

WILDLIFE ECOLOGY

AN ANALYTICAL APPROACH

AARON N. MOEN

Cornell University

with a foreword by Douglas L. Gilbert
Colorado State University

W. H. FREEMAN AND COMPANY

SAN FRANCISCO



3 3755 000 97486 5

ARLIS

Alaska Resources Library & Information Services
Library Building, Suite 111
3211 Providence Drive
Anchorage, AK 99508-4634

This document is copyrighted material.

Alaska Resources Library and Information Services (ARLIS) is providing this excerpt in an attempt to identify and post all documents from the Susitna Hydroelectric Project.

This book is identified as APA no. 3215 in the Susitna Hydroelectric Project Document Index (1988), compiled by the Alaska Power Authority.

It is unable to be posted online in its entirety. Selected pages are displayed here to identify the published work.

The book is available at call number TK1425.S8A23 no.3215 in the ARLIS Susitna collection.

Copyright © 1973 by W. H. Freeman and Company

No part of this book may be reproduced by any mechanical, photographic, or electronic process, or in the form of a phonographic recording, nor may it be stored in a retrieval system, transmitted, or otherwise copied for public or private use without written permission of the publisher.

Printed in the United States of America

2 3 4 5 6 7 8 9

Library of Congress Cataloging in Publication Data

Moen, Aaron N 1936-
Wildlife ecology.

Bibliography: p.

1. Zoology—Ecology. 2. Wildlife management.
3. Ruminantia. I. Title.
QH541.M54 599'.735'045 73-6833
ISBN 0-7167-0826-4

CONTENTS

Foreword	<i>xiii</i>
Preface	<i>xv</i>
Acknowledgments	<i>xvii</i>

PART 1

LIFE, INTERACTIONS, AND ECOLOGICAL MODELING

1	PRODUCTIVITY GRADIENTS	3
	1-1 The concept of life	3
	1-2 The role of the analytical ecologist	4
	1-3 Dead or alive	5
	1-4 Productivity of the individual	5
	1-5 The natural mosaic	7
	1-6 Interspecies interaction	10
	1-7 Intraspecies interaction	11
	1-8 Reproductive patterns	12
	1-9 A theoretical mosaic	13
2	INTERACTIONS BETWEEN ORGANISMS AND ENVIRONMENT	16*
	2-1 Functional relationships	16
	2-2 The scope of the environment	21
	OPERATIONAL, POTENTIAL, AND HISTORICAL RELATIONSHIPS	21
	TIME	24
	ASSOCIATED RELATIONSHIPS	25
	HABITAT EVALUATION	26
3	ECOLOGICAL MODELING AND SIMULATION	32
	3-1 Mathematical models	33
	3-2 The analytical model in ecology	36

PART 2
THE DISTRIBUTION OF MATTER AND ENERGY
IN TIME AND SPACE

4	SOIL, WATER, AND TOPOGRAPHY	43
4-1	Soil	44
	PHYSICAL CHARACTERISTICS	44
	SOIL PROFILE	46
	SOIL WATER	46
	CHEMICAL CHARACTERISTICS	47
	BIOLOGICAL CHARACTERISTICS	48
4-2	Soil classification in transition	51
4-3	Eutrophication	52
4-4	Biogeochemical cycles	53
5	WEATHER IN RELATION TO PHYSICAL CHARACTERISTICS	57
5-1	The distribution of sunlight	57
	THE ATMOSPHERE	60
5-2	Atmospheric water	62
5-3	Precipitation	62
	RAIN	62
	RAINFALL IN RELATION TO SOIL AND TOPOGRAPHY	66
	SNOW	68
	CONDUCTIVITY	69
5-4	Snow cover in relation to kinetic energy	69
	WINDPACK	69
	THE EFFECT OF WINDBREAKS	70
	SNOWFALL INTERCEPTION	72
	THE ROLE OF SNOW IN A PRECIPITATION-CANOPY-SUBSTRATE MODEL	72
	THE EFFECT OF SNOW DISTRIBUTION ON ANIMALS	72
6	WEATHER AND THE PROCESSES OF THERMAL EXCHANGE	75
6-1	The four modes of heat transfer	75
6-2	Radiant energy exchange	76
	THE ELECTROMAGNETIC SPECTRUM	76
	SOLAR RADIATION	77
	INFRARED RADIATION	78
	ATMOSPHERIC TRANSMISSION AND ABSORPTION CHARACTERISTICS	78
	ATMOSPHERIC EMISSION	80
	RADIATION FROM PHYSICAL AND BIOLOGICAL OBJECTS	84
	EMISSIVITY AND REFLECTIVITY OF SNOW	85
	RADIANT TEMPERATURE IN RELATION TO AIR TEMPERATURE	85

6-3 Instrumentation for measuring radiation	90
6-4 Convection	92
AIR MOVEMENT	92
MEAN VELOCITY WIND PROFILES	93
6-5 Convective heat loss	94
6-6 Conduction	97
6-7 Heat loss by evaporation	98
6-8 Conclusion	103

PART 3 METABOLISM AND NUTRITION

7 ENERGY METABOLISM	109
7-1 Basal metabolism and associated terminology	110
USES FOR MEASUREMENTS OF BASAL METABOLIC RATE	110
CONDITIONS FOR MEASUREMENT	110
ASSOCIATED TERMINOLOGY	112
7-2 Measurements of basal metabolic rate	112
DIRECT METHODS	112
INDIRECT METHODS	112
CALCULATION OF HEAT PRODUCTION	113
7-3 Metabolic rates of ruminants	115
RELATIONSHIPS OF BODY WEIGHT	115
METABOLIC RATES OF WILD RUMINANTS	116
FASTING METABOLISM OF DOMESTIC RUMINANTS	120
7-4 Metabolic rates of other animals	120
7-5 Factors influencing energy metabolism and heat production	123
THE RELATIONSHIP BETWEEN HEAT PRODUCTION AND SURFACE AREA	126
HEAT INCREMENTS DUE TO DIET	127
HEAT INCREMENTS DUE TO ACTIVITY	127
NONSHIVERING THERMOGENESIS	127
SEX DIFFERENCES	128
REPRODUCTIVE CONDITION	128
RHYTHMIC CHANGES IN THE BASAL METABOLIC RATE	129
INSULATION CHARACTERISTICS	129
WEATHER	130
PATHOGENS AND PARASITES	130
7-6 Social and psychological effects on heat production	130
8 DIGESTION	135
8-1 The definition of digestion	135
8-2 A research philosophy	135
8-3 Chemical composition of food materials	136
WATER	137
NITROGENOUS SUBSTANCES—CRUDE PROTEIN	137
CARBOHYDRATES—NITROGEN-FREE EXTRACT	138

CARBOHYDRATES—CRUDE FIBER	138
ETHER EXTRACT	138
ASH	138
SUMMARY OF PROXIMATE ANALYSIS	139
8-4 The nutritive evaluation of forages	139
8-5 The alimentary canal	141
ANATOMY	141
HISTOLOGY	144
8-6 Mechanical and secretory processes in digestion	145
INGESTION	147
SALIVATION AND MASTICATION	147
RUMINATION	147
STOMACH AND INTESTINAL MOVEMENTS	147
DEFECATION	149
8-7 Chemical processes of digestion	149
RUMEN MICROORGANISMS	150
FERMENTATION	151
pH	153
8-8 Products of fermentation	153
HEAT ENERGY	153
GASES	153
VOLATILE FATTY ACIDS	154
PROTEIN	156
VITAMINS AND MINERALS	157
8-9 Passage of digesta through the gastrointestinal tract	157
8-10 Digestion and absorption in the gastrointestinal tract	159
8-11 Summary	159
9 INGESTION AND NUTRIENT UTILIZATION	164
9-1 Variations in nutrient intake	164
SEASONAL VARIATIONS	164
INDIVIDUAL VARIATIONS	165
9-2 Regulation of nutrient intake	166
RELATIONSHIP TO WEIGHT	166
RELATIONSHIP TO ENERGY EXPENDITURE	167
CONTROL OF INTAKE	167
9-3 Energy utilization	171
PATHWAYS OF ENERGY UTILIZATION	172
NET ENERGY FOR MAINTENANCE	175
NET ENERGY FOR PRODUCTION	176
SUMMARY OF ENERGY UTILIZATION	176
9-4 Protein utilization	176
9-5 Efficiency of nutrient utilization	177
DIGESTION COEFFICIENTS	177
NET ENERGY AND PROTEIN COEFFICIENTS	177
METABOLIC EFFICIENCY	178
9-6 Body growth	179
9-7 Summary	182

PART 4
BEHAVIORAL FACTORS IN RELATION TO
PRODUCTIVITY

10	THE ORGANISM AS A FUNDAMENTAL UNIT IN A POPULATION	189
	10-1 Energy, matter, and time	190
	10-2 Biological chronology	191
 11	 INTRASPECIES INTERACTION	 206
	11-1 Sensory perception	206
	11-2 Protective behavior and family ties	213
	11-3 Movement patterns	214
	11-4 Feeding behavior	216
	11-5 Rest	216
	11-6 Play	217
	11-7 Social order	217
	DOMINANCE PATTERNS	217
	11-8 Radio telemetry and behavioral analyses	218
 12	 INTERSPECIES INTERACTION	 225
	12-1 Predator-prey relationships	226
	12-2 Factors affecting predation rates	228
	12-3 Energetic considerations	230
	TROPHIC LEVELS	232
	12-4 Man as a predator	235
	12-5 Parasites and pathogens	236
	12-6 Competition	238
	12-7 Conclusion	238

PART 5
ENERGY FLUX AND THE ECOLOGICAL
ORGANIZATION OF MATTER

13	THERMAL ENERGY EXCHANGE BETWEEN ORGANISM AND ENVIRONMENT	245
	13-1 Thermal energy exchange	245
	13-2 The concept of homeothermy	246
	REGIONS OF THERMAL EXCHANGE	247
	ANALYSES OF HOMEOTHERMIC RELATIONSHIPS	249
	13-3 Measurement of thermal parameters	250
	CONDUCTION COEFFICIENTS	250
	TEMPERATURE-PROFILE MEASUREMENTS	253

18-4	Population requirements for protein	400
18-5	Population requirements for energy	400
18-6	Other population dimensions	400
19	PREDICTING POPULATION DYNAMICS	404
19-1	Ecological productivity gradient	404
19-2	The relative importance of different variables	405
	ANIMAL REQUIREMENTS	405
	RANGE SUPPLY	406
	FACTORS AFFECTING BOTH ANIMAL REQUIREMENTS AND RANGE SUPPLY	406
19-3	Factors to consider in population analyses	408
19-4	Population analyses for $n = 1, 2, \dots, n$	408
	MORPHOLOGICAL AND PHYSIOLOGICAL CONSIDERATIONS	409
	BEHAVIORAL CONSIDERATIONS	410
	A THEORETICAL AVERAGE DEER	410
19-5	Time in relation to biological events	411
	SEASONAL CHANGES IN ANIMALS AND PLANTS	411
	THE IMPORTANCE OF SEASONAL CHANGES	412
	VARIATIONS IN THE TIME OF BREEDING	413
20	ECOLOGICAL ANALYSES AND DECISION-MAKING PROCEDURES	418
20-1	The simulation of management practices	418
	BIOLOGICAL CONSIDERATIONS	419
	SOCIAL AND ECONOMIC CONSIDERATIONS	419
	POLITICAL CONSIDERATIONS	420
20-2	Conclusion	420
APPENDIXES		
A-1	Weights and Measurements	425
A-2	Weather, Thermal Factors, and the Julian Calendar	428
A-3	Weight and Metabolic Weight	432
A-4	Radiant Temperature in Relation to Air Temperature	433
A-5	Surface Area in Relation to Weight	436
A-6	Symbols	438
A-7	Reference Books	440
A-8	Instructions for Contributors to the Professional Literature	442
	INDEX	445

FOREWORD

In recent years, environmental problems have created great general concern. Thus, the time has come when a revitalized and more effective approach to the management of natural resources is necessary. This is especially true in light of increased human populations.

In the past, individual abuses of the natural resources have been treated as isolated problems—an approach doomed to failure. Instead, individual abuses can be seen as parts of a larger problem: the increasing pressure of an expanding population on dwindling nature resources. That problem often appears overwhelming. In seeing it, many have given up in despair. But a great problem may be broken down; each part can be attacked separately and perhaps solved. Bit by bit the big problem becomes solvable. The importance of each issue, whether it be protein availability, harvest of females, or disposal of waste pollutants, depends on the particular role of the issue in the overall environmental structure.

Wild animals, and the management of them are a vital part of the environmental "machine," a part that also is made of smaller parts. Age, sex, and time of year affect the physiology of an individual animal. These, together with nutritional factors, genetic history, and features of the physical environment, combine in the complex system that determines the interactions between an animal, other organisms, and the land.

It is the essence of the wildlife manager's job that he understand the system and be able to work with it. He must understand how an organism fits into the ecosystem. He must understand the effects of the organism on its total environment and the effects of the environment on the organism.

In *Wildlife Ecology: an analytical approach*, Professor Moen has analyzed this natural system. He evaluates each component and welds them together into a unified whole. Although most of the examples deal with white-tailed deer, the concepts are applicable to the other wild ruminants and, indeed, to all organisms.

Professor Moen's creative research and dedication have produced a work in which traditional pieces of wildlife management—numbers and conditions of animals, nutritive values of range plants, behavior patterns—are at last presented as parts of a greater whole. This book should be made available to every wildlife professional, whether technician, manager, biologist, conservation officer, administrator or researcher. It is an important publication and the time for it has come.

Douglas L. Gilbert

Colorado State University
Fort Collins, Colorado
September 1972

PREFACE

Rapid advances in analytical capabilities within the last fifteen years have made it possible for the ecologist to do things within a time dimension that were unheard of a few years ago. The capabilities for rapid analyses pose a threat to the discipline of ecology, however, because there can be a tendency to use numbers, large quantities of them, hoping by some magical means of computer analysis to find some relationships emerge.

The reorganization of numbers within a computer program of storage and computation is nothing more than a rapid bookkeeping system. Computers used in such a way do not usually help much in gaining insight into the mechanisms that are operating in the natural world. They tend to promote a false sense of security.

The real benefits of computer analyses emerge if they are used to extend the analyst's capabilities for analyzing the relationship between one factor or force and another factor or force in the ecosystem. It is important to realize that the human mind must always be ahead of the computer, with the electronic system doing rapid computations that are too numerous and time-consuming to do in any other manner. This suggests that the first models built by analytical ecologists are of necessity very simple ones. Let them be no more complex than the model builder can fully comprehend, insuring that he knows not only the capabilities of his analytical model but also its weakness. A progression of such simple models will result in more complex, working models that represent a *known* portion of the ecosystem.

In this book I have aimed at promoting the building of simple but workable models. They do not require large computer centers for their use; small desk-top computing systems are entirely adequate. In fact, many of the models suggested can be done manually, with the principles of model building illustrated just as

well. Thus the book should be of interest to ecology classes in many types of educational institutions, from the small college to the major university. I am convinced that, wherever the student is located, the major factor that will determine his progress in ecology is his ability to think, along with the guidance of a professor who stimulates thinking about meaningful ecological relationships.

Aaron N. Moen

April 1973

ACKNOWLEDGMENTS

The completion of a book is not possible without the help of many people. My own efforts have been made possible through the kind direction and guidance given to me by my parents on their farm in western Minnesota. The opportunities for contact with wild animals and native plants in that area stirred within me an interest to pursue an understanding of the relationships between organism and environment.

My academic career in the field of natural resources began under the guidance of Dr. Max Partch at St. Cloud State College. His enthusiasm for teaching in the field impressed me greatly. Dr. William H. Marshall, of the University of Minnesota, gave me opportunities, freedom, and responsibility as I pursued a Ph.D. The most significant academic work that permitted me to delve into the energy relationships of deer at that time was that of Helenette Silver and her colleagues at the New Hampshire Fish and Game Department and the University of New Hampshire. Without her pioneering efforts in the field of energy metabolism of white-tailed deer, my Ph.D. dissertation could not have started me on the challenging research on the energetics of a free-ranging animal.

I wish to thank the many friends I have made in the field of wildlife management, especially the deer biologists in the State of New York who always provide stimulating interaction as we proceed together to understand this most important resource in New York State. My colleagues at Cornell, especially Dr. Peter Van Soest of the Department of Animal Science, have provided many insights into the animal-environment relationships currently under investigation. Dr. Douglas L. Gilbert, formerly at Cornell and now at Colorado State University, has discussed big-game management with me on many occasions. Dr. Donald Ordway and his staff of aerodynamic engineers have been of great help in our thermal analyses at the BioThermal Laboratory.

Dr. Dwight A. Webster, former head of the Department of Natural Resources, and the administrators of the Agricultural Experiment Station at Cornell have all been most helpful as I established a research program at the BioThermal Laboratory. Funds for research at the Laboratory have been contributed through the Pittman-Robertson Federal Aid program, Project W-124-R, and the New York State Department of Environmental Conservation. Additional funds from the Agricultural Experiment Station at Cornell, the Cornell Research Grants Committee, the National Science Foundation, The Loyalhanna Foundation, and the National Rifle Association have helped support the work at the BioThermal Laboratory.

The staff at the Laboratory has contributed significantly to the work that is described in this text. My respect for the abilities and dedication of my students cannot be fully expressed by acknowledgment but will be manifested by their contributions in the future. I must recognize the help and accomplishments of former students, especially Dr. Keith E. Evans and Dr. Deborah S. Stevens. The work of Nadine L. Jacobsen and Charles T. Robbins, both Ph.D. candidates studying the energy relationships of deer, has provided much insight into the complex animal-environment relationships that are the focus of study at the Laboratory. William Armstrong, laboratory technician, has helped in the design and construction of research equipment and in the care of our experimental deer herd. Richard E. Reynolds, foreman at the Ithaca Game Farm, has contributed much to the program with his help in the construction of the deer pens, maintenance of the facilities, and continual attention to our needs. Eleanor Horwitz offered many fine suggestions on ways to improve the manuscript. I appreciate her efforts to convince me to say things in the simplest way possible.

Students in my courses have raised many stimulating questions. I wish that each one of them could participate actively rather than passively in the educational process of research and discovery.

Finally, the help and encouragement of my wife, Sharon, and of Ronald, Thomas, Daniel, and Lindy cannot be fully expressed in words. It has often been impossible to keep up with some of the domestic duties confronting every husband and father because of the urgency of research according to a biological clock and my own intense interest in the subject. As Tom (age 9) said when I suggested I might write another book, "Oh no, not another five years of that!"