THE NATURAL HISTORY OF MOSQUITOES

By MARSTON BATES

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To

LEWIS WENDELL HACKETT

ABLE EXPONENT OF THE IMPORTANCE OF
TRYING TO SEE THE WORLD FROM THE
POINT OF VIEW OF THE MOSQUITO

FOREWORD

THIS book was written in the small Colombian town of Villavicencio, "east of the Andes and west of nowhere," if I may borrow the phrase used by my wife as a book title. I hope that the critical reader will keep this circumstance in mind. If the material had been assembled at one of the great centers of learning, more judgment could have been used in the selection and rejection of bibliographic references; as it is, the use of a given reference may not mean that the particular author has produced the best work, but that his paper happened to be available for study. Even more than this, I regret my inability to place the various and diverse bits of fact that have accumulated about mosquitoes in proper perspective with the general fields of the different biological sciences. Such a project would have required not only general library facilities, but also frequent contact and discussion with other biologists specializing in the different fields. This lack of opportunity for frequent discussion with colleagues having other special interests is perhaps the greatest disadvantage of an isolated tropical post.

There may be a credit side to the fact that the book was written in Villavicencio. While library facilities and the opportunity to consult with colleagues were lacking, I at least was in constant contact with mosquitoes. The material of the book accumulated over a period of several years during which the work of the Villavicencio laboratory was concerned first with the transmission of yellow fever and later with the biology of the anopheline vectors of malaria. Problems of mosquito biology thus intruded themselves constantly during the composition of the manuscript, and chapters and paragraphs were separated by excursions into specific research projects or by the daily incidents of laboratory management. This may make for uneven writing, but there is at least the hope that it has also added a spark of life to the inherently tedious compilation of the literature on mosquito behavior.

Various friends have read parts of different drafts of the manuscript, and I am particularly grateful for suggestions received from Dr. R. B. Hill, Dr. L. W. Hackett, Dr. Paul Russell, Dr. Max Theiler and Dr. R. M. Taylor of the Rockefeller Foundation; Dr. L. E. Rozeboom of Johns Hopkins University; Dr. A. D. Hess of the Tennessee Valley Authority; and Dr. Harold Trapido of the Gorgas Memorial Laboratory. Mr. Melville Grosvenor and Mr. Edwin Wisherd of the National Geographic Society have helped me with photographic problems, and some of the illustrations used here have been published in the Magazine of their Society, and also in the book by Nancy Bell Bates, "East of the Andes, and West of Nowhere," published by Charles Scribner's Sons. My thanks are due to the various authors and (in the case of copyright material) to the publishers for permission to use the material that has been quoted in the present text. To itemize these debts would merely clutter up this foreword; the extent and nature of my obligations is clear from the text citations and the bibliography. Last for acknowledgement, but most important of all, is my debt to Miss Helen Booth, who has typed the whole manuscript several times and spent endless hours nursing the cards of our indexes of the mosquito literature, thus making the book possible.

I doubt whether I would ever have managed to finish the manuscript without the sympathetic encouragement of my chiefs in the Rockefeller Foundation, especially of Dr. G. K. Strode, the director of the International Health Division, of Dr. A. J. Warren, the associate director, and of Dr. H. B. van Wesep, the chief of the Publications Division. They cannot be held to share any responsibilities for my opinions or statements; but since the book has taken a great deal of time and energy that would otherwise have been devoted to active research, it represents in fact a contribution from the International Health Division. I can thus only hope that it represents a contribution to knowledge, and hence, however indirectly and minutely, bears some relation to the welfare of mankind throughout the world.

MARSTON BATES

Baltimore, Maryland
January, 1949

LIST OF PLATES

Between pages 208 and 209

1. Larval habitats: marshy zones in lakes
2. Larval habitats: marshes and ponds
3. Larval habitats: coastal areas of brackish water
4. Larval habitats: Egyptian village pond
5. Larval habitats: tropical forest pool
6. Larval habitats: seepage and pools in streams
7. Larval habitats: side pools in open streams
8. Larval habitats: tree holes
9. Larval habitats: plant containers in tropical forest
10. Larval habitats: palm leaves and bamboo stems
11. Mosquito technique: field study of larvae
12. Mosquito technique: captures in tropical forest
13. Mosquito technique: large laboratory cages
14. Mosquito technique: stable traps baited with donkeys
15. Mosquito technique: laboratory apparatus
16. Mosquito technique: methods of handling adults

CONTENTS

I. Introduction 1

II. The Environment of the Adult 13
The Adult Habitat 14
Time of Flight 17
Activity Rhythms 22
Resting Places 23
Laboratory Study of Orientation Reactions 26

III. Survival and Dispersal 32
Longevity of the Adult 32
Distance of Flight 36
Seasonal Distribution 41

IV. The Sexual Behavior of Mosquitoes 49
Factors Influencing Swarm Formation 51
Sexual Selection and Differences in Female Behavior . . 57
Inheritance of Epigamic Behavior Patterns 59
Special Types of Behavior 61
Hybridization Experiments 62
Gynandromorphs 64

V. Food Habits of the Adult 66
Factors Governing the Search for Food 66
Studies of Host Preference 72
Mechanism of Biting 76
Food of Males 79
Special Food Habits 80

VI. Egg Development and Oviposition 82
Necessity for Blood 82
Effect of Type of Blood on Egg Development . . . 84
Fat Production During Hibernation 86
Other Factors Influencing Egg Development 88
Digestion of Blood 89
Ovarian Stages 91

Manner of Laying Eggs 92
Selection of Oviposition Site 95

VII. Mosquito Eggs 100
Egg Structure 101
Variation in Eggs 103
Field Studies of Eggs 104
Embryonic Development 105
Hatching Stimulus 107

VIII. The Larval Environment 112
Temperature 114
Light 120
Movement 122
Surface Characters 123
Dissolved Gases 123
Hydrogen-Ion Concentration 124
Nitrates and Organic Materials 125
Inorganic Salts 127

IX. The Physiology and Behavior of Larvae 129
Food Requirements 129
Methods of Feeding 132
Predacious Larvae 135
Growth 137
Hibernation in the Larval Stage 139
Respiration 141
Larval Behavior 142

X. The Biological Environment of the Larva 147
Microbiota 150
Vegetation 153
Parasites 157
Predators 158
Competition 161

XI. The Classification of Larval Habitats 163
Classifications of Habitats 164
Outline of a Scheme for Breeding-Place Classification . 167

XII. The Pupal Stage 179
The Ecological Function of the Pupa 181
Pupal Behavior 183

XIII. Mosquitoes in Relation to Other Organisms 186
Mosquitoes as Parasites 187
Mosquitoes as Prey 189

Mosquitoes as Hosts 190
Mosquitoes as Vectors 195
Mosquitoes as Vectors of Dermatobia 197
Mosquitoes as Vectors of Filaria 198

XIV. Mosquitoes as Vectors of Viruses 201
Yellow Fever 203
Dengue 206
Western Equine Encephalitis 207
Eastern Equine Encephalitis 208
Venezuelan Equine Encephalitis 209
St. Louis Encephalitis 209
Japanese B Encephalitis 210
West Nile Virus 210
Lymphocytic Choriomeningitis 210
Rift Valley Fever 211
Other Neurotropic Viruses from Mosquitoes 211
Equine Infectious Anemia 213
Fowl Pox 214
Rabbit Myxoma 214
Adaptations and Relationships Among the Mosquito Transmitted Viruses 214
Mosquito Infection with Entomotropic Viruses . . . 217
The Extrinsic Incubation Period 220
Virus Transmission 221

XV. Mosquitoes as Vectors of Plasmodia 223
Types of Plasmodia 225
Development of the Plasmodium in the Mosquito . . 229
Factors Governing Mosquito Infection 231
Mosquito Transmission 236

XVI. The Species Problem 239
Anopheles maculipennis 244
Anopheles punctulatus 246
Anopheles stephensi 247
Anopheles gambiae 248
The Subgenus Nyssorhynchus of Anopheles 249
Culex pipiens 249
Specific Characters 250
Possible Mechanism of Speciation 253

XVII. The Classification of Mosquitoes 257
The Principles of Animal Classification 260
Generic Groupings in Mosquitoes 265

XVIII. The Distribution of Mosquitoes 271
Faunal Regions 272
The Range of Specific Populations 280
Fossil Mosquitoes 285

XIX. Techniques in Mosquito Study 286
Field Studies: Larvae 287
Field Studies: Adults 290
Larval Culture 292
Laboratory Manipulation 296
Laboratory Colonization 301

XX. The Strategy of Mosquito Research 304

Appendix. Systematic List of Mosquito Species 311

Bibliography 323

Index 369

LIST OF TABLES

I. Vertical distribution of common forest mosquitoes in the region of Villavicencio, Colombia 16

II. Recaptures of marked *Anopheles culicifacies* in flight-range experiments of Russell, Knipe, Rao, and Putnam 38

III. Life-history calendar of Danish mosquitoes 45

IV. Results of experiments in which males of *Anopheles atroparvus* were left with females of various species 58

V. The effect of various blood components on egg production in *Aëdes aegypti* 85

VI. Egg production of *Aëdes aegypti* following ingestion of blood from different species of vertebrates 87

VII. Length of eclosion period of eggs of *Aëdes aegypti* in relation to previous "conditioning" period 108

VIII. Effect of overcrowding on pupation period and mortality of *Aëdes aegypti* larvae at 27° C 139

IX. Relation of rate of growth to concentration of Lilly liver extract 343 in *Aëdes aegypti* 139

X. Relation between the breeding of *Anopheles quadrimaculatus* and type of vegetation 155

XI. Summary of laboratory experiments with infection of mosquitoes with yellow-fever virus 204

XII. Transmission of yellow-fever virus to baby mice by feedings of individual mosquitoes 222

XIII. Comparison of regional faunas 279

XIV. Distribution of mosquito subgenera by faunal regions . . 279

LIST OF FIGURES

1. Relative abundance of *Anopheles gambiae* and *Aëdes africanus* at different heights in the Mamirimiri Forest, Uganda, during the wet season 16

2. Biting time of three diurnal forest mosquitoes on the Island of Marajó, Brazil 19

3. Relation of biting cycle of the nocturnal *Anopheles gambiae* and the diurnal *Eretmapodites* to the daily cycles of temperature and relative humidity 21

4. Longevity of *Anopheles culicifacies* in an outdoor cage in relation to seasonal changes in temperature and humidity . . . 35

5. Stages in the introduction of the fascicle by *Aëdes aegypti* in biting, as observed in the web of the frog's foot 77

6. *Harpagomyia* mosquito taking food from the mouth of a *Cremastogaster* ant 81

7. Diagram to show pattern of water currents in "eddy" feeding of larvae 133

8. Geographical distribution of the North American populations of the *Anopheles maculipennis* group 255

9. Construction of ingress baffle with horizontal opening for "Egyptian-type" stable trap 291

CHAPTER I

INTRODUCTION

> Natural history is encumbered by multitudes of facts which are recorded only because they are easy to record.—L. C. MIALL

Mosquitoes in general, and the malaria carriers in particular, have been the subject of a tremendous amount of study, whose results have been reported in a voluminous literature. Much of this literature is an uncritical accumulation of facts that were easy to record, or of facts that were related to some momentarily fashionable subject of study, or of facts that were needed for the attainment of some immediately practical objective. As a mere accumulation of facts the literature represents, as Miall has stated, an encumbrance: but it is an encumbrance waiting to be converted into an orderly and useful structure of knowledge.

Facts form the raw material of science—the bricks from which our model of the universe must be built—and we are rightly taught to search for sound and solid facts, for strong and heavy bricks that will serve us well in building foundations, for clean and polished bricks that will fit neatly into ornamental towers. But while accumulating the bricks may be a contribution to science, we must take care that the pile does not become a hopelessly discouraging jumble. For science itself is not brickmaking—it is, at the workaday and technical level, bricklaying; and at the creative and artistic level, architecture, the designing of an edifice that will utilize all the bricks to the very best advantage.

The metaphor, of course, cannot be carried too far. The bricklayers and the architects of science are always acquiring strange, new, and beautiful bricks that make it necessary to tear their careful building down and start over. It is an unending, dreamlike game that seems to be limitless—the model of the universe will never be done, nor does any part of it seem to have a comfortable or dependable permanence. But still the bricks, as bricks, cannot be left in a jumbled pile,

and we have the task of organizing them into some sort of a pattern, however transient.

The pile of facts about mosquitoes is an impressive accumulation, one that should be useful to all biologists if only the assortment were a little better organized. Yet, as soon as one starts sorting out these facts, one finds how incomplete they are, how many more are needed if any decent theoretical structure is to be built. The bricks are not overly abundant; it is simply that they need to be sorted according to their size and shape.

That, then, is the object of this book. It certainly can do no harm, and it may serve as a convenience to the architects of biological theory. Even with all of the work that has been done on mosquitoes, the final impression of such a review is that a great deal more work is needed before we can achieve any real understanding of mosquito behavior. So the object is a double one—to indicate the needs as well as outline the resources.

Much that has been written about mosquitoes is concerned directly with methods of killing them, or of recognizing species that are dangerous as vectors of specific diseases; but the problems both of control and of identification have led to a great deal of biological work with implications that go far beyond the immediate practical objectives. Mosquito control and mosquito identification have both been the subject of many excellent and useful reviews, but in recent years no attempt has been made to summarize the knowledge that we have acquired concerning mosquitoes as living animals. The reports of original researches are scattered through a wide range of periodicals, many in medical journals not commonly available in purely biological libraries. As a result, this work has hardly been noticed by the students of biological theory, who view mosquitoes as something to be swatted, rather than as potential sources of information about the biological processes that govern the bewildering organic world that we inhabit.

The biological study of insects has in general been hampered by the tremendously complex problems of classification: before the behavior and physiology of the animals could be studied it has been necessary to name them, and this has led to what may seem to be an undue emphasis on morphology and taxonomy in entomological writing. It is only in certain groups (such as mosquitoes and butterflies) or in certain regions (such as Europe or parts of the United

States) that this primary task of classifying and describing has proceeded to a stage where the accumulation of significant observations on habit and behavior becomes practical. Much of this preliminary work remains to be done even in groups of insects of agricultural importance, because agricultural entomology has been largely developed in the temperate zone or in very restricted regions of the tropics. The importance of mosquitoes as vectors of human disease has led to their study in all parts of the world. The diseases carried by mosquitoes are particularly characteristic of tropical and relatively backward regions, which has furnished the incentive for intensive work in many such areas, while the temperate-zone fauna has been studied because of its convenient access from the great centers of learning. The result is an unusually even geographical distribution of effort. Mosquitoes are probably as completely described from the points of view of species taxonomy and life history as any group of insects; their only rivals in this respect would be certain groups that are highly prized by collectors, such as some of the families of butterflies.

It is interesting to compare mosquitoes with other groups of insects in this matter of being "well known." In general, it seems to be true that the groups of insects that have received the most attention belong to one of three classes: those that are of economic importance, those that are especially adapted to laboratory manipulation, and those that are particularly attractive to collectors. An indication of the extent to which various insects have been used in biological studies may be gained by tabulating the number of page references in the indexes of general textbooks. Wigglesworth's *Principles of Insect Physiology* (1939) furnishes a convenient guinea pig for such analysis. *Apis*, the honey bee, has considerably more page references (66) in the index than any other insect, while *Drosophila* is not far behind *Apis* in physiological studies, and in any book on genetics and evolution it is cited with overwhelmingly greater frequency than any other insect. In recent years various students in Europe and America have started making field studies of the "natural history" of *Drosophila*, and our information on this group will no doubt soon be as well rounded as it is extensive.

The history of the *Drosophila* studies is interesting, since it demonstrates what might be called the "law of the multiplication of the potential value of a subject of study": the more that is known about a given animal or group of animals, the more valuable it becomes for

further work. *Drosophila* was used at first because of the ease with which it could be manipulated in the laboratory; as studies accumulated, it became increasingly valuable for new studies merely because of the background provided by this earlier work, a process that seems to continue indefinitely, though one would expect that in the long run some limit would be met.

The order of frequency of reference to insects in Wigglesworth's index deserves further consideration. After *Apis* comes *Dytiscus*, the water beetle, with 49 references; then *Periplaneta* (cockroach) with 42; *Tenebrio* (meal worm) also with 42; *Drosophila* with 41 and *Calliphora* (blowfly) with 38. The mosquito genera come well down on the list (*Culicidae*, 11 references; *Culex*, 21; *Anopheles*, 11; *Aëdes*, 8), though the combined references make a respectable showing for the family. These various genera have been studied primarily because they are easily adapted to laboratory manipulation. Physiologists are, in fact, often criticized by other workers for using such insects for their studies instead of important pests. They use the cockroach not because it is economically an important animal, but because it is easily encountered and raised in their laboratories. Physiologists have given little attention to butterflies, because they are rather difficult to handle in the laboratory. Yet from the point of view of taxonomy and geographical distribution, butterflies are perhaps the best known large group of insects because they have been so extensively collected in all parts of the world.

The fact that diverse groups of insects have been studied from widely divergent points of view, and the resultant scattering of effort, is unavoidable in view of the nature of man and of insects. It seems, none the less, unfortunate from the point of view of the development of a unified and integrated biological science—in other words, from the point of view of the development of a general knowledge of the nature of life processes.

The scatter effect is increased by the course, perhaps largely accidental, that the biological sciences have followed in specialization. We have two widely diverging types of specialization: according to group studied and according to point of view. The first type of specialization gives us entomologists, ornithologists, herpetologists and conchologists; the second, physiologists, histologists, cytologists, and geneticists. In many cases—the taxonomists and the morphologists furnish good examples—both types of specialization may be combined,