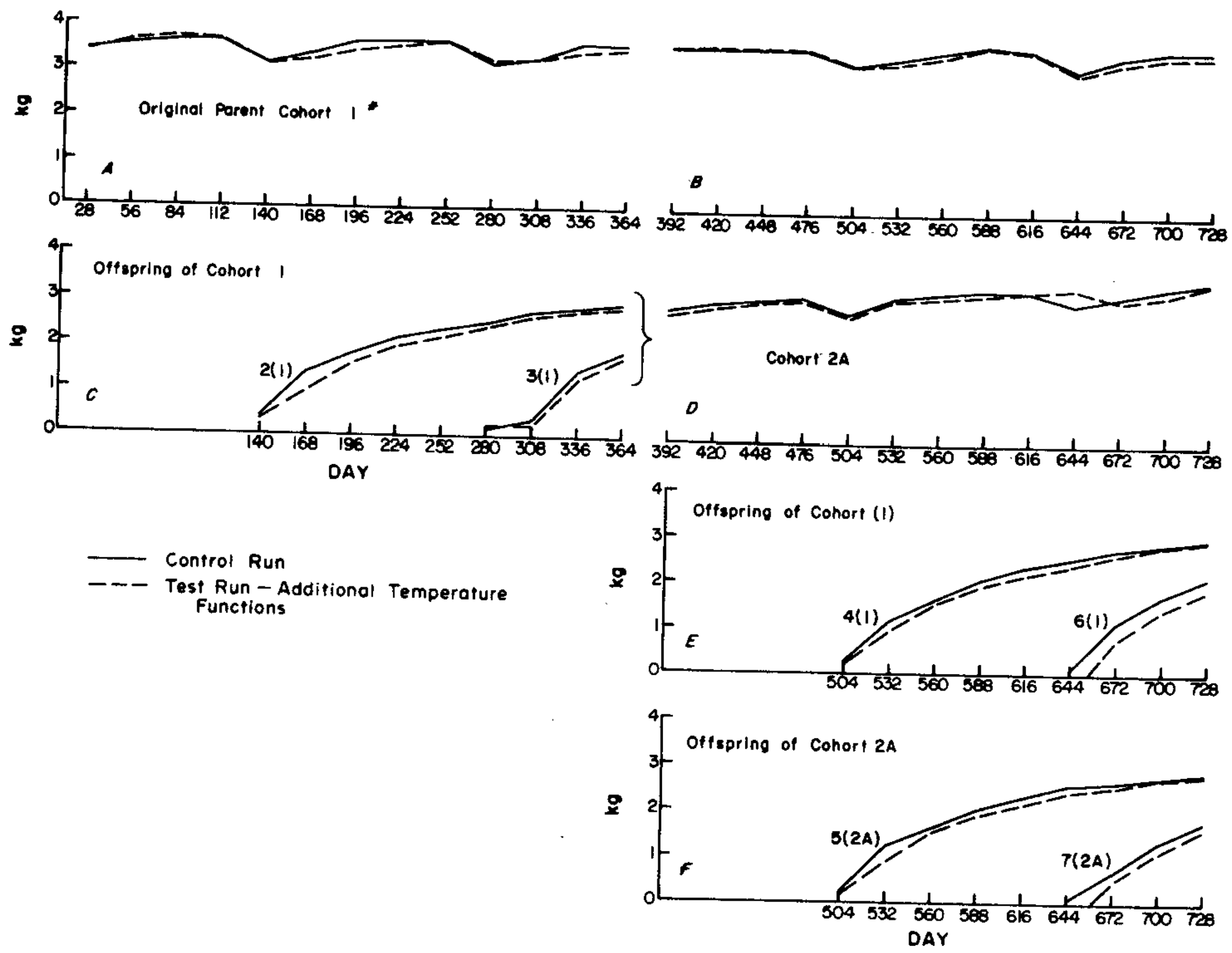

Fig. 14. Jackrabbit Weights (kg) for 2-year Model Run. See Fig. 6 for *.

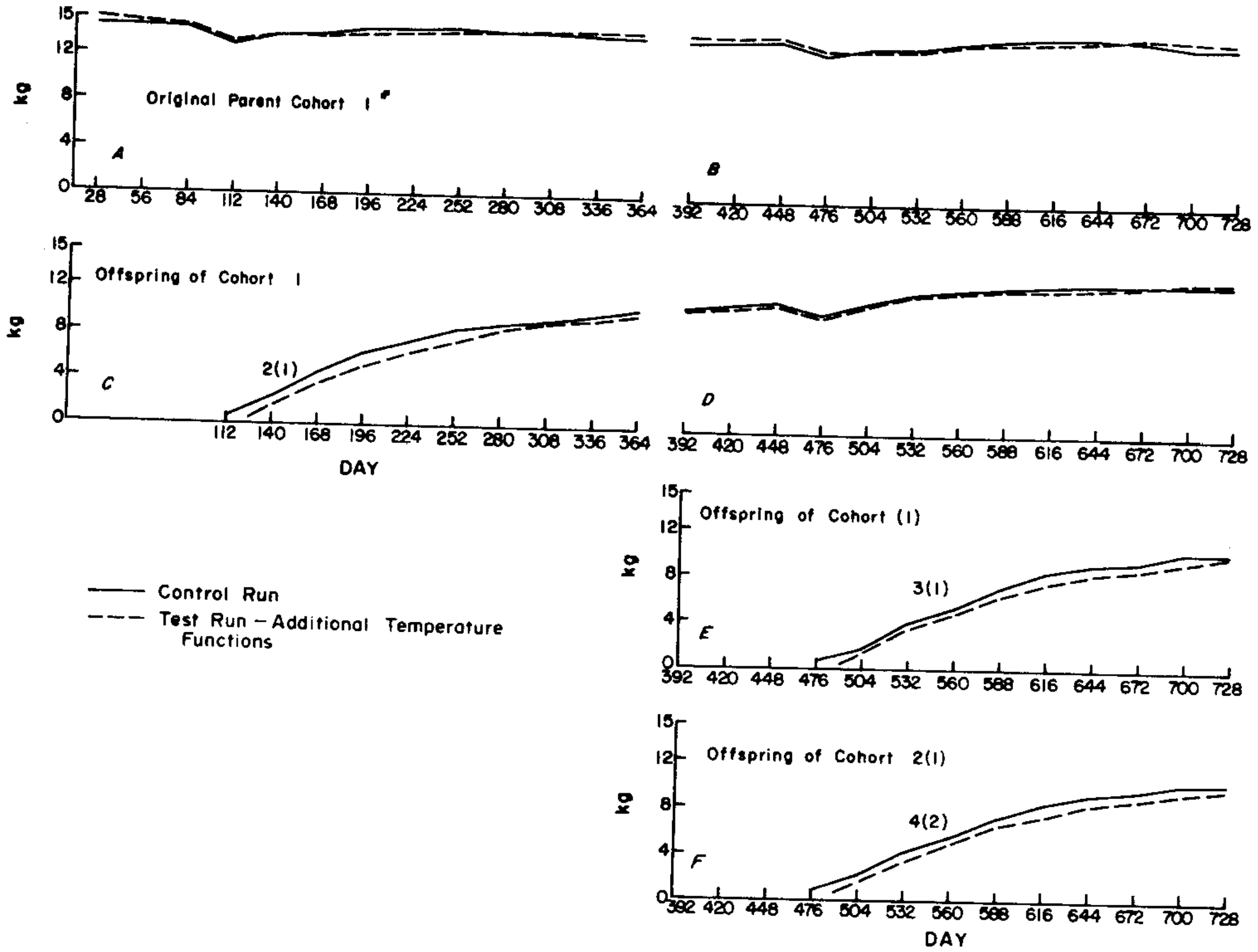

Fig. 15. Coyote Weights (kg) for 2-year Model Run. See Fig. 6 for *.

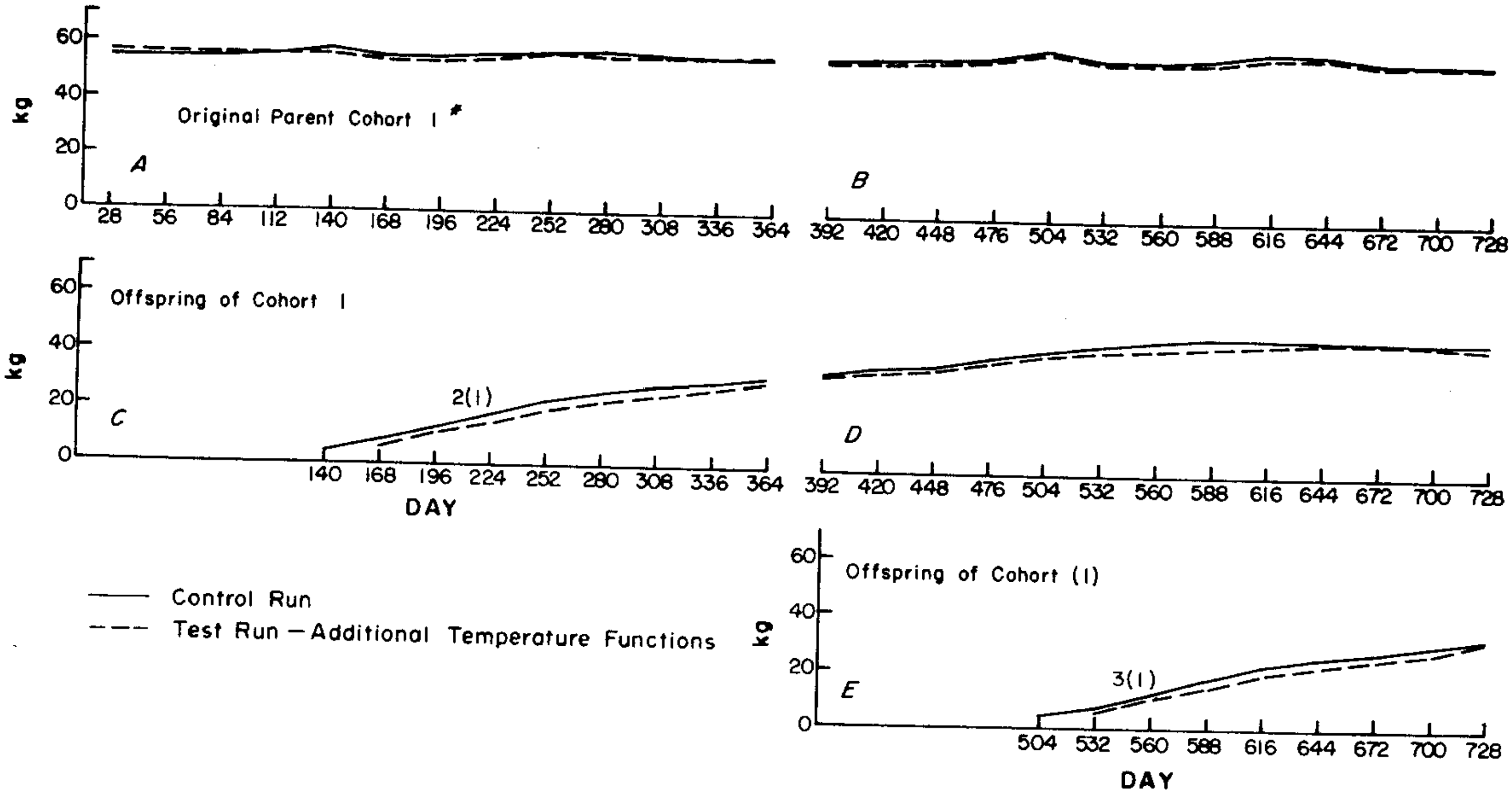

Fig. 16. Sheep Weights (kg) for 2-year Model Run. See Fig. 6 for *.

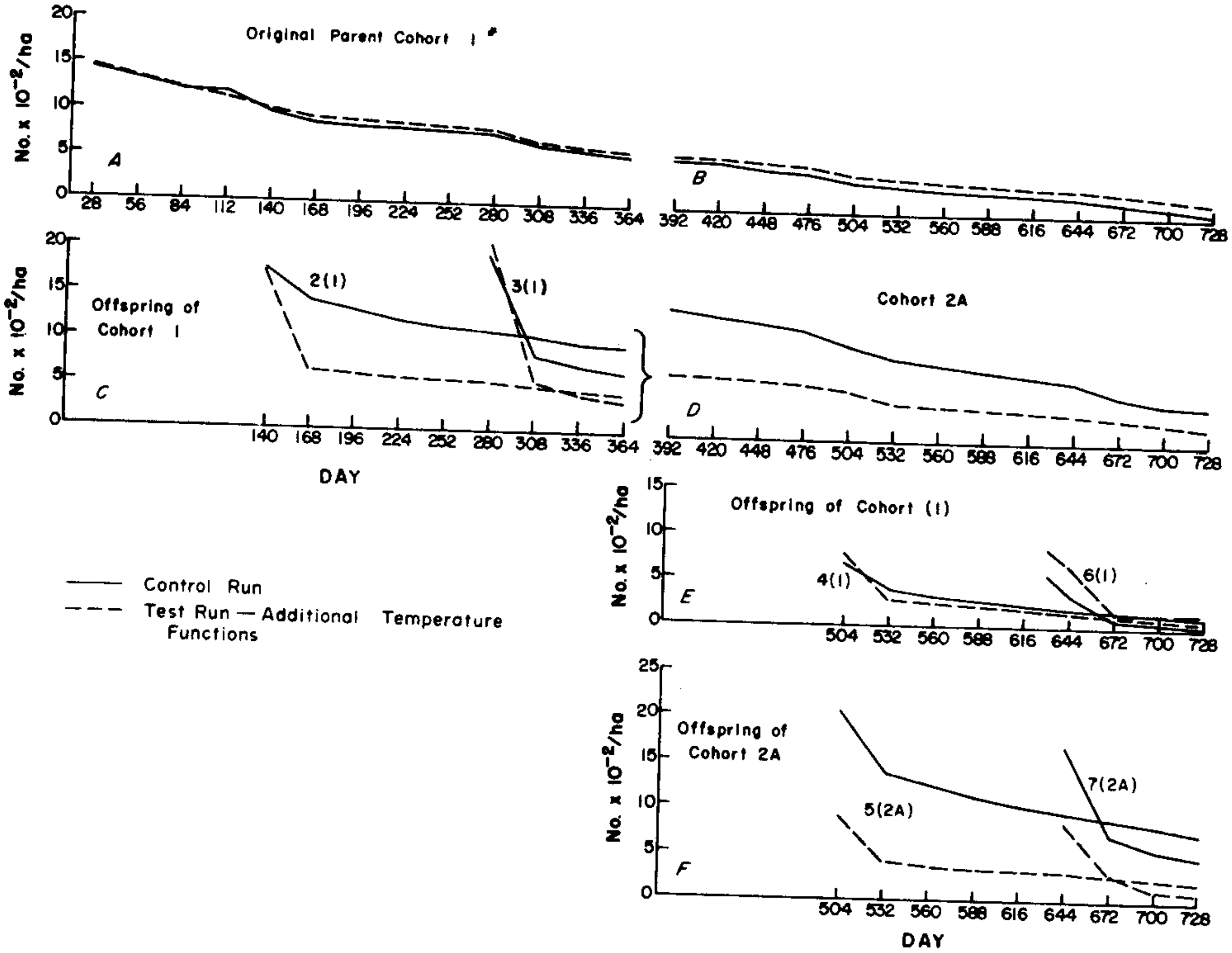

Fig. 17. Jackrabbit Densities (no. × 10^{-2}/ha) for 2-year Model Run. See Fig. 6 for *.

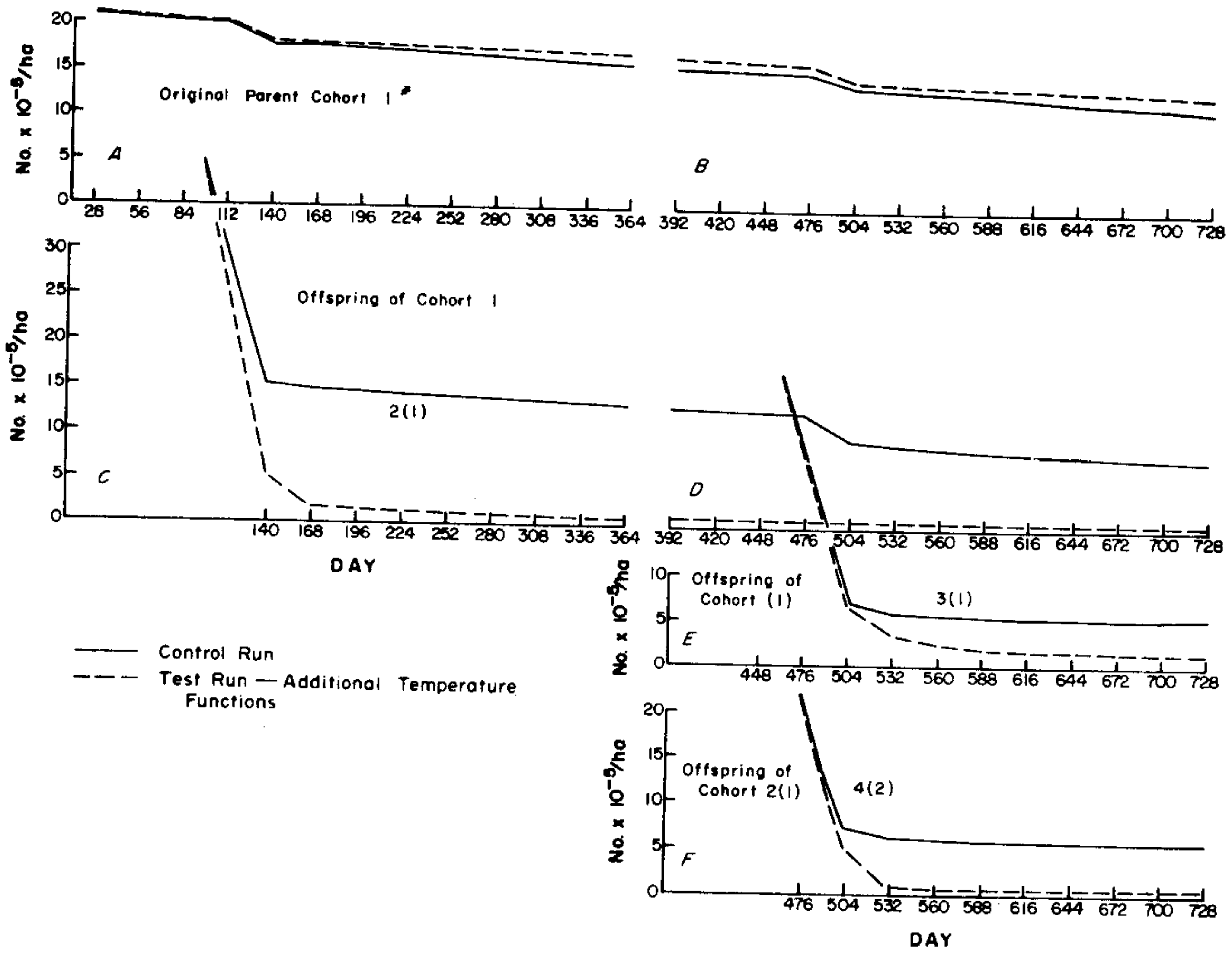

Fig. 18. Coyote Densities (no. × 10^{-5}/ha) for 2-year Model Run. See Fig. 6 for *.

CHAPTER VII

COMBINED ALTERATIONS OF GROWTH FUNCTION AND AMBIENT TEMPERATURE EFFECTS

The results of altering the original submodel structure with respect to the growth function and the temperature function are known. An additional test combining these two changes is proposed as a test of internal communication between these two major functions and the processes they control.

HYPOTHESIS 4

Inclusion of the alternate growth function (Eq. 3) and the temperature functions (Eq. 6, 7, 8) will result in output lying between the extremes produced in the tests using these functions individually.

METHOD OF TESTING

The results of including both these substitute functions will be reviewed with respect to:

1.) Patterns of weight gain
2.) Reproductive patterns
3.) Calculated increase in metabolism for the young
4.) Animal densities

RESULTS

Patterns of Weight Gain

The patterns of weight gain for all species addressed are shown to be similar to those produced by the alteration of the growth function alone. Although slightly lower in all instances (Fig. 19 through 22), the weights describe a pattern of slow growth at first, followed by an increased rate of gain, leading to a higher final adult weight. This adult weight tends to converge with that of adults in the control run (Fig. 19-B, D).

As before, this pattern is found to provide an overall advantage, both for the survival of the individual and for increased reproduction.

Reproductive Patterns

The pattern of weight gain lies between that of the control run and that for the growth function alone. Thus, the numbers of reproductions for deer mice and sheep are shown to increase in response to the growth function (Fig. 19-E, G, H, I; 22-E), although one fewer generation is produced for deer mice (Fig. 19-C). This too is an intermediate response, indicating that the temperature functions are having their effects through delaying births beyond the seasonal limit. While similar patterns of slightly later births and slower weight gain are seen in other species, the delay is not sufficient to eliminate any other reproductions. Thus, the growth function seems to have more effect in this situation.

Increase in Metabolic Rate for the Young

The results of the increased metabolic need calculated for the young are seen, as in the test using the temperature functions alone to penalize the very young. This is best illustrated in the drops in density for jackrabbits and coyotes (Fig. 23, 24); however, in both cases, the declines are noted to be less severe than those in the temperature function test. Thus, it appears that the altered growth function has a mitigating effect.

Animal Densities

The overall result of combining the two functions appears to be the immediate decline in numbers of young in a pattern intermediate to the individual test results. However, this decline is, nevertheless, greater than in the control run (Fig. 23, 24), indicating that the effect of the temperature functions prevails here. Once the initial growth has been achieved, the shape of the density curve closely resembles that of the control at a level determined by initial animal number. This, in turn, reflects the numbers of reproducing adults.

As before, the coyote decline pattern appears unnaturally abrupt at the time of birth; however, the general pattern is similar to that exhibited by the jackrabbit.

The net result of this test appears to be an increase in population for jackrabbits, deer mice, and sheep, while there is a net decline apparent in coyotes. This could possibly result from the unnatural decline described.

CONCLUSIONS

Hypothesis 4

Inclusion of the alternate growth function (Eq. 3) and the temperature functions (Eq. 6, 7, 8) will result in output lying between the extremes produced in the tests using these functions individually.

This hypothesis is accepted as the combined effects are found to be a compromise of earlier responses. The temperature functions, operating to increase food demand for the young, make the expected weight more difficult to attain and result in the increased initial death rate. On the other hand, the growth function acts to increase initial weight gain, providing an advantage for the young and, therefore, an increase in population through increase reproductions. The net increase in population indicated for most animals observed indicates the more pronounced effect of the growth function in this combination.

These results further support the general submodel framework as a stable acceptable foundation upon which such alterations appear to operate as expected.

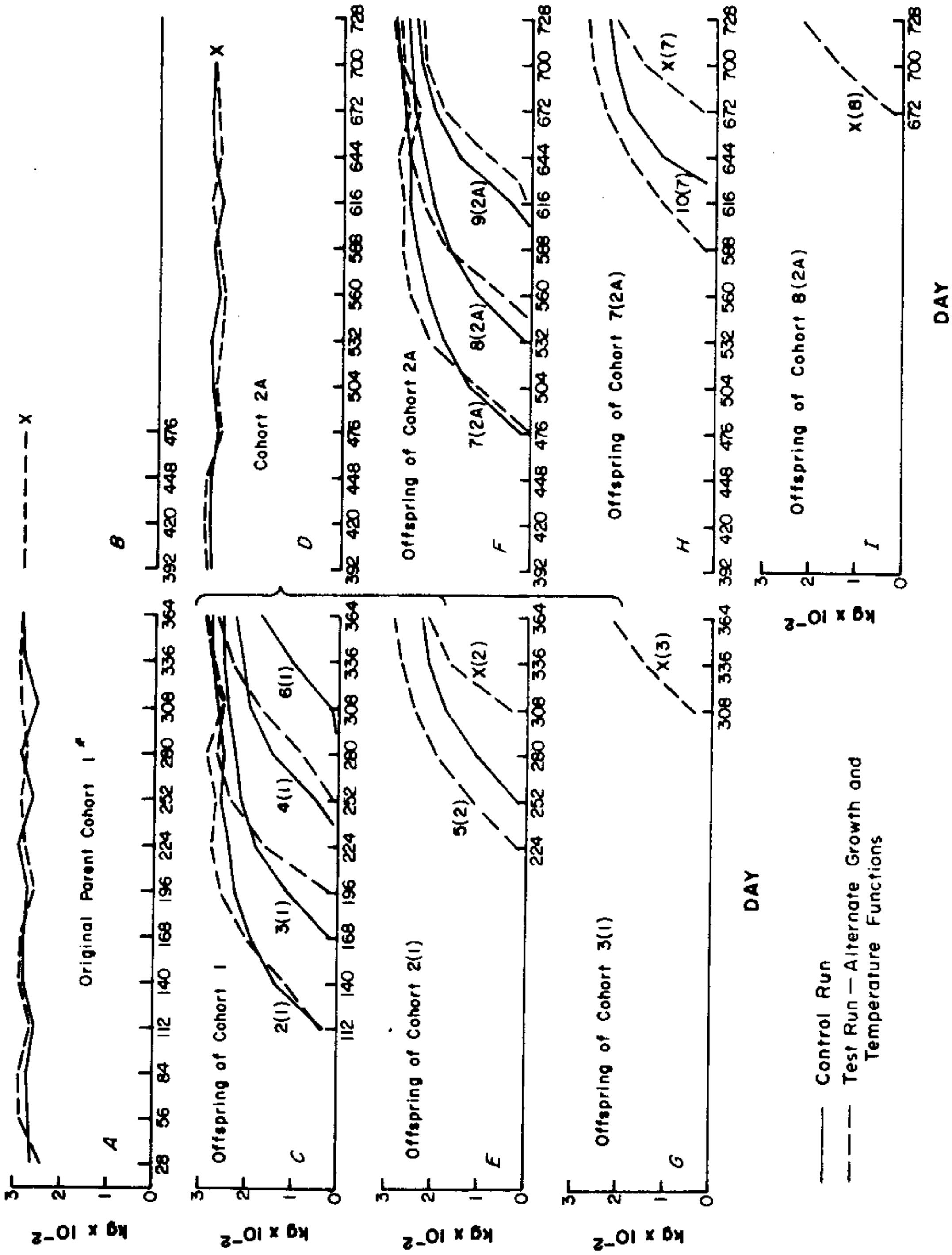

Fig. 19. Deer Mouse Weights (kg × 10^{-2}) for 2-year Model Run. See Fig. 6 for *.

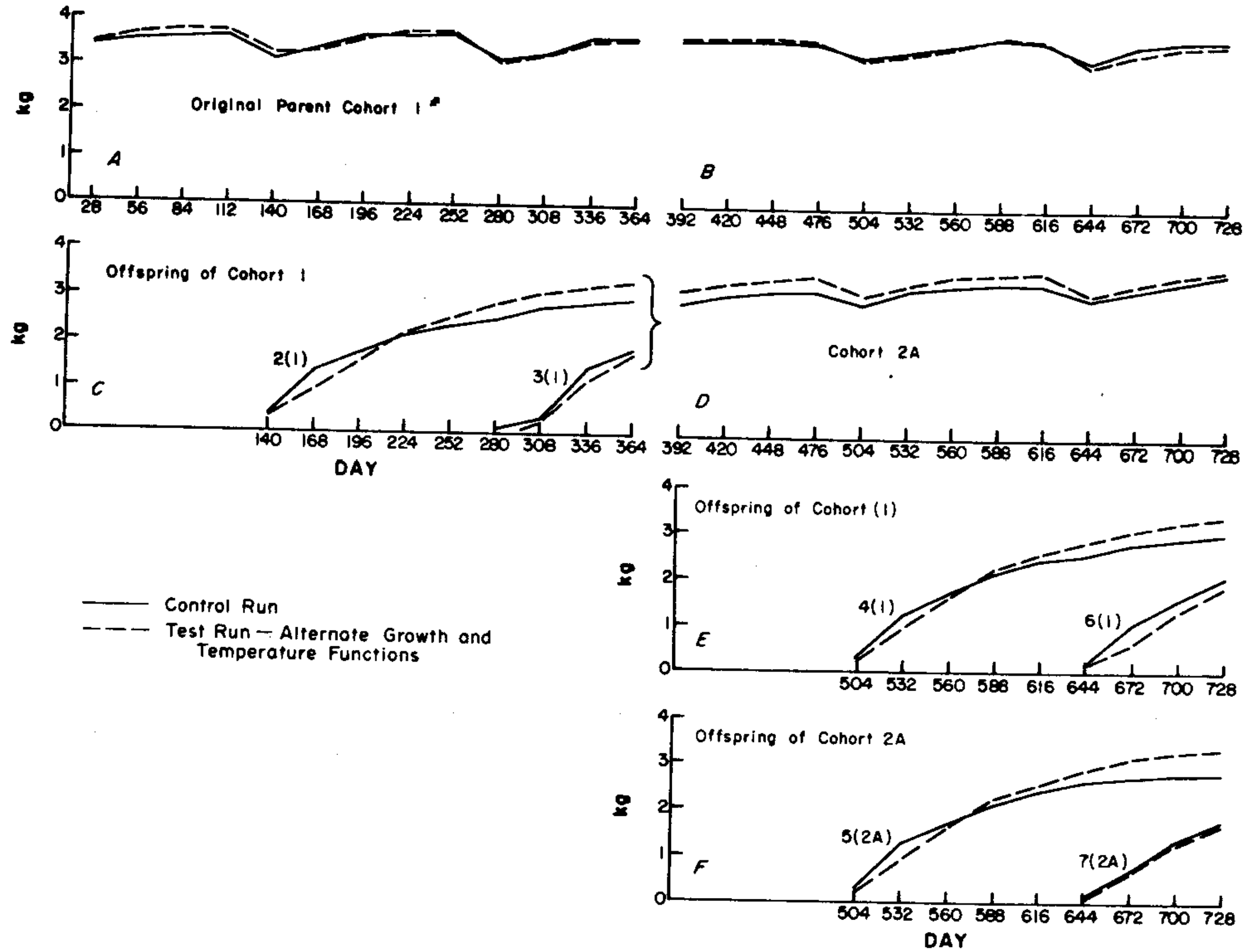

Fig. 20. Jackrabbit Weights (kg) for 2-year Model Run. See Fig. 6 for *.

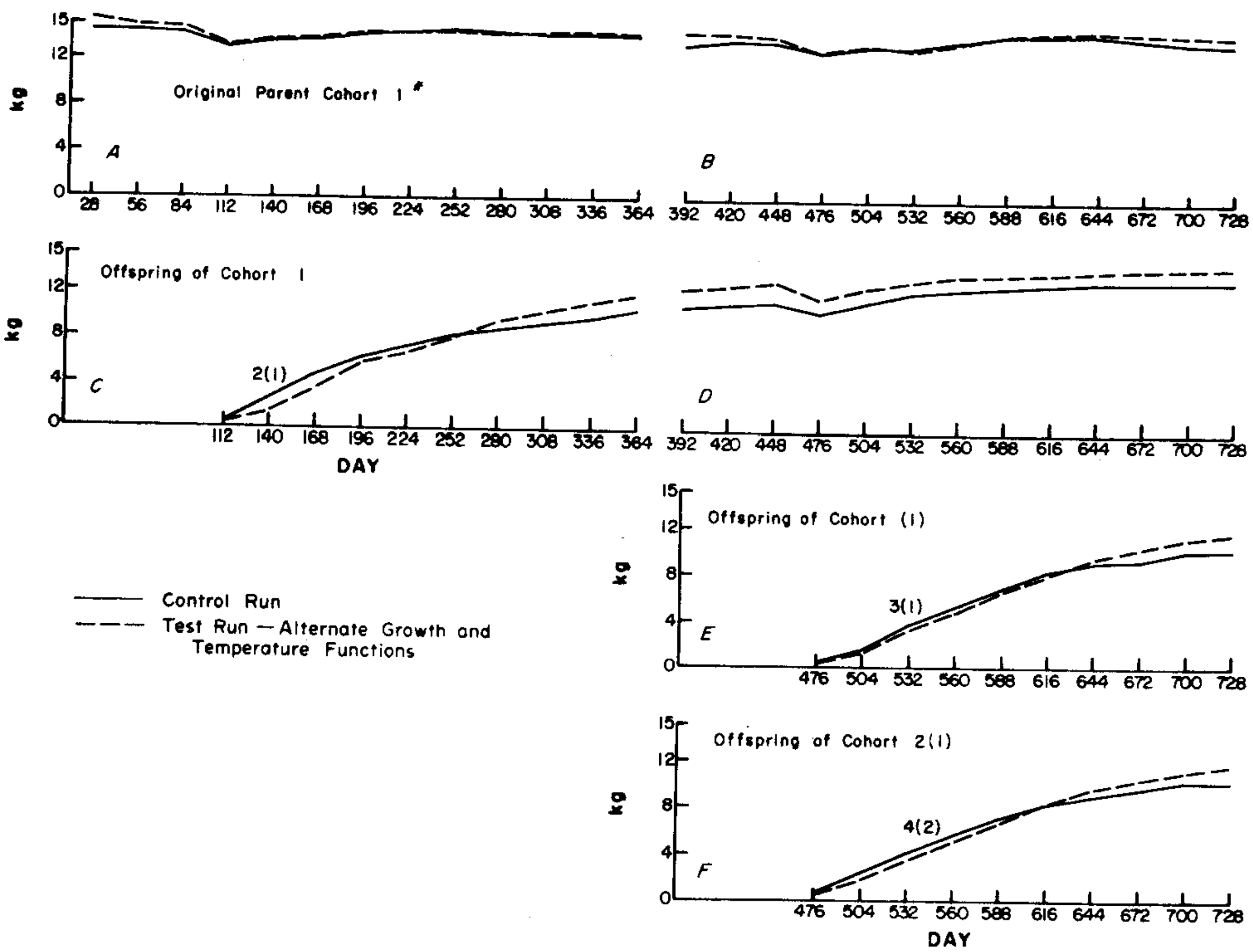

Fig. 21. Coyote Weights (kg) for 2-year Model Run. See Fig. 6 for *.

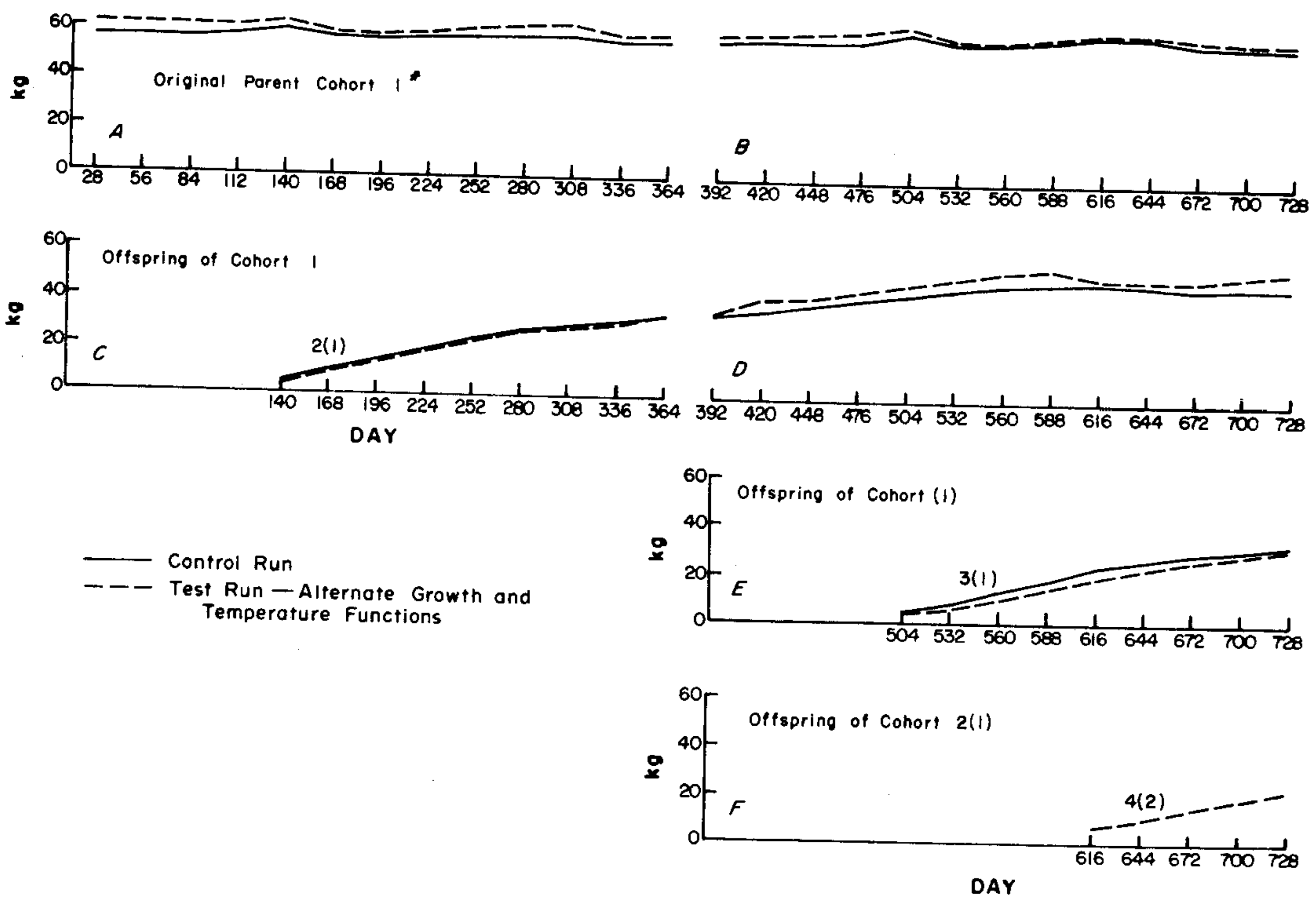

Fig. 22. Sheep Weights (kg) for 2-year Model Run. See Fig. 6 for *.

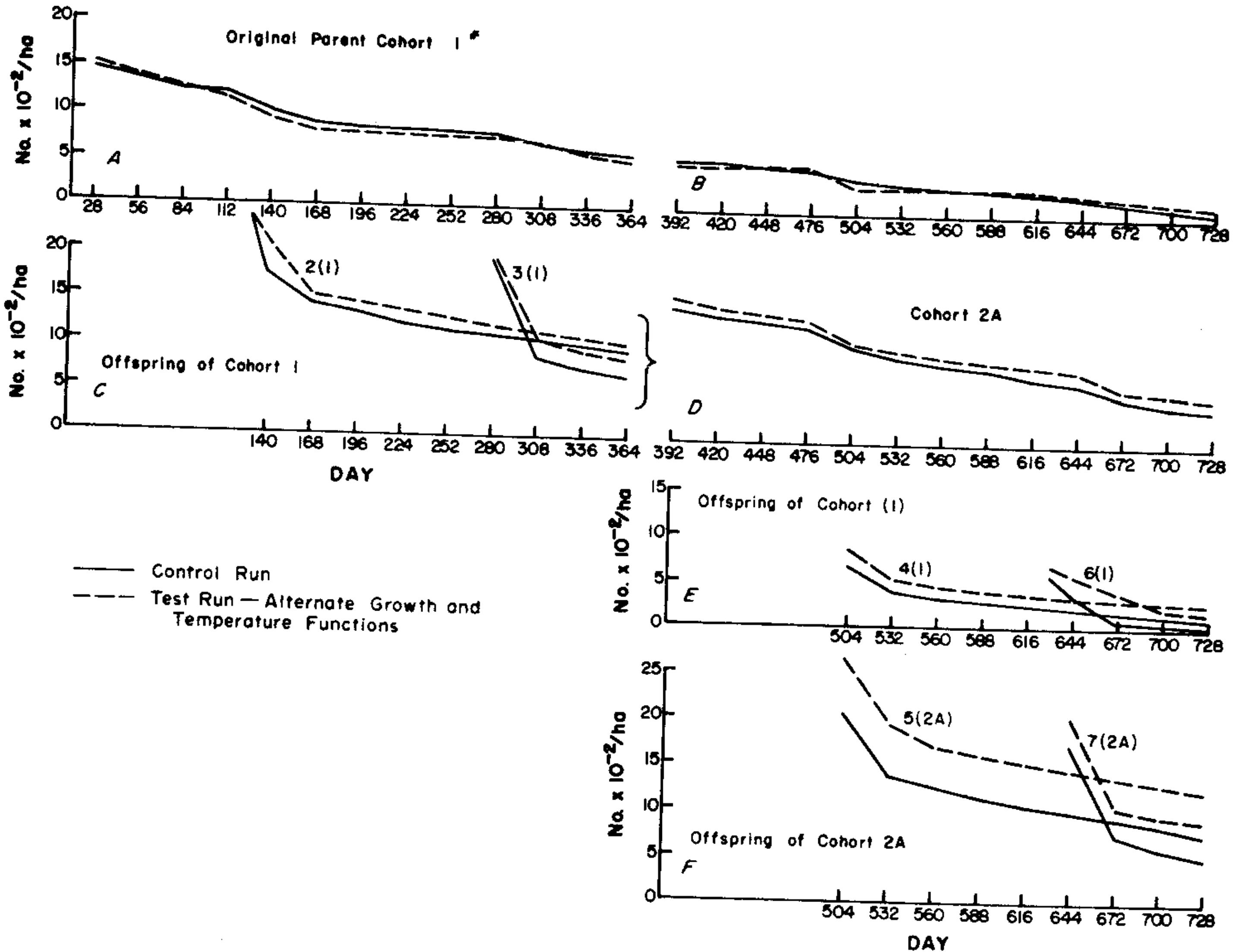

Fig. 23. Jackrabbit Densities (no. × 10^{-2}/ha) for 2-year Model Runs. See Fig. 6 for *.

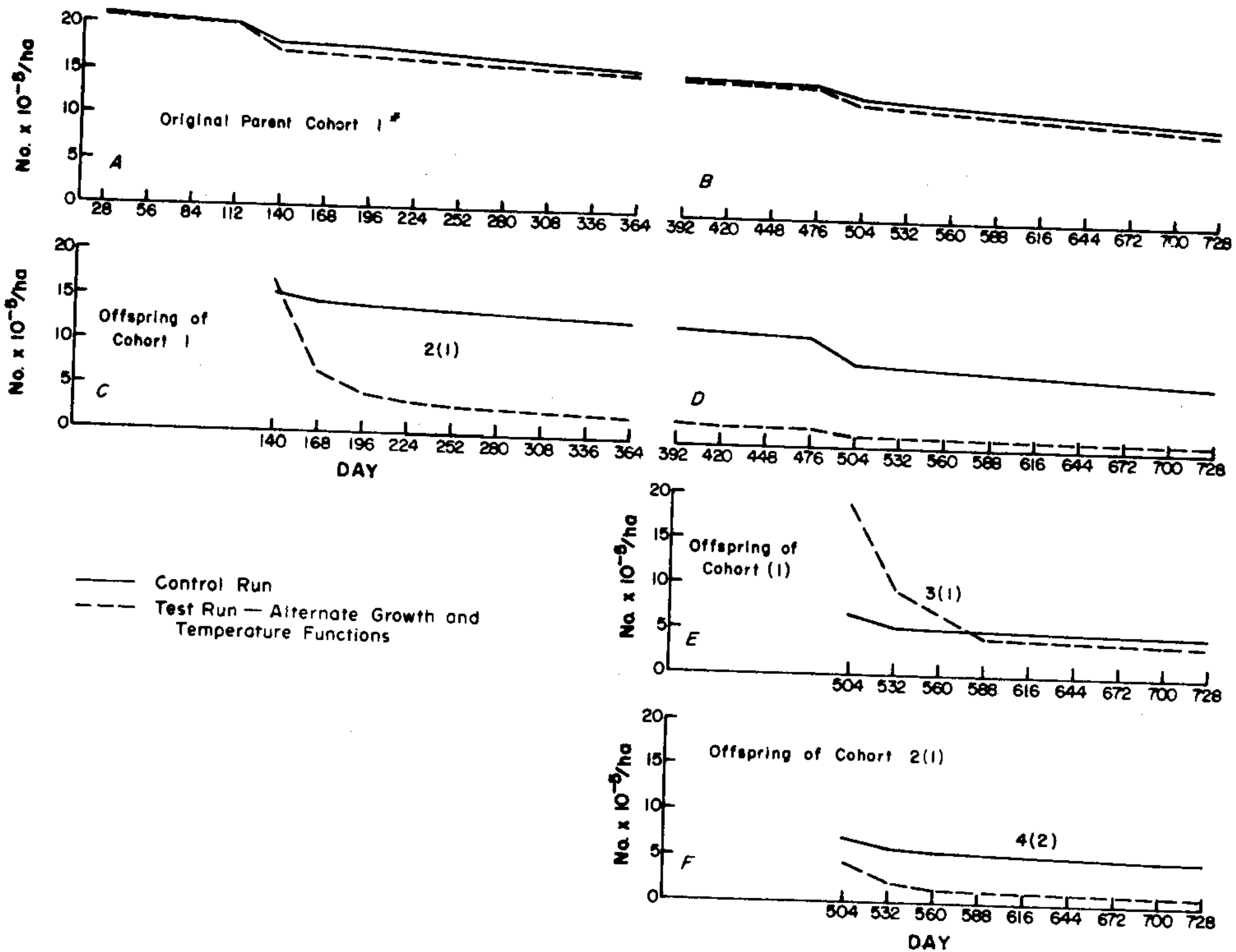

Fig. 24. Coyote Densities (no. × 10^{-5}/ha) for 2-year Model Run. See Fig. 6 for *.

CHAPTER VIII

SUBSTITUTION OF ALTERNATE PARAMETER FOR CALCULATING METABOLIC WEIGHT

The present submodel uses the following regression equation for relating body weight to fasting metabolism or metabolic weight (Kleiber, 1961):

$$FM = 70\ W^{0.75} \tag{9}$$

where: FM = Fasting metabolism (kcal)

W = Animal weight (kg)

This formulation has grown out of a series of studies attempting to link fasting metabolism with some measureable attribute of the body. As early as 1883, Max Rubner experimenting with dogs, determined that the fasting metabolism per kilogram body weight decreased with the increasing size of the animal (Blaxter, 1967). When "size" was expressed as surface area, however, all dogs produced the same relative amount of heat. Though a generalization, which found its greatest difficulty in the accurate measurement of surface area, this law pointed the way for further studies. Both Kleiber and Brody suggested that fasting metabolism should be related to some expression of body weight, a more easily measured value. Brody's studies (1945) support the formulation:

$$FM = 70.5\ W^{0.73} \tag{10}$$

where: FM = Fasting metabolism (kcal)

W = Animal weight (kg)

whereas, Kleiber (1961) has determined Equation (9) to be more precise. While authorities differ upon which value is acceptable and, thus, present their data in different ways, "both Brody's and Kleiber's equations are just as much generalizations as was Rubner's so many years ago" (Blaxter, 1967, pg. 89).

HYPOTHESIS 5

The substitution of Brody's metabolic weight calculation (Eq. 10) for that of Kleiber (Eq. 9) will alter the mechanics of the submodel, producing observable changes in output which are related to reduced metabolic weight.

METHOD OF TESTING

The results of the substitution is compared with the control output on the basis of:

1.) Pattern of weight gain
2.) Reproductive patterns
3.) Calculated increase in metabolism for the young
4.) Animal densities

RESULTS

Pattern of Weight Gain

The substitution appears to change the output very little, much of the data remaining identical (Compare Tables 1 and 9 in Appendix). For this reason no attempt has been made to graph differences in output. Instead, the maximum change for each species has been calculated and is presented as follows:

Table 4. Comparison of Weight Output When Substituting Equation 10.

Animal	Maximum Weight Deviation	Time for Weight to Return to Standard
Deer mouse	+ 1.0%	Within 100 days
Jackrabbit	+ 3.2%	28 days
Coyote	- 0.4%	Within 1/2 year
Sheep	- 0.7%	Within 1/2 year

Thus, all animals are seen to exhibit some change in weight, this change occurring early in life and being corrected to match that of the control run well within the test period of two years. A general pattern does not present itself, the magnitudes and persistences of these changes appearing to be controlled by species specific parameters.

Reproductive Patterns

No change in reproductive pattern is apparent, the timing of reproductions remaining the same in all cases and the numbers of young produced remaining the same as in the control.

Calculated Increase in Metabolic Rate for the Young

No distinct pattern emerges for the early effects of the metabolic weight change upon the young, a variety of weight changes resulting. As these persist for varying lengths of time, the secondary effect of change in death rate, as seen in density change, presents a varied pattern.

Animal Densities

Differences in densities show no marked pattern that appears to be directly related to the individual species' characteristics (Table 5):

Table 5. Comparison of Density Output When Substituting Equation 10.

Animal	Maximum Density Difference
Deer mouse	+ 2.0%
Jackrabbit	+ 1.1%
Coyote	- 0.1%
Sheep	- 0.6%

In general, an increase in density accompanies an increase in weight, a reasonable result based on submodel mechanics and finding from previous tests. These density changes are achieved early and then maintained at a relatively constant rate throughout the test period. This indicates that the effect is operating principally on the young.

CONCLUSIONS

Hypothesis 5

The substitution of Brody's metabolic weight calculation (Eq. 10) for that of Kleiber (Eq. 9) will alter the mechanics of the submodel, producing observable changes in output which are related to reduced metabolic weight.

This hypothesis is accepted as the hypothesized changes are observed; however, as the changes stabilize within the test period, it appears that the two functions would perform equally well in the submodel, as it should have the latitude to operate upon either of these functions.

CHAPTER IX

CONSTRUCTION AND EVALUATION OF SURVIVAL CURVES FROM OUTPUT

Survivorship curves are a standard technique for evaluating biological populations. Here they are utilized to compare the modeled population responses to submodel alterations. These curves provide an estimate of living populations of animals (analogs of data collected in nature) and illustrate the existing population structure by depicting the proportional size of each age class (Quick, 1973).

Survivorship curves are constructed by plotting the number of living animals at a given age (1_x) against age (x) (Southwood, 1968). Slobodkin (1961) described four basic types of survival curves (Fig. 25). These are:

Type I - mortality acts most severely on the older members
Type II - the numbers of individuals dying per unit time is constant
Type III - the mortality rate is constant
Type IV - mortality acts most severely on the younger members.
(Southwood, 1968)

These curve types typify population structures of different species and indicate their dynamics. Thus, responses of the various species to submodel alterations will be evaluated by examining these population parameters.

HYPOTHESIS 6

Changes in survival curves in response to altering the growth function and including the temperature functions will support the earlier findings that:

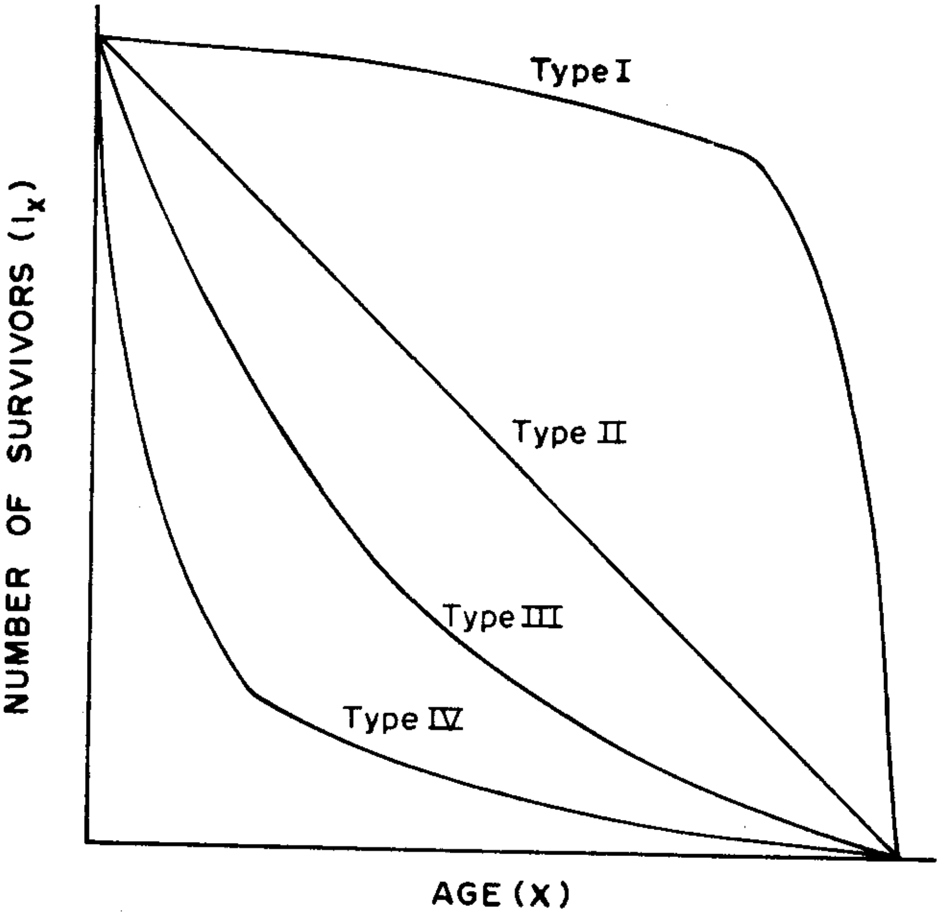

Fig. 25. Types of Survivorship Curves (after Slobodkin in Southwood, 1968).

1.) The altered growth function provides a survival advantage for the young.

2.) The temperature functions impose a survival disadvantage upon the young.

METHOD OF TESTING

The simulated survival curves were constructed by calculating population numbers for each age class in proportion to the original population, which is set at 1000 for ease of comparison. These (1_x) values are then plotted against time.

Since the submodel combines all new age classes into one population at the end of the year, data for complete survival curves are not available. By utilizing age classes which begin early in the year, and thus retain their identity for the longest period of time, a partial pattern for a single cohort can be observed. As it has been previously determined that those changes in population patterns which occur do so early in life, their effects are expected to be visible within this partial survival curve. The results of these calculations are illustrated in Figs. 26 through 28.

RESULTS

The survival curves resulting from the control run for deer mice appear, in general, to be between Type II and Type III. The substitution of the alternate growth function is seen to raise the survival curve slightly for the youngest members (Fig. 26). In general, this tends to straighten the curve, altering it slightly in the direction of Type II. The inclusion of the temperature functions causes a steeper decline in the curves at the outset, after which the pattern shows little change (Fig. 26). This is in keeping with expectations of a survival disadvantage imposed on the young and alters the survival curve slightly in the direction of Type III.

Survival curves for jackrabbits appear, in general, to represent Type III. Responses to the submodel alterations are similar, although more pronounced (Fig. 27). The weight function test causes the curves to shift in the direction of Type II, while the temperature test lowers the early populations and shifts the pattern toward Type IV. The reduced effect observed for deer mice is attributed to the averaging of their weights in the temperature function calculations (see Chapter VI) in an attempt to model their more protected condition. As stated in Chapter IV, deer mouse data were combined in an attempt to represent a more protected condition for the young. This was done by averaging the weights for all members of the species and applying the temperature function to the species as a whole. Thus, survival curves for deer mice reflect a less extreme disadvantage for the very young. This is evidenced in the less pronounced initial drop in number for this species. In all other species, each cohort was addressed individually, the survival curves thus representing the precise effect of the temperature function on a given cohort.

Survival curves for coyotes show no resemblance to any of the standard types described, although the test run altering temperature functions results in a curve approximating a Type IV response. A distinct drop in parent numbers corresponding to each birth date (Fig. 28). While the relative population responses for both test runs follow the general pattern set by the other two species, the weight advantage awarded to young coyotes appears to be relatively slight. On the other hand, the responses to temperature effects are extremely pronounced.

CONCLUSIONS

Hypothesis 6

Changes in survival curves in response to altering the growth function and including the temperature functions will support the earlier findings that:

1.) The altered growth function provides a survival advantage for the young.

2.) The temperature functions impose a survival disadvantage upon the young.

This hypothesis is accepted for all three species under consideration, as they are shown to illustrate the above results through this different method. However, the results shown for the coyote follow an abrupt pattern of decline which should be explained. It is suggested that parameters governing death in this species are not operating as they should with respect to the population as a whole throughout the year. In conjunction with this sudden population drop, the coyote responses to the submodel stresses appear to lower the population to a more pronounced extent than would be expected from the pattern set by other species. It is suggested that these disadvantages are first a response to parent loss, resulting in increased mortality for the dependent young. This effect tends then to mask the positive result expected from the inclusion of the growth function alteration.

Thus, the examination of survival curves might be done as a means of validating the population dynamics of species while a model is being constructed. This could obviate the possibility of overlooking internal errors whose effects are hidden before the final output is determined. In addition, this method provides an excellent means of assessing population responses to stresses imposed to test a consumer model, as is the case here.

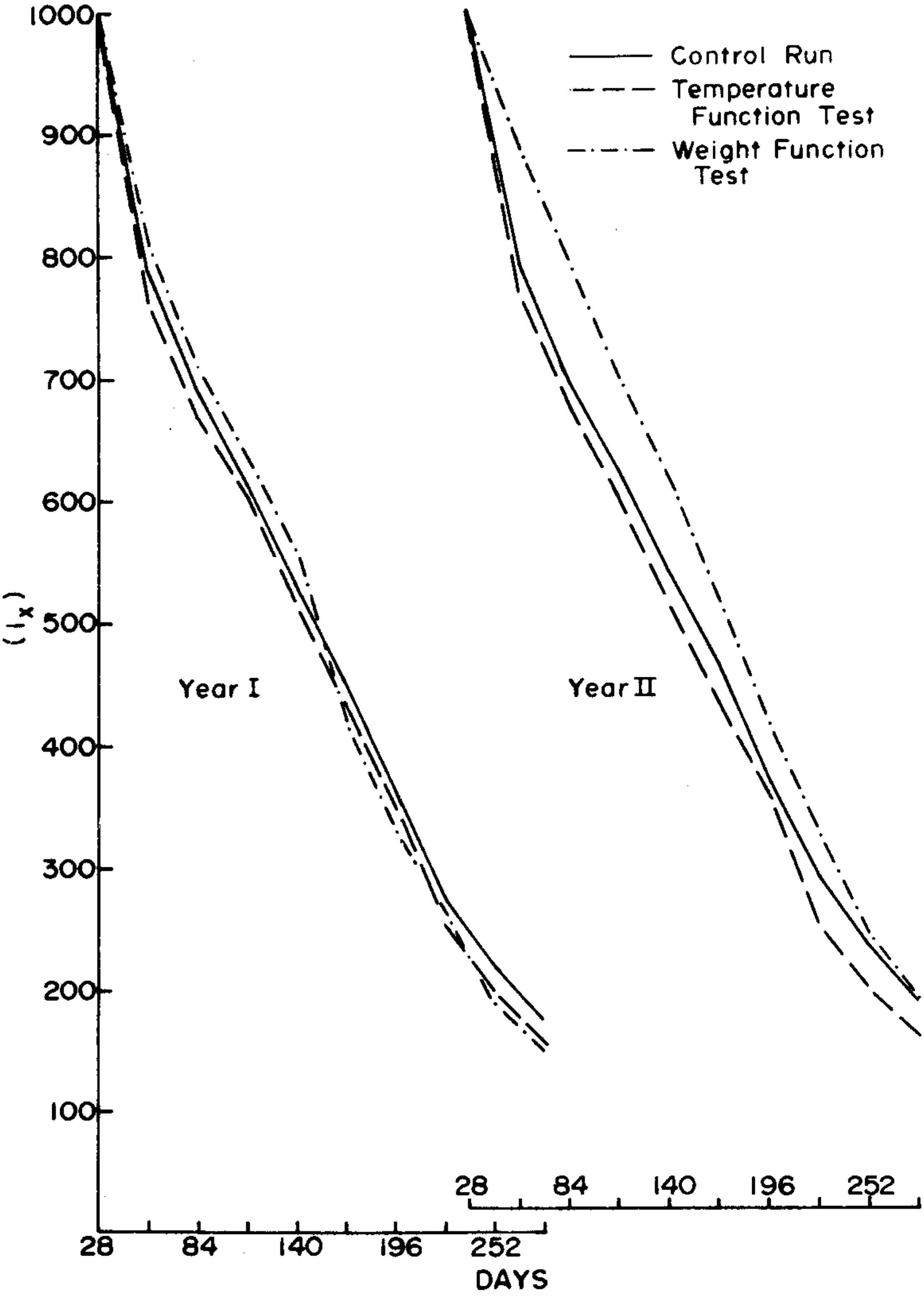

Fig. 26. Survivorship Curves - Deer Mice.

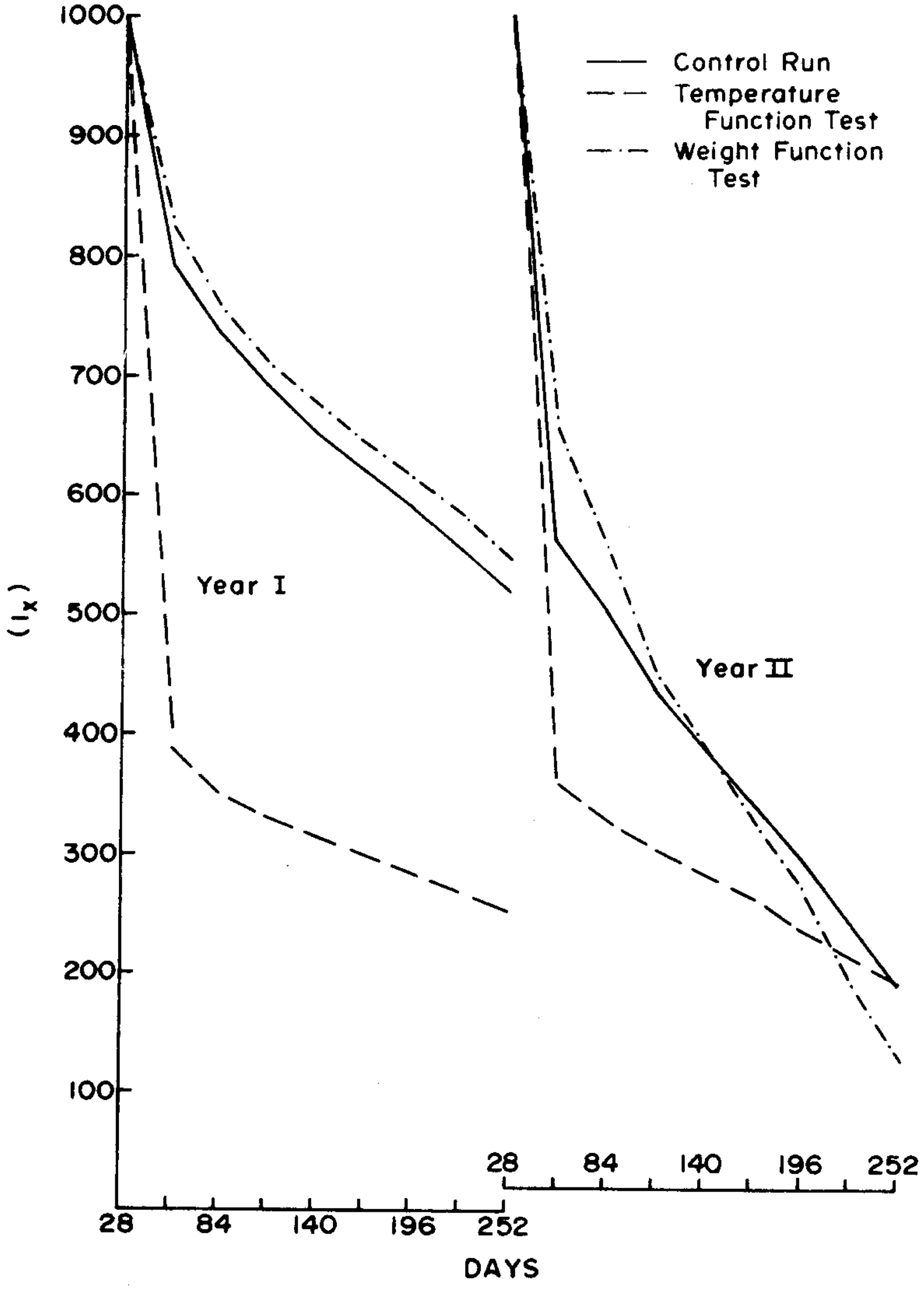

Fig. 27. Survivorship Curves - Jackrabbits.

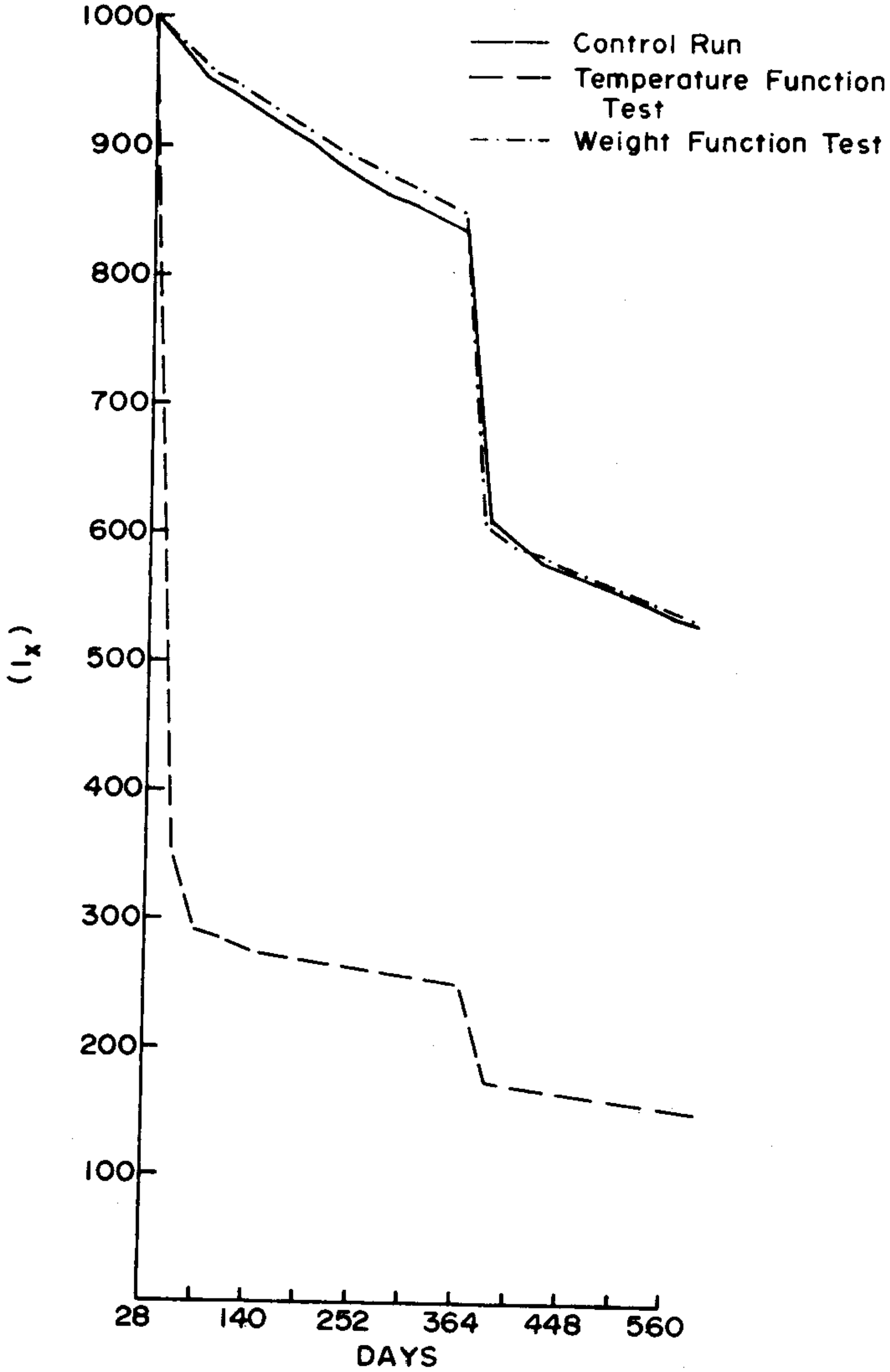

Fig. 28. Survivorship Curves - Coyotes.

CHAPTER X

DISCUSSION

The purpose of this investigation has been to explore several means of assessing the performance of the Mammalian Consumer Submodel of the ecosystem model ELM.

The initial review of objectives for the submodel with respect to the main model objectives resulted in the conclusion that the major subgoal of creating a canonical representation for grassland mammalian species is both feasible and essential to the operation of the total model.

Concern has centered on the validity of the internal mechanisms reflected as changes in output stemming from changes in submodel structure or components. To observe this the following alterations and additions to the submodel were devised and implemented.

1.) The threshold value governing reproduction was examined and compared with reproductive data for a variety of mammals. As such data are quite variable, there was no precise validation for the given value; however, support for the concept of species similarity with respect to this developmental stage can be found (Brody, 1945; Ricklefs, 1967). The choice of values, then remains a matter of experimentation.

2.) Two substitutions were made in the submodel framework. An alternate parameter in the metabolic weight function (Brody, 1945) was utilized, and the Von Bertalanffy growth function was fit into the framework. Each of these functions has a key role in the submodel operation. The rationale for making such substitutions lies in the contention that a new, although quite similar submodel is thereby created. Output comparisons will, then, provide a second viewpoint for observing internal operations.

When such tests were run, confidence in the submodel structure was supported, as new output was in keeping with expectations based on the nature of the new functions included and on their respective roles in the submodel.

3.) The addition of functions to alter energy demands as a function of ambient temperatures was made in an effort to test the submodel's ability to accept additional complexity and produce biologically acceptable and interpretable results. Output from this test indicated that the submodel has this capability and, therefore, has the latitude to be adapted to different situations and modeling questions.

4.) A combination test, consisting of substituting the Von Bertalanffy growth function and including the critical temperature functions simultaneously was made, the hypothesis being that the new output would reflect a compromise of the outputs observed for the individual tests. This was found to be the case, and further supports the soundness of the model framework and internal communication.

5.) Survival curves were constructed as a means of observing population trends through the use of a standard biological technique. The presence of an unlikely survival pattern for coyotes indicated that errors can be present in the submodel, their effects being subsequently hidden in a final output that appears to be appropriate. Thus, it is suggested that survival curves be used for validation of species population dynamics during the construction of such a model.

In general, the investigations carried out in this study lend confidence to the canonical structure of the submodel as it presently exists and in its capabilities for adaptation to new, related modeling questions. It appears that such techniques of studying model structure by making alterations and additions serves as a useful means of assessing the biological processes as they are modeled.

The alteration of the submodel framework through the substitution of equally acceptable functions essentially creates a second similar model which can be expected to yield different though equally acceptable results. It is suggested that this approach may be the most efficient means of identifying and adjusting parameter values which are not providing the proper latitude to operate within both acceptable biological frameworks. Since, to be truly general, a biological model should have this capability, such testing is useful in locating parameters in need of adjustment and in testing for the best overall value for each. This method is preferable to a "trial and error" approach to parameter testing.

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APPENDIX

Table 1. Animal Weights, Control Run (two years)

	Jackrabbits (kg)							Coyotes (kg)					Deer Mice (kg × 10⁻²)										Sheep (kg)		
Day/Cohort*	1	2(1)	3(1)					1	2(1)			Day/Cohort	1	2(1)	3(1)	4(1)	5(2)	6(1)					1	2(1)	
28	3.48							14.3				28	2.54										54.5		
56	3.50							14.2				56	2.65										54.4		
84	3.52							14.2				84	2.72	(0.137)									54.6		
112	3.53	(0.184)**						12.8	0.737			112	2.52	0.213									55.0		
140	3.18	0.398						13.3	2.22			140	2.77	1.47									58.9	3.70	
168	3.43	1.28						13.8	4.55			168	2.81	1.97	0.137								55.0	7.75	
196	3.54	1.73						14.1	6.12			196	2.73	2.24	1.15								55.0	12.8	
224	3.56	2.07						14.2	7.34			224	2.83	2.42	1.82	(0.137)							55.8	17.7	
252	3.57	2.39						14.3	8.21			252	2.60	2.54	2.13	0.565	0.137						55.8	21.9	
280	3.12	2.49	0.184					14.3	8.91			280	2.83	2.51	2.34	1.59	1.07	0.137					57.7	24.9	
308	3.30	2.64	0.655					14.2	9.51			308	2.60	2.70	2.50	2.01	1.78	0.157					56.5	27.5	
336	3.52	2.79	1.41					14.0	9.98			336	2.80	2.80	2.60	2.28	2.12	1.34					55.6	29.9	
364	3.59	2.93	1.82					14.0	10.4			364	2.85	2.79	2.68	2.45	2.34	1.88					55.7	32.1	
	1	2A***		4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)		1			2A			7(2A)	8(2A)	9(2A)	10(7)	1	2(1)	3(1)
392	3.59	2.88						13.8	10.7			392	2.85			2.77							56.5	34.6	
420	3.59	3.06						13.9	11.0			420	2.85			2.82							57.1	36.7	
448	3.60	3.16						14.0	11.5			448	2.85			2.83			(0.137)				57.5	35.5	
476	3.59	3.24		0.184	0.184			12.7	10.5	0.737	0.737	476	2.85			2.59			0.211				57.9	42.1	
504	3.25	2.92		0.355	0.366			13.4	11.5	1.92	2.02	504				2.79			1.40				61.0	43.6	3.70
532	3.47	3.18		1.17	1.17			13.8	12.1	4.00	4.04	532				2.84			1.92	0.137			57.9	46.6	6.90
560	3.59	3.35		1.69	1.69			14.0	12.5	5.69	5.70	560				2.72			2.22	1.04			57.7	48.2	12.1
588	3.60	3.42		2.05	2.06			14.2	12.9	7.15	7.16	588				2.85			2.42	1.77			58.4	45.9	17.4
616	3.60	3.45		2.32	2.32	(0.185)		14.3	13.1	8.26	8.26	616				2.62			2.55	2.13	0.137	0.137	60.6	49.0	22.2
644	3.25	3.01		2.50	2.51	0.207	0.165	14.4	13.3	9.05	9.05	644				2.84			2.55	2.35	1.59	1.15	60.1	48.4	25.4
672	3.51	3.23		2.64	2.66	1.11	0.755	14.2	13.3	9.66	9.66	672				2.85			2.71	2.50	2.02	1.81	58.5	47.8	28.1
700	3.62	3.50		2.81	2.60	1.62	1.49	14.0	13.3	10.2	10.2	700				2.85			2.76	2.61	2.29	2.15	57.5	47.7	30.6
728	3.64	3.53		2.94	2.95	2.18	1.90	14.0	13.3	10.6	10.6	728							2.79	2.69	2.45	2.37	57.6	48.2	33.2

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

Table 2. Animal Densities, Control Run (two years)

Day/Cohort*	Jackrabbits (No. = 10^{-3}/ha)						Coyotes (No. = 10^{-5}/ha)			
	1	2(1)	3(1)				1	2(1)		
28	14.3						21.5			
56	13.2						21.0			
84	12.2						20.6			
112	12.2	27.2					20.1	40.2		
140	9.86	17.8					17.6	15.3		
168	8.86	14.1					17.6	14.9		
196	8.64	13.1					17.5	14.6		
224	8.39	12.3					17.4	14.4		
252	8.11	11.6					17.2	14.2		
280	7.84	11.0	19.6				17.1	14.0		
308	6.39	10.5	8.34				16.9	13.8		
336	5.95	9.91	7.19				16.8	13.6		
364	5.60	9.27	6.52				16.7	13.4		
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)
392	5.31	14.3					16.5	13.2		
420	5.03	13.6					16.3	13.1		
448	4.74	13.0					16.1	12.9		
476	4.49	12.4	11.0	30.5			16.0	12.8	31.7	22.9
504	3.87	10.5	6.92	20.7			13.6	9.33	7.00	6.99
532	3.43	9.07	3.92	13.9			13.2	9.09	5.80	6.07
560	3.17	8.56	3.46	12.8			13.0	8.87	5.69	5.95
588	2.88	8.02	3.03	11.9			12.8	8.74	5.58	5.84
616	2.60	7.49	2.68	11.0	(6.05)**		12.6	8.61	5.48	5.73
644	2.16	6.98	2.37	10.2	3.49	17.4	12.4	8.48	5.38	5.63
672	1.74	5.44	20.5	9.50	1.16	7.82	12.3	8.35	5.28	5.53
700	1.37	4.83	1.66	8.72	0.518	6.57	12.1	8.22	5.19	5.43
728	0.979	4.25	1.26	7.86	0.0014	5.67	11.9	8.10	5.10	5.43

Day/Cohort	Deer Mice (No. = 10^{-1}/ha)						Sheep (No. = 10^{-2}/ha)		
	1	2(1)	3(1)	4(1)	5(2)	6(1)	1	2(1)	
28	17.4						16.5		
56	13.4						16.5		
84	10.3						16.5		
112	8.04	14.9					16.5		
140	7.05	11.8					16.5	24.5	
168	6.21	10.3					16.5	24.5	
196	5.13	9.18	8.96				16.5	24.5	
224	4.20	7.97	7.55				16.5	24.5	
252	3.31	6.80	6.47	5.47			16.5	24.5	
280	2.43	5.35	5.46	4.29	9.15		16.5	24.5	
308	1.96	4.06	4.52	3.57	7.59	3.65	16.5	24.5	
336	1.43	3.24	3.64	2.94	6.34	2.36	16.5	24.5	
364	1.10	2.59	2.90	2.40	5.28	1.91	16.5	24.5	
	1	2A	7(2A)	8(2A)	9(2A)	10(7)	1	2(1)	3(1)
392	0.917	11.7					16.5	24.5	
420	0.768	9.92					16.5	24.5	
448	0.623	8.65					16.5	24.5	
476	0.492	7.69	14.4				16.5	24.5	
504		6.52	11.4				16.5	24.5	23.6
532		5.70	10.0				16.5	24.5	23.6
560		4.76	8.96	8.40			16.5	24.5	23.6
588		3.87	7.79	7.08			16.5	24.5	23.6
616		3.11	6.66	6.06	5.24		16.5	24.5	23.6
644		2.22	5.32	5.13	3.86	9.04	16.5	24.5	23.6
672		1.75	4.21	4.28	3.19	7.50	16.5	24.5	23.6
700		1.33	3.39	3.49	2.63	6.28	16.5	24.5	23.6
728			2.74	2.83	2.18	5.30	16.5	24.5	23.6

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

Table 3. Animal Weights, Alternate Growth Function (two years)

Day/Cohort*	Jackrabbits (kg) 1	2(1)	3(1)				Coyotes (kg) 1	2(1)		
28	3.58						14.4			
56	3.60						14.3			
84	3.60						14.3			
112	3.66						12.7	0.836		
140	3.20	0.419					13.3	3.02		
168	3.47	1.20					13.8	4.22		
196	3.58	1.80					14.1	6.10		
224	3.60	2.31					14.2	7.79		
252	3.60	2.66					14.3	9.08		
280	3.06	2.91	0.209				14.4	10.2		
308	3.31	3.11	0.660				14.1	11.0		
336	3.54	3.27	1.37				13.7	11.5		
364	3.61	3.40	1.93				13.7	11.9		
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)
392	3.61	3.28					13.4	12.2		
420	3.61	3.46					13.5	12.5		
448	3.61	3.54					13.7	12.9		
476	3.61	3.56					12.3	11.7	0.730	0.836
504	3.23	3.17	0.385	0.382			13.4	12.9	1.64	1.76
532	3.49	3.42	1.10	1.11			13.7	13.4	3.66	3.68
560	3.61	3.57	1.74	1.75			14.0	13.8	5.58	5.60
588	3.62	3.59	2.28	2.29			14.2	14.0	7.58	7.58
616	3.62	3.59	2.68	2.69			14.3	14.2	9.18	9.18
644	3.25	3.13	2.93	2.95	0.209	0.209	14.4	14.3	10.4	10.4
672	3.68	3.37	3.10	3.14	0.339	0.854	14.2	14.1	11.3	11.3
700	3.75	3.60	3.28	3.28		1.56	13.9	13.8	11.9	11.9
728		3.61	3.41	3.41		2.12	13.8	13.8	12.4	12.4

Day/Cohort	Deer Mice (kg × 10⁻²) 1	2(1)	3(1)	4(1)	5(2)	6(1)	X(2)†	X(3)†		Sheep (kg) 1	2(1)	3(1)	
28	2.77									60.3			
56	2.84									60.3			
84	2.84	(0.164)								60.4			
112	2.54	0.250								60.6			
140	2.82	1.56								64.5	4.06		
168	2.84	2.30	0.164							60.2	7.31		
196	2.75	2.63	1.12							60.3	11.2		
224	2.85	2.76	2.08	(0.164)	0.164					61.0	15.7		
252	2.59	2.73	2.51	0.619	1.24					62.6	20.2		
280	2.83	2.83	2.72	1.73	2.10		(0.164)	(0.164)		61.9	23.9		
308	2.56	2.67	2.58	2.38	2.55	0.164	0.901	0.805		60.2	27.5		
336	2.80	2.84	2.81	2.67	2.73	1.37	1.90	1.84		59.0	30.9		
364	2.85	2.85	2.84	2.78	2.81	2.17	2.45	2.42		59.0	34.2		
		2A	7(2A)	8(2A)	9(2A)	10(7)	X(7)†	X(8)†		1	2(1)	3(1)	4(2)
392	2.85	2.83								59.7	37.1		
420	2.85	2.85								60.2	40.9		
448	2.85	2.85								60.5	43.6		
476	2.85	2.55	0.250							60.8	46.1		
504		2.79	1.46							63.8	50.6	4.06	
532		2.85	2.04	0.164						60.2	54.5	6.73	
560		2.68	2.61	0.925						60.6	56.7	10.7	
588		2.85	2.76	1.96		0.164				61.2	57.7	15.5	4.06
616		2.59	2.76	2.49	(0.164)**	1.32				63.0	52.9	20.6	7.30
644		2.84	2.44	2.71	1.67	2.16	(0.164)	(0.164)		62.0	52.9	24.6	11.7
672		2.85	2.70	2.51	2.34	2.58	0.957	0.693		60.2	53.5	20.3	16.0
700		2.85	2.85	2.83	2.67	2.74	1.99	1.82		59.8	54.7	33.6	20.4
728			2.85	2.84	2.78	2.81	2.49	2.42		59.0	55.8	35.8	24.9

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

† Additional groups not present in control run.

Table 4. Animal Densities, Alternate Growth Function (two years)

Day/Cohort*	Jackrabbits (No. × 10⁻²/ha)						Coyotes (No. × 10⁻³/ha)			
	1	2(1)	3(1)				1	2(1)		
28	14.3						21.5			
56	13.2						21.0			
84	12.1						20.6			
112	11.1	26.9					20.1	40.2		
140	9.31	20.8					16.9	29.4		
168	8.38	17.1					16.9	28.8		
196	8.14	15.8					16.8	28.3		
224	7.85	14.8					16.7	27.9		
252	7.53	14.1					16.5	27.5		
280	7.20	13.4	18.0				16.4	27.1		
308	5.57	12.8	10.2				16.2	26.8		
336	5.09	12.1	8.75				16.1	26.4		
364	4.69	11.3	7.78				15.9	26.1		
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)
392	4.37	17.1					15.7	25.8		
420	4.66	16.3					15.6	25.5		
448	3.76	15.6					15.4	25.3		
476	3.50	14.9	8.61	36.7			15.2	25.0	29.4	47.2
504	2.89	12.6	5.88	29.1			11.2	17.7	8.35	17.9
532	2.46	11.0	3.87	23.4			11.0	17.3	6.18	14.9
560	2.18	10.4	3.27	21.6			10.9	17.1	6.06	14.6
588	1.82	9.67	2.74	20.0			10.7	16.8	5.94	14.4
616	1.47	8.95	2.32	18.7			10.6	16.5	5.83	14.1
644	1.04	7.50	1.97	17.4	3.06	20.8	10.4	16.3	5.66	13.7
672	0.597	6.18	1.60	16.3	0.939	10.8	10.2	16.1	5.56	13.5
700	0.185	5.43	1.18	15.1		9.19	10.0	15.8	5.46	13.2
728		4.71	0.757	13.9		7.98	9.87	15.6	5.37	13.0

Day/Cohort	Deer Mice											Sheep (No. × 10⁻²/ha)		
	1	2(1)	3(1)	4(1)	5(2)	6(1)	x(2)†	x(3)†				1	2(1)	
28	16.8											16.5		
56	13.0											16.5		
84	10.0											16.5		
112	7.85	14.7										16.5		
140	6.81	11.9										16.5		
168	5.97	10.4										16.5	24.6	
196	4.94	9.38	8.63									16.5	24.6	
224	4.00	8.22	7.27									16.5	24.6	
252	3.26	6.19	6.19	1.11	4.95							16.5	24.6	
280	2.35	4.95	5.17	9.15	3.74							16.5	24.6	
308	1.83	3.94	4.16	7.68	3.05	3.27	6.65	6.95				16.5	24.6	
336	1.26	2.85	3.03	6.35	2.43	1.74	5.29	5.52				16.5	24.6	
364	0.918	2.21	2.38	5.18	1.91	1.34	4.33	4.52				16.5	24.6	
	1				2A	7(2A)	8(2A)	9(2A)	10(7)	x(7)†	x(8)†	1	2(1)	3(1)
392	0.741				16.9							16.5	24.6	
420	0.570				14.5							16.5	24.6	
448	0.393				12.6							16.5	24.6	
476	0.241				11.2	16.8						16.5	24.6	
504					9.26	14.8						16.5	24.6	
532					8.02	13.3	11.9					16.5	24.6	23.7
560					6.84	11.7	9.98					16.5	24.6	23.7
588					5.43	8.69	8.50	7.06	15.6			16.5	24.6	23.7
616					4.43	7.03	7.07	5.03	12.9			16.5	24.6	23.7
644					3.15	5.51	5.51	4.11	10.9	12.7	12.5	16.5	24.6	23.7
672					2.41	4.07	4.03	3.25	8.99	9.47	9.06	16.5	24.6	23.7
700					1.69	3.15	3.15	2.58	7.38	7.49	6.92	16.5	24.6	23.7
728						3.10	3.10	2.61	7.37	6.15	5.64	16.5	24.6	23.7

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

† Additional groups not present in control run.

Table 5. Animal Weights, Additional Temperature Functions (two years)

Day/Cohort*	Jackrabbits (kg)						Coyotes (kg)					Bear Mice (kg × 10^{-3})						Sheep (kg)		
	1	2(1)	3(1)				1	2(1)			Day/Cohort	1	2(1)	3(1)	4(1)	5(2)		1	2(1)	
28	3.46						15.0				28	2.36						56.2		
56	3.51						14.5				56	2.59						55.0		
84	3.53						14.3				84	2.69						54.9		
112	3.55	(0.184)**					12.9	0.737			112	2.49	0.210					55.0		
140	3.19	0.324					13.3	1.72			140	2.69	1.23					57.2		
168	3.35	0.959					13.6	3.46			168	2.79	1.85					53.4	6.01	
196	3.47	1.53					13.8	4.99			196	2.58	2.16	0.137				53.6	10.2	
224	3.53	1.91					14.0	6.16			224	2.78	2.37	1.51				54.2	14.6	
252	3.57	2.19					14.1	7.19			252	2.84	2.51	1.98	0.137	0.137		55.9	19.2	
280	3.13	2.40	0.196				14.2	8.07			280	2.72	2.46	2.25	1.00	0.849		56.5	22.8	
308	3.30	2.61	0.573				14.3	8.81			308	2.83	2.66	2.43	1.76	1.68		56.3	25.8	
336	3.48	2.77	1.29				14.3	9.44			336	2.85	2.74	2.56	2.11	2.07		55.7	28.3	
364	3.57	2.90	1.73				14.3	9.99			364	2.85	2.79	2.65	2.33	2.31		55.7	30.7	
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)		1	2A	7(2A)	8(2A)	9(7)	19(2A)	1	2(1)	3(1)
392	3.59	2.79					14.2	10.4			392	2.85	2.74					56.3	33.2	
420	3.60	2.99					14.2	10.9			420	2.85	2.81					56.8	35.4	
448	3.60	3.12					14.3	11.3			448	2.85	2.83					57.2	37.2	
476	3.60	3.21	(0.184)	0.184			12.9	10.3	0.737	0.737	476	2.85	2.85	0.209				57.6	38.9	
504	3.25	2.90	0.323	0.337			13.2	11.5	1.80	1.86	504		2.75	1.22				60.0	42.0	
532	3.43	3.14	0.960	0.980			13.7	11.9	3.49	3.51	532		2.83	1.85	0.137			56.4	44.7	6.01
560	3.55	3.30	1.53	1.53			13.9	12.3	5.00	5.00	560		2.63	2.06	0.571			56.7	46.6	10.2
588	3.60	3.39	1.91	1.91			14.1	12.6	6.18	6.17	588		2.81	2.37	1.56			57.2	47.6	14.6
616	3.61	3.45	2.18	2.18	(0.184)		14.2	12.8	7.20	7.20	616		2.59	2.51	2.01	0.137	0.137	58.8	48.2	19.2
644	3.22	3.48	2.40	2.40	0.245	0.184	14.3	13.1	8.08	8.08	644		2.76	2.46	2.26	1.15	0.848	59.2	48.3	22.8
672	3.40	3.21	2.62	2.61	0.742	0.475	14.4	13.2	8.84	8.83	672		2.84	2.66	2.44	1.82	1.68	58.7	48.0	25.8
700	3.56	3.41	2.81	2.80	1.40	1.22	14.3	13.4	9.47	9.47	700		2.85	2.74	2.56	2.15	2.07	57.9	47.8	28.3
728	3.62	3.52	2.95	2.92	1.80	1.68	14.3	13.5	10.0	10.0	728			2.79	2.66	2.36	2.31	57.0	48.0	30.7

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

Table 6. Animal Densities, Additional Temperature Functions (two years)

Day/Cohort*	Jackrabbits (No. = 10^{-2}/ha)						Coyotes (No. = 10^{-2}/ha)			
	1	2(1)	3(1)				1	2(1)		
28	14.4						21.5			
56	13.4						21.0			
84	12.4						20.5			
112	11.5	27.8					20.1	40.2		
140	9.99	17.3					18.0	5.21		
168	9.20	6.64					17.9	1.87		
196	9.03	6.19					17.8	1.51		
224	8.82	5.84					17.7	1.48		
252	8.58	5.54					17.6	1.45		
280	8.20	5.27	20.9				17.4	1.43		
308	6.81	5.00	5.58				17.3	1.41		
336	6.47	4.70	4.34				17.1	1.39		
364	6.17	4.40	3.98				17.0	1.38		
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)
392	5.94	6.91					16.8	1.36		
420	5.70	6.59					16.7	1.34		
448	5.47	6.29					16.5	1.32		
476	5.25	6.02	12.9	14.8			16.3	1.31	32.6	2.29
504	4.55	5.05	7.80	9.13			14.4	0.923	6.95	0.346
532	4.10	4.32	2.83	4.03			14.2	0.890	3.06	0.268
560	3.90	4.11	2.58	3.71			14.0	0.877	2.51	0.221
588	3.70	3.89	2.39	3.45			13.8	0.864	2.44	0.217
616	3.50	3.68	2.22	3.22	(8.40)**		13.6	0.851	2.40	0.213
644	3.19	3.48	2.06	3.01	7.10		13.4	0.838	2.35	0.209
672	2.67	2.79	1.87	2.77	1.73	8.62	13.2	0.826	2.31	0.206
700	2.46	2.52	1.67	2.51	1.35	1.57	13.0	0.813	2.27	0.202
728	2.26	2.32	1.48	2.27	1.15	1.37	12.8	0.800	2.23	0.198

Day/Cohort	Deer Mice (No. = 10^{-1}/ha)						Sheep (No. = 10^{-2}/ha)		
	1	2(1)	3(1)	4(1)	5(2)		1	2(1)	
28	18.2						16.5		
56	12.3						16.5		
84	9.16						16.5		
112	7.14	13.3					16.5		
140	6.12	10.2					16.5		
168	5.12	9.00					16.5	23.3	
196	4.49	8.02	9.15				16.5	23.3	
224	3.33	6.90	6.08				16.5	23.3	
252	2.75	5.71	5.20	10.4	5.23		16.5	23.3	
280	2.13	4.70	4.44	7.62	3.50		16.5	23.3	
308	1.63	3.36	3.63	6.27	2.89		16.5	23.3	
336	1.31	2.65	2.90	5.26	2.40		16.5	23.3	
364	1.05	2.12	2.30	4.35	1.97		16.5	23.3	
	1	2A	7(2A)	8(2A)	9(2A)	10(7)	1	2(1)	3(1)
392	0.893	8.10					16.5	23.3	
420	0.757	6.75					16.5	23.3	
448	0.626	5.87					16.5	23.3	
476	0.507	5.02	9.77				16.5	23.3	
504		4.37	7.53				16.5	23.3	
532		3.72	6.61				16.5	23.3	22.9
560		3.28	5.89	5.51			16.5	23.3	22.9
588		2.45	5.06	4.50			16.5	23.3	22.9
616		2.04	4.19	3.85	3.87		16.5	23.3	22.9
644		1.56	3.46	3.39	2.68	5.69	16.5	23.3	22.9
672		1.20	2.48	2.70	2.24	4.69	16.5	23.3	22.9
700		0.944	1.96	2.16	1.86	3.94	16.5	23.3	22.9
728			1.58	1.72	1.53	3.29	16.5	23.3	22.9

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

Table 7. Animal Weights, Combined Growth and Temperature Functions

Day/Cohort*	Jackrabbits (kg) 1	2(1)	3(1)	Coyotes (kg) 1	2(1)	Day/Cohort	Deer Mice (kg × 10⁻²) 1	2(1)	3(1)	4(1)	5(2)	X(2)†	X(3)†	Sheep (kg) 1	2(1)
28	3.52			15.2		28	2.42							60.5	
56	3.61			14.6		56	2.76							60.4	
84	3.62			14.5		84	2.84	(0.164)						60.4	
112	3.62	(0.184)**		12.8	0.836	112	2.54	0.247						60.5	
140	3.21	0.346		13.4	1.59	140	2.74	1.30						62.7	3.70
168	3.40	0.930		13.6	3.19	168	2.83	2.12	(0.164)					58.7	6.04
196	3.52	1.57		13.8	4.97	196	2.57	2.53	0.572					54.9	9.33
224	3.58	2.08		14.0	6.64	224	2.80	2.72	1.65	0.164				59.4	13.2
252	3.60	2.51		14.1	8.12	252	2.85	2.65	2.30	1.07	0.164			60.8	17.6
280	3.09	2.84	0.184	14.2	9.24	280	2.69	2.81	2.62	1.98	0.986	(0.164)	(0.164)	61.1	21.6
308	3.29	3.07	0.528	14.3	10.2	308	2.83	2.54	2.46	2.47	1.93	0.409	0.355	60.3	25.3
336	3.49	3.25	1.23	14.4	11.0	336	2.85	2.78	2.73	2.69	2.45	1.51	1.45	59.3	28.7
364	3.58	3.37	1.80	14.4	11.7	364	2.85	2.85	2.83	2.79	2.69	2.24	2.20	59.1	32.1

Day/Cohort*	Jackrabbits (kg) 1	2A***	4(1)	5(2A)	6(1)	7(2A)	Coyotes (kg) 1	2(1)	3(1)	4(2)
392	3.60	3.18					14.4	12.2		
420	3.61	3.38					14.4	12.7		
448	3.61	3.49					14.4	13.1		
476	3.61	3.55	0.184	0.184			12.7	11.8	0.836	0.836
504	3.22	3.17	0.349	0.351			13.4	12.8	1.68	1.75
532	3.43	3.38	0.939	0.936			13.6	13.2	3.22	3.25
560	3.56	3.52	1.57	1.57			13.9	13.5	4.98	4.99
588	3.61	3.59	2.09	2.09			14.1	13.8	6.65	6.65
616	3.62	3.60	2.51	2.51			14.2	14.0	8.13	8.11
644	3.14	3.11	2.84	2.84	0.184	0.184	14.3	14.1	9.24	9.24
672	3.36	3.31	3.09	3.08	0.640	0.574	14.4	14.2	10.2	10.2
700	3.56	3.51	3.27	3.26	1.33	1.27	14.4	14.3	11.0	11.0
728	3.63	3.60	3.41	3.39	1.87	1.84	14.4	14.4	11.7	11.7

Day/Cohort	Deer Mice (kg × 10⁻²) 1	2A	7(2A)	8(2A)	9(2A)	10(7)	X(7)†	X(8)†	Sheep (kg) 1	2(1)	3(1)	4(2)
392	2.85	2.79							59.6	35.6		
420	2.85	2.85							60.3	41.4		
448	2.85	2.85	(0.164)						60.3	41.6		
476	2.85	2.54	0.247						60.5	44.2		
504		2.75	1.30						62.8	48.2	3.70	
532		2.84	2.12	(0.164)					59.2	51.8	6.04	
560		2.57	2.53	0.570					59.7	54.3	9.33	
588		2.80	2.72	1.65	0.164				60.0	55.8	13.2	3.70
616		2.85	2.65	2.30	1.07	(0.164)			61.4	51.1	17.6	6.47
644		2.70	2.81	2.62	1.98	0.988	(0.164)	(0.164)	61.6	51.1	21.7	9.54
672		2.83	2.54	2.46	2.47	1.93	0.408	0.355	60.6	51.6	25.3	13.6
700		2.85	2.78	2.73	2.69	2.45	1.51	1.45	59.5	52.8	28.7	17.4
728			2.85	2.83	2.79	2.68	2.24	2.20	59.2	53.9	32.1	21.3

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

† Additional groups not present in control run.

Table 8. Animal Densities, Combined Growth and Temperature Functions (two years)

	Jackrabbits (No. × 10^{-2}/ha)						Coyotes (No. × 10^{-5}/ha)					Deer Mice (No. × 10^{-1}/ha)								Sheep (No. × 10^{-2}/ha)			
Day/Cohort*	1	2(1)	3(1)				1	2(1)			Day/Cohort	1	2(1)	3(1)	4(1)	5(2)	X(2)†	X(3)†		1	2(1)		
28	14.4						21.5				28	18.0								16.5			
56	13.3						21.0				56	12.2								16.5			
84	12.4						20.6				84	9.13								16.5			
112	11.4	27.7					20.1	43.2			112	7.22	13.6							16.5			
140	9.69	22.0					17.1	17.2			140	6.02	10.8							16.5			
168	8.76	15.0					17.1	6.75			168	5.03	9.51							16.5	22.4		
196	8.57	14.1					17.0	4.42			196	4.37	8.46	7.39						16.5	22.4		
224	8.35	13.3					16.7	3.48			224	3.24	7.39	6.15						16.5	22.4		
252	8.10	12.7					16.7	2.99			252	2.64	5.86	5.24	10.3					16.5	22.4		
280	7.83	12.1	19.6				16.6	2.87			280	2.05	4.51	4.41	8.61	3.40				16.5	22.4		
308	6.11	11.6	11.1				16.4	2.83			308	1.52	3.69	3.68	7.24	2.80	7.64	7.38		16.5	22.4		
336	5.75	11.1	9.48				16.3	2.80			336	1.20	2.65	2.69	6.00	2.30	5.00	4.92		16.5	22.4		
364	5.46	10.5	8.76				16.1	2.76			364	0.944	2.06	2.09	4.91	1.88	4.12	4.06		16.5	22.4		
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)		1	2A	7(2A)	8(2A)	9(2A)	10(7)	X(7)†	X(8)†	1	2(1)	3(1)	4(2)
392	5.24	15.4					15.9	2.73			392	0.799	14.4							16.5	22.4		
420	5.01	14.8					15.8	2.70			420	0.664	12.1							16.5	22.4		
448	4.79	14.2					15.6	2.67			448	0.534	10.5							16.5	22.4		
476	4.58	13.7	11.3	33.7			15.4	2.64	30.8	5.05	476	0.420	9.37	17.6						16.5	22.4		
504	3.84	11.6	8.48	26.7			12.9	1.96	18.5	2.98	504		7.71	13.9						16.5	22.4		
532	3.36	10.3	5.51	18.5			12.8	1.91	9.15	1.71	532		6.45	12.3						16.5	22.4	21.5	
560	3.16	9.97	4.98	17.2			12.6	1.88	6.16	1.18	560		5.60	10.9	9.51					16.5	22.4	21.5	
588	2.96	9.27	4.60	16.2			12.4	1.86	4.87	0.935	588		4.17	9.54	7.94					16.5	22.4	21.5	
616	2.97	8.78	4.26	15.2	(6.50)**	20.8	12.2	1.83	4.18	0.809	616		3.41	7.58	6.79	13.4				16.5	22.4	21.5	27.0
644	2.47	8.12	3.95	14.3	5.94	20.8	12.0	1.80	4.03	0.773	644		2.60	5.85	5.74	11.3	4.44			16.5	22.4	21.5	27.0
672	1.97	6.45	3.65	13.4	3.02	11.3	11.8	1.77	3.95	0.759	672		1.99	4.81	4.81	9.50	3.69	8.48	8.51	16.5	22.4	21.5	27.0
700	1.77	5.98	3.35	12.6	2.42	9.86	11.6	1.74	3.89	0.746	700		1.55	3.47	3.53	7.52	3.05	6.58	6.52	16.5	22.4	21.5	27.0
728	1.59	5.57	3.07	11.8	2.12	9.06	11.4	1.72	3.82	0.743	728			2.72	2.77	6.53	2.52	5.46	5.41	16.5	22.4	21.5	27.0

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.

†Additional groups not present in control run.

Table 9. Animal Weights, Alternate Metabolic Weight Parameter (two years)

Day/Cohort*	Jackrabbits (kg)						Coyote (kg)			
	1	2(1)	3(1)				(1)	2(1)		
28	3.48						14.3			
56	3.50						14.2			
84	3.52						14.2			
112	3.53	(0.184)**					12.8	0.737		
140	3.18	0.356					13.3	2.22		
168	3.43	1.28					13.7	4.53		
196	3.54	1.73					14.0	6.10		
224	3.56	2.07					14.2	7.31		
252	3.57	2.30					14.3	8.18		
280	3.12	2.48	0.184				14.3	8.88		
308	3.30	2.64	0.661				14.2	9.48		
336	3.52	2.79	1.41				14.0	9.95		
364	3.59	2.93	1.82				14.0	10.4		
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)
392	3.59	2.87					13.8	10.7		
420	3.59	2.06					13.9	11.0		
448	3.60	3.16					14.0	11.4		
476	3.59	3.23	0.184	0.184			12.7	10.5	0.737	0.737
504	3.25	2.92	0.357	0.368			13.4	11.5	1.93	2.02
532	3.47	3.18	1.17	1.18			13.7	12.0	3.98	4.02
560	3.59	3.35	1.69	1.69			14.0	12.5	5.65	5.67
588	3.60	3.42	2.05	2.06			14.2	12.8	7.11	7.12
616	3.60	3.45	2.32	2.32	(0.184)		14.3	13.1	8.22	8.22
644	3.25	3.01	2.50	2.51	0.281	0.185	14.4	13.3	9.01	9.02
672	3.50	3.23	2.65	2.66	1.11	0.780	14.2	13.3	9.63	9.63
700	3.62	3.49	2.81	2.80	1.63	1.49	14.0	13.3	10.2	10.2
728	3.63	3.53	2.96	2.95	1.83	1.90	14.0	13.3	10.6	10.6

Day/Cohort	Deer Mice (kg × 10^{-2})						Sheep (kg)		
	1	2(1)	3(1)	4(1)	5(2)	6(1)	1	2(1)	
28	2.55						54.6		
56	2.65						54.5		
84	2.72	(0.137)					54.6		
112	2.53	0.209					55.0		
140	2.77	1.49					58.7	3.70	
168	2.81	1.97	0.137				54.7	7.68	
196	2.74	2.24	1.17				54.7	12.7	
224	2.83	2.42	1.83	(0.137)			55.5	17.6	
252	2.61	2.55	2.14	0.566	0.137		57.5	21.7	
280	2.83	2.52	2.35	1.60	1.11	0.137	57.6	24.8	
308	2.60	2.70	2.50	2.02	1.79	0.148	55.6	27.4	
336	2.80	2.76	2.61	2.28	2.13	1.36	55.7	29.7	
364	2.85	2.79	2.69	2.45	2.35	1.89	55.7	32.0	
	1	2A	7(2A)	8(2A)	9(2A)	10(7)	1	2(1)	3(1)
392	2.84	2.78					56.5	34.5	
420	2.85	2.82					57.0	36.5	
448	2.85	2.83	0.137				57.5	38.3	
476	2.85	2.59	0.211				57.9	40.0	
504		2.80	1.42				60.8	43.4	3.73
532		2.84	1.94	0.137			57.3	46.3	6.84
560		2.73	2.23	1.08			57.5	48.0	11.9
588		2.85	2.42	1.78			58.1	48.8	17.2
616		2.62	2.55	2.14	0.137	0.137	60.3	49.0	22.1
644		2.84	2.56	2.35	1.60	1.17	60.1	48.4	25.3
672		2.85	2.71	2.50	2.03	1.82	58.6	47.9	28.0
700		2.85	2.76	2.61	2.29	2.16	57.5	47.7	30.5
728			2.79	2.69	2.46	2.37	57.6	48.2	33.1

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data avereraged and incremented. This becomes group 2A.

Table 10. Animal Densities, Alternate Metabolic Weight Parameter (two years)

Day/Cohort	Jackrabbits (No. × 10⁻²/ha)						Coyotes (No. × 10⁻⁵/ha)				Day/Cohort	Deer Mice (No. × 10⁻¹/ha)						Sheep (No. × 10⁻⁴/ha)		
	1	2(1)	3(1)				1	2(1)				1	2(1)	3(1)	4(1)	5(2)	6(1)	1	2(1)	
28	14.3						21.5				28	17.4						16.5		
56	13.2						21.0				56	13.4						16.5		
84	12.2						20.6				84	10.3						16.5		
112	11.2	27.2					20.1	40.1			112	8.08	14.9					16.5		
140	9.70	17.3					17.6	15.3			140	6.98	11.8					16.5		
168	8.88	13.7					17.6	14.8			168	6.16	10.3					16.5	24.3	
196	8.67	12.7					17.5	14.6			196	4.78	8.21	8.17				16.5	24.3	
224	8.41	11.9					17.4	14.4			224	3.93	8.01	6.88				16.5	24.3	
252	8.15	11.3					17.2	14.1			252	3.03	6.85	5.90	4.94			16.5	24.3	
280	7.87	10.7	19.7				17.1	13.9			280	2.19	5.41	4.98	3.80	9.36		16.5	24.3	
308	6.42	10.2	8.56				16.9	13.7			308	1.76	4.16	4.13	3.15	7.77	3.28	16.5	24.3	
336	5.99	9.62	7.43				16.8	13.6			336	1.26	3.33	3.34	2.60	6.50	2.09	16.5	24.3	
364	5.64	9.01	6.75				16.6	13.4			364	0.978	2.66	2.66	2.12	5.42	1.70	16.5	24.3	
	1	2A***	4(1)	5(2A)	6(1)	7(2A)	1	2(1)	3(1)	4(2)		1	2A	7(2A)	8(2A)	9(2A)	10(7)	1	2(1)	3(1)
392	5.36	14.2					16.5	13.2			392	0.813	11.4					16.5	24.3	
420	5.08	13.5					16.3	13.1			420	0.681	9.76					16.5	24.3	
448	4.80	12.9					16.2	12.9			448	0.551	8.52					16.5	24.3	
476	4.55	12.3	11.0	30.5			16.0	12.7	31.5	22.9	476	0.435	7.57	14.1				16.5	24.3	
504	3.91	10.4	7.05	20.7			13.4	9.24	7.12	7.04	504		6.12	11.3				16.5	24.3	
532	3.47	9.01	4.10	14.0			13.2	8.91	5.90	6.11	532		5.54	9.90				16.5	24.3	23.4
560	3.22	8.51	3.63	13.0			13.0	8.78	5.79	6.00	560		4.63	8.84	8.22			16.5	24.3	23.4
588	2.93	7.98	3.21	12.0			12.8	8.65	5.68	5.88	588		3.79	7.71	6.93			16.5	24.3	23.4
616	2.65	7.46	2.85	11.2	6.05		12.6	8.53	5.57	5.77	616		2.92	6.60	5.94	4.85		16.5	24.3	23.4
644	2.21	6.95	2.54	10.4	3.53	17.4	12.4	8.40	5.47	5.67	644		2.10	5.20	5.04	3.56	8.95	16.5	24.3	23.4
672	1.80	5.43	2.21	9.65	1.19	7.54	12.2	8.27	5.37	5.57	672		1.65	4.14	4.21	2.94	7.43	16.5	24.3	23.4
700	1.44	4.83	1.83	8.88	.575	6.34	12.1	8.14	5.28	5.48	700		1.26	3.34	3.44	2.43	6.23	16.5	24.3	23.4
728	1.06	4.27	1.42	8.01	.001	5.48	11.9	8.02	5.19	5.47	728			2.71	2.80	2.01	5.26	16.5	24.3	23.4

* Each group is identified by a cohort number followed by the identification number for its parent group.

** Weights in parentheses represent birth weights of animals born between recorded days.

*** At the end of each year all animals born in that year are grouped as one, their data averaged and incremented. This becomes group 2A.