

H. H. MITCHELL

**COMPARATIVE  
NUTRITION OF MAN  
AND DOMESTIC ANIMALS**

**VOLUME 2**

Comparative Nutrition  
of Man and  
Domestic Animals

VOLUME II

COPYRIGHT © 1964, BY ACADEMIC PRESS INC.

ALL RIGHTS RESERVED

NO PART OF THIS BOOK MAY BE REPRODUCED IN ANY FORM  
BY PHOTOSTAT, MICROFILM, OR ANY OTHER MEANS,  
WITHOUT WRITTEN PERMISSION FROM THE PUBLISHERS

ACADEMIC PRESS INC.

111 FIFTH AVENUE  
NEW YORK 3, N. Y.

*United Kingdom Edition*

Published by  
ACADEMIC PRESS INC. (LONDON) LTD.  
BERKELEY SQUARE HOUSE  
BERKELEY SQUARE, LONDON, W.1

*Library of Congress Catalog Card Number 62-13115*

PRINTED IN GREAT BRITAIN BY THE WHITEFRIARS PRESS LTD.  
LONDON AND TONBRIDGE

## PREFACE

The purpose of this treatise is to present a critical and, in some respects, provocative discussion and summary of present knowledge in the selected segment of the field of comparative nutrition indicated in the title. The literature relating to this most recent approach to the study of nutrition exists mainly in journals and in sections of books devoted to a much larger coverage with emphasis on the physiology or the biochemistry rather than the more practical phases of nutrition. The particular segment of comparative nutrition chosen for treatment here, namely, that relating to man and domestic animals, was dictated by the availability of pertinent information bearing on the practical phases of the subject, such as nutrient requirements and the extent to which the animal body can utilize the nutrients in its food supply.

The treatise had its inception in a graduate course in comparative nutrition at the University of Illinois, developed during a period of some thirty years. In parallel with the development of the course, an experimental research program was pursued concerned with studies of the chemical growth and nutritive requirements (including energy) of poultry, swine, sheep, and cattle, and later of human subjects. This program was often carried out in co-operation with the various Divisions of the Departments of Animal Science and the Departments of Physiology, of Home Economics, and of Medicine in the College of Medicine in Chicago. My colleague Dr. T. S. Hamilton and I planned and guided the biochemical phases of most of these studies. The results of these correlated (if sometimes only loosely so) investigations supplied much of the basic material for many of the chapters in this treatise.

The primary purpose of the volumes is to present and correlate, in a quantitative fashion, the nutrient requirements of man and his domesticated animals and the factors that modify these quanta; the similarities and dissimilarities among the different species of animals are pointed out. Considerable discussion has also been given to the background information, largely biochemical in nature, concerning the various nutrients, their functions, and their participation in the energy transactions of the body.

The treatise was written with the training and the interests of graduate students in mind, particularly those students majoring in nutrition, physiology, home economics, or biochemistry, or those majoring in some branch of animal science and minoring in nutrition. A basic course in organic chemistry and in biochemistry is essential, while some knowledge of animal physiology or zoology and of statistics is helpful.

The treatment of the subject matter of the book is unique in that net nutrient requirements are expressed in terms of animal expenditures and storages, factored into their ultimate terms: maintenance, growth, activity, reproduction, etc. These net requirements are converted into dietary requirements after due considerations of the wastages of dietary nutrients in the course of their assimilation in the body. These two lines of nutritional enquiry are distinct in the techniques required for their measurement and in the factors that determine their magnitude, if the ultimate goals of the science of nutrition are to be completely attained and the flexibility in the application of its principles preserved.

In the Division of Animal Nutrition, the participation of Dr. B. C. Johnson, the late Dr. Harry Spector, Dr. J. B. Shields, Dr. R. M. Forbes, Mr. W. T. Haines, and Miss Jesse R. Beadles, now deceased, in some phases of the above-mentioned research program was important to the success of this work, as well as that of the many graduate students who contributed in one capacity or another to limited segments of the researches. In the investigations requiring the cooperation of other Divisions in the Department of Animal Science, the author acknowledges with gratitude the participation of Dr. L. E. Card, Dr. W. E. Carroll, and Dr. W. G. Kammlade. In studies requiring the participation of other Departments in the University, the assistance of Dr. F. R. Steggerda, Dr. Julia O. Holmes, Dr. Janice M. Smith, Miss Beula McKey, and the late Dr. Robert W. Keeton is gratefully acknowledged.

Occasionally the opportunity arose to prepare critical reviews of the areas with which the research program of the Division was concerned. The cooperation of Dr. F. J. McClure, of Mrs. Elizabeth Curzon, and of Miss Marjorie Edman was highly important to whatever success these reviews may have attained.

In the preparation of these volumes, the author takes pleasure in acknowledging the generosity of the University of Illinois in extending to him the use of its facilities, including office space, during his retirement from active service. To the members of the staff of the College of Agriculture he is indebted for advice in many pertinent problems. In particular he acknowledges with gratitude the assistance of Miss Marjorie Edman, with whom he has been associated for many years in joint authorship of scientific papers and in the discussion of nutritional problems as they arose. Miss Edman has assumed much of the responsibility in tracking down publications pertinent to the book coverage, in the documentation of the various chapters of the book, and in the supervision of the preparation of the manuscript for the publisher. Her help has been invaluable.

To my wife I wish to express my deep gratitude for her forbearance during my virtual seclusion during the years of preparation of the book, for her encouragement and her patience with the slow progress made, and for the

active parts she has taken in the arduous proofreading required in such an undertaking, of material quite foreign to her interests, often expressed in terms unintelligible to the layman. The author here expresses his appreciation to Mrs. Alma White for her generous help in handling the considerable volume of correspondence associated with the preparation of these volumes, and to Mrs. Rita Ellis for typing much of the final copy of the manuscript.

The author gladly acknowledges his gratitude to his colleagues in nutrition for the use of quotations from their publications, and to those publishers and editors of scientific journals and books who gave their permission to use charts and data that have appeared in their publications, realizing as most of them have, that their responsibilities as custodians of the storehouse of contemporary scientific knowledge impels a relaxation of the rights given to them by copyright in order to promote the widest use of such knowledge for the advancement of science.

In the preparation of the manuscript of this book for publication it has been a pleasure to work with the staff of Academic Press. Their comments and suggestions have contributed much to the style and readability of the text. While the author accepts full responsibility for errors that seem inevitably to creep into such an undertaking as this, he is confident that their number has been considerably reduced because of this competent cooperation of the publishers.

H. H. MITCHELL

Urbana, Illinois

## CONTENTS OF VOLUME I

### *Section I: The Nutrient Requirements of the Animal Body. Requirements Represented by Nutrient Expenditures*

1. The Maintenance Requirement of Energy: The Basal Metabolism
2. The Maintenance Requirement of Energy: The Activity Increment
3. The Maintenance Requirement of Protein
4. The Water Requirements for Maintenance
5. The Mineral Requirements of Maintenance
6. The Nutrient Requirements for Muscular Work
7. The Nutrient Requirements for Growth and Senescence
8. The Storage of Nutrients in the Body, with Particular Reference to Fattening and Obesity
9. The Nutrient Requirements for Mammalian Reproduction
10. The Nutrient Requirements for Lactation
11. The Nutrient Requirements for Egg Production

AUTHOR INDEX

SUBJECT INDEX

## INTRODUCTION

The science of nutrition deals primarily with the interactions between the animal body and its food supply with the ultimate purpose of defining quantitatively the fully adequate food supply for any combination of animal functions and for any type of internal and external stress. Obviously, this purpose can best be realized most economically, not by studying all possible combinations of animal functions, but, in so far as possible, by studying animal functions each in turn with reference to the nutrient expenditures or storages involved—in growth, activity, reproduction, lactation, etc.—and the conditions, within the animal or in the environment, that modify these methods of nutrient disposal. In this way, nutrient requirements can be assessed for each function under any given set of conditions.

In combining these assessed expenditures and storages of nutrients to obtain a total nutrient requirement of an animal of given species, age, sex, and physiological status, it cannot be assumed that "the whole is the sum of its parts," because the imposition of one function upon another may result in stimulation or inhibition of one or both functions. Thus, pregnancy stimulates basal metabolism while inhibiting lactation. These interrelationships among animal functions need further study, particularly quantitative study, for the attainment of the most satisfactory results in practical nutrition.

Fully adequate diets or rations, thus visualized as the ultimate goal of nutritional research, are of necessity well-balanced diets or rations. A balanced diet may be defined as one containing proportions of each of the essential nutrients large enough to promote maximum performance of those animal functions with respect to which the diet is balanced, but not so large as to impair in any way the well-being of the animal consuming it or of any of its tissues, or to depress the net energy content of the diet. The carbohydrate and fat content of a balanced diet should be sufficient in amount to permit the full use of the essential nutrients to perform their specific functions in the body, but not so great as to impair physically the maximum performance of all organs of the body.

In addition, the balanced diet must contain no injurious (or toxic) factors, or at most such amounts of such factors as are innocuous to the animal consuming it.

In realizing experimentally the attainment of balanced diets or rations, any dietary modification that induces an increase in the rate of growth of an experimental animal, or any other indication of improvement in nutritive condition, is *prima facie* evidence of an improvement in the balance of the diet. A corollary to this statement is that dietary modifications that do not



produce indications of improved nutritive conditions do not improve the dietary balance.

Looking at it another way, those dietary modifications that induce indications of improvement in the nutritive condition of experimental animals increase the nutritive value of the basal diet per gram consumed. This means a better utilization of its contained energy. However, the penalty in energy wastage associated with the consumption of an unbalanced diet may not be apparent in the case of animals like the beef calf that have been bred (and fed) to fatten and grow simultaneously.

Hence, the utilization of the metabolizable energy of a completely balanced diet is maximal, and the same for all such diets for each animal function, but varies from species to species.

Hence, also the nutritive value of feeds is specific and characteristic for the various feeds only with respect to their content of nutrients and their digestibility. The extent to which the absorbed nutrients are utilized in the body is dependent upon (1) the way in which feeds are combined in the diet, and (2) the animal functions they support.

Quoting E. B. Forbes, "... an individual foodstuff expresses its normal and characteristic nutritive value ... only as it is a part of a ration which is qualitatively complete and quantitatively sufficient, for the conditions existing."

Of the balanced ration, it may be said that the more of it that is consumed, the better nourished will be the animal with reference to which the ration is balanced, up to the point of repletion of its requirements. On the other hand, the greater the consumption of a ration deficient in one or more essential nutrient the less well nourished an animal will be and the quicker will deficiency symptoms appear.

Nutrient requirements revealed by investigations on experimental animals can be expressed only in terms of the animal, not of its food supply. The expression of nutrient requirements in terms of dietary proteins, dietary minerals, available energy, and vitamins requires quantitative evaluation of the losses of dietary nutrients in the course of their assimilation, in digestion, and in metabolism. If an animal expends or stores (or both) 6000 calories of energy, and from a given food supply loses 40% of its energy in its assimilation, the dietary requirement of energy will be 10,000 calories. The situation is greatly complicated by the fact that food energy losses in the course of assimilation vary with the nutritive adequacy of the diet for the functions it is serving in the animal it is nourishing, with the conditions of feeding, and with the purposes for which the energy is used in the body.

Thus, two lines of nutritional investigation, the one relating to the animal and the other to its food supply, are distinct in the techniques required for their prosecution and in the factors that modify the magnitude

of the results obtained. The two lines of study should not be confused where the most complete understanding of the results is desired and the most complete attainment of the ultimate purposes of the science of nutrition is the end in view.

Different species of animals differ in their biochemical and nutritional behavior, but most often these differences are quantitative in nature rather than qualitative. Certain broad principles may be formulated that describe the metabolic and nutritional behavior of many species of animals. These are the basic principles of the science of nutrition upon which predictions of nutritional behavior in particular cases may be made. The existence of such principles among animals justifies the use of many different species in studying particular nutritional problems, depending upon their adaptability to the experimental techniques that must be employed and, at times, upon the degree to which they can cooperate with the investigator in securing the desired ends. They justify, also, the carrying over of experimental findings from one species to another, at least until direct study of all species is attained. Thus, the principles governing the nutritional behavior of man are no more to be distinguished from the principles governing the nutritional behavior of farm animals than from the principles governing the nutritional behavior of the albino rat and of other laboratory animals, experiments on which so much of the science of physiology, including nutrition, has been derived.

However, it must always be remembered that, superimposed upon the apparent fixity of nutritional behavior among species of animals there are secondary and specific modifications that reflect adaptations to different environmental conditions. These are the modifications that distinguish one species from another. They may be evolutionary in character and genetic in persistence, taking generations to develop and requiring eons of time. Within any one species, adaptations to changes in environment and in food supply may occur in relatively short intervals of time, in weeks or months, or possibly years. These are the adaptations that necessitate the conception of a nutrient requirement as a range of values, symmetrically including a mean measure, rather than the mean itself.

Scarcity of the necessary nutritional data of the required character and precision have limited the species coverage, and prevented any considerable consideration of some domestic species, such as the cat and the dog, which it would otherwise have been desirable to have included in the discussions in the following chapters.

The adaptability of animal life to environmental changes is one of its most characteristic features, permitting its continuance under catastrophic geologic changes and its distribution throughout the earth with its varied climates, in sea, land, and air. Among the homoiothermic animals, the

homeostatic mechanisms regulating the constancy of body temperature, of the hydrogen ion concentration of the fluids and tissues, of the character and kinetics of its enzyme systems, are aided by the buffering action of the adaptation processes.

The statements made thus far may seem to the reader to be largely dogmatic and opinionated. It will be the purpose of the various chapters in the two volumes of this treatise to establish their validity or at least their rationality. An important purpose of the discussions to follow will be to harmonize the available knowledge of the nutrition of man with that of the nutrition of farm animals. In fact, human nutrition can profit from the revelations of investigations of the nutrition and biochemistry of farm animals much more than it has up to the present. Conversely, college courses in animal nutrition can be made more interesting to agricultural students by the demonstrations that much of what we know of animal nutrition is applicable to the students themselves.

The discussions in the following chapters will be divided into four sections, in accordance with the ideas stated above:

Section I. Nutrient Requirements in Terms of Body Expenditures and Storages: Chapters 1 through 11. This constitutes Volume 1.

Section II. Vitamin Requirements in Terms of Dietary Equivalents: Chapters 12, 13, and 14. This section marks a necessary departure from the plan mapped out above, because of the lack of quantitative information on vitamin expenditures at the present writing.

Section III. The Wastage of Nutrients during Assimilation. Net Nutrient Values: Chapters 15 through 20.

Section IV. Fulfillment. Chapter 21, with tables and discussion illustrating the factorization, integration, and adaptation of dietary requirements to changing conditions.

A critical discussion of available knowledge in any discipline inevitably involves evaluation of methods as well as the results of research. This situation may be resolved in either one of two ways, i.e., disregard investigations of doubtful significance, or discuss such investigations with such reservations as their design and interpretation may dictate. If the literature in a certain area of knowledge seems to be only in part ambiguous in significance, only the better contributions need be considered, but if the literature in respect to an important phase of a subject under discussion is wholly ambiguous from the standpoint of methodology, then it becomes the painful

duty of a reviewer to point out the specific items with respect to which an investigation is vulnerable, such as improper controls, failure to assess the magnitude of experimental random errors by statistical analysis, disregard of the limitations of isotope-tracer techniques, improper use of correlation coefficients.

As R. A. Fisher has well said: "A clear grasp of simple and standardized statistical procedures will . . . go far to elucidate the principles of experimentation; but these procedures are themselves only the means to a more important end. Their part is to satisfy the requirements of sound and intelligible experimental design, and to supply the machinery for unambiguous interpretation."

## CONTENTS

PREFACE . . . . .	vii
CONTENTS OF VOLUME I . . . . .	xv
INTRODUCTION . . . . .	xvii

### Section II: VITAMIN REQUIREMENTS IN TERMS OF DIETARY EQUIVALENTS

#### 12. The Dietary Requirements for the Fat-Soluble Vitamins and Vitamin C

I. Introduction . . . . .	3
II. Vitamin A . . . . .	7
III. Vitamin D . . . . .	28
IV. Vitamin E (The Tocopherols) . . . . .	35
V. Vitamin K . . . . .	45
VI. Vitamin C: Ascorbic Acid . . . . .	49
References . . . . .	66

#### 13. The Dietary Requirements for the B Vitamins

I. Introduction . . . . .	75
II. Thiamine . . . . .	78
III. Riboflavin . . . . .	95
IV. Nicotinic Acid (Niacin) . . . . .	107
V. Pyridoxine (Vitamin B <sub>6</sub> ) . . . . .	120
VI. Pantothenic Acid . . . . .	129
VII. Vitamin B <sub>12</sub> (The Cobalamin Derivatives) . . . . .	134
VIII. Pteroylglutamic Acid (Folic Acid) and Related Substances . . . . .	145
IX. Biotin . . . . .	150
X. Choline and Inositol . . . . .	157
References . . . . .	158

## 14. Vitamin Requirements in Panorama

I. The Basic Requirements for Vitamins Under Nonstress Conditions . . . . .	177
II. Variability in Vitamin Requirements . . . . .	185
III. The Beneficial Effects of Levels of Vitamin Intake Higher than Basic Requirements . . . . .	188
IV. Vitamin Requirements Under Conditions of Stress . . . . .	212
V. Vitamins as Pharmacologic Agents . . . . .	253
VI. The Formulation of Vitamin Recommendations for Reasonable Health Security . . . . .	257
References . . . . .	265

## Section III: THE UTILIZATION OF DIETARY NUTRIENTS

## 15. An Interpretive Interlude

I. Introduction . . . . .	283
II. The Comparability of Net Nutrient Requirements for Animals of Different Species . . . . .	284
III. Animal Size and Productivity . . . . .	286
IV. Methodology . . . . .	290
V. The Measurement of Precision . . . . .	302
VI. The Dermal Losses of Nutrients . . . . .	305
References . . . . .	305

## 16. The Nutrients Contained in Foods

I. The Analysis of Food Materials . . . . .	309
II. Conutrients . . . . .	322
References . . . . .	349

## 17. Nutrient Wastage in Digestion: Absorption

I. Introduction . . . . .	361
II. The Agents of Digestion: Enzymes . . . . .	362
III. The Agents of Digestion: Gastrointestinal Microorganisms . . . . .	367
IV. The Regulation of the Digestive Processes . . . . .	385

17. Nutrient Wastage in Digestion: Absorption—*contd.*

V. The Waste Products of Digestion: The Feces . . . . .	387
VI. The Measurement of Digestibility . . . . .	388
VII. The Results of Digestion Experiments . . . . .	419
VIII. Gastrointestinal Absorption . . . . .	432
References . . . . .	449

## 18. The Wastage of Nutrients in Metabolism: Energy

I. Introduction . . . . .	471
II. Metabolizable Energy . . . . .	480
III. Factors Affecting the Net Availability of Metabolizable Energy (N.A.M.E.) and the S.D.A. . . . .	489
IV. The Causation of the S.D.A. of Foods . . . . .	541
V. Methods of Expressing the Fully Available Energy of Rations and Diets . . . . .	547
References . . . . .	554

## 19. The Wastage of Nutrients in Metabolism: Protein and Amino Acids

I. Introduction . . . . .	567
II. The Biological Evaluation of the Nutritive Values of Proteins . . . . .	575
III. Chemical Evaluation of the Nutritive Value of Proteins . . . . .	611
IV. The Quantitative Nutritional Evaluation of Proteins from Their Amino Acid Make-up . . . . .	615
V. The Biological Justification for Chemical Methods of Assessing Protein Nutritional Quality . . . . .	636
References . . . . .	645

## 20. The Wastage of Nutrients in Metabolism: Minerals and Vitamins

I. The Wastage of Minerals . . . . .	661
II. The Wastage of Dietary Vitamins in Their Assimilation in the Animal Body . . . . .	691
References . . . . .	695

*Section IV: FULFILLMENT*

## 21. Fulfillment

I. A Summary of Prior Discussions of Nutritional Problems with a Glimpse into the Future . . . . .	705
II. Illustrations of the Integration of Factored Requirements and Utilizations of Nutrients and Energy . . . . .	732
III. Finale . . . . .	777
References . . . . .	780
AUTHOR INDEX . . . . .	789
SUBJECT INDEX . . . . .	824



*Section II*

**VITAMIN REQUIREMENTS  
IN TERMS OF DIETARY EQUIVALENTS**