FRONTIERS OF BIOLOGY Editors: A NEUBERGER AND E. L. TATUM

PHEROMONES

Martin C. DIRCH

PHEROMONES

Edited by

Martin C. BIRCH

Department of Entomology and Nematology, University of California at Davis, Davis, California, U.S.A.



1974

NORTH-HOLLAND PUBLISHING COMPANY - AMSTERDAM • LONDON AMERICAN ELSEVIER PUBLISHING COMPANY, INC. - NEW YORK

© North-Holland Publishing Company - 1974

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior permission of the copyright owner.

Library of Congress Catalog Card Number: 73-88157

North-Holland ISBN: 0 7204 7133 8 American Elsevier ISBN: 0 444 10604 9

PUBLISHERS:

NORTH-HOLLAND PUBLISHING COMPANY – AMSTERDAM NORTH-HOLLAND PUBLISHING COMPANY, LTD. – LONDON

SOLE DISTRIBUTORS FOR THE U.S.A. AND CANADA: AMERICAN ELSEVIER PUBLISHING COMPANY, INC. 52 VANDERBILT AVENUE, NEW YORK, N.Y. 10017

PRINTED IN THE NETHERLANDS

PHEROMONES

NORTH-HOLLAND RESEARCH MONOGRAPHS

FRONTIERS OF BIOLOGY

VOLUME 32

Under the General Editorship of
A. NEUBERGER

London

and

E. L. TATUM

New York



NORTH-HOLLAND PUBLISHING COMPANY AMSTERDAM • LONDON

General preface

The aim of the publication of this series of monographs, known under the collective title of 'Frontiers of Biology', is to present coherent and up-to-date views of the fundamental concepts which dominate modern biology.

Biology in its widest sense has made very great advances during the past decade, and the rate of progress has been steadily accelerating. Undoubtedly important factors in this acceleration have been the effective use by biologists of new techniques, including electron microscopy, isotopic labels, and a great variety of physical and chemical techniques, especially those with varying degrees of automation. In addition, scientists with partly physical or chemical backgrounds have become interested in the great variety of problems presented by living organisms. Most significant, however, increasing interest in and understanding of the biology of the cell, especially in regard to the molecular events involved in genetic phenomena and in metabolism and its control, have led to the recognition of patterns common to all forms of life from the bacteria to man. These factors and unifying concepts have led to a situation in which the sharp boundaries between the various classical biological disciplines are rapidly disappearing.

Thus, while scientists are becoming increasingly specialized in their techniques, to an increasing extent they need an intellectual and conceptual approach on a wide and non-specialized basis. It is with these considerations and needs in mind that this series of monographs, 'Frontiers of Biology' has been conceived.

The advances in various areas of biology, including microbiology, biochemistry, genetics, cytology, and cell structure and function in general will be presented by authors who have themselves contributed significantly to these developments. They will have, in this series, the opportunity of bringing together, from diverse sources, theories and experimental data, and of integrating these into a more general conceptual framework. It is unavoidable, and probably even desirable, that the special bias of the individual authors will become evident in their contributions. Scope will also be given for presentation of new and challenging ideas and hypotheses for which complete evidence is at present lacking. However, the main emphasis will be on fairly complete and objective presentation of the more important and more

rapidly advancing aspects of biology. The level will be advanced, directed primarily to the needs of the graduate student and research worker.

Most monographs in this series will be in the range of 200—300 pages, but on occasion a collective work of major importance may be included somewhat exceeding this figure. The intent of the publishers is to bring out these books promptly and in fairly quick succession.

It is on the basis of all these various considerations that we welcome the opportunity of supporting the publication of the series 'Frontiers of Biology' by North-Holland Publishing Company.

E. L. TATUM
A. NEUBERGER, Editors

Preface

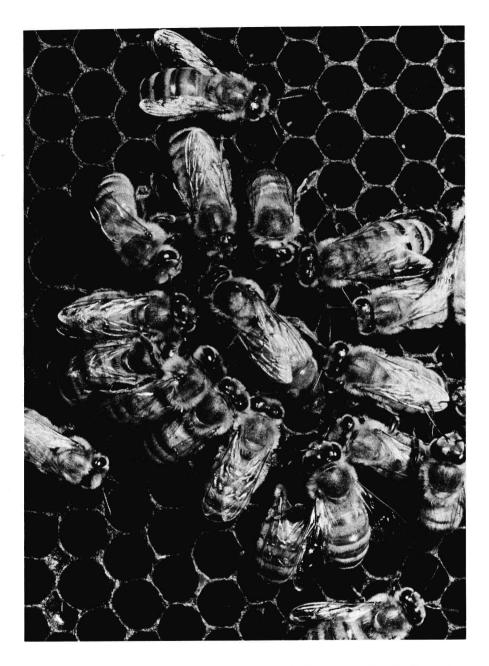
Previous books on pheromones have either emphasized the chemistry of pheromones, practical utilization of chemical determinants of behavior, or a variety of topics in the area of chemoreception. None has primarily emphasized the biology of pheromones throughout the animal kingdom or attempted to cover animal pheromones as a single topic. The study of pheromones demands an involvement with the behavior of animals, but that involvement has usually been kept to a minimum. There has been a strong tendency with the insect work to concentrate on chemical isolation, identification and synthesis, and the technology of field deployment — the behavior of compounds rather than the behavior of insects. Mammalian pheromone research has had a somewhat different approach. Partly due to the greater complexities of the secretions involved, chemistry has lagged behind here: behavior has had more emphasis, although, as with the insect work, it has for the most part been restricted to laboratory animals in situations that cannot easily be translated to natural populations.

The current situation merely reveals how little we know about the way pheromones actually influence the behavior and population dynamics of animals. The biological basis for pheromone research needs a much greater input, especially since pheromones are currently being heralded as one of the most promising new tools for management of pest populations. They are clearly going to be used with, or without, a sound knowledge of the underlying biology.

Hence, this book is concerned with the biology of pheromones, avoiding techniques, chemistry and cataloguing of identifications, all of which are indispensable but have tended to crowd out the biology. The book concentrates on the two main groups studied to date — the insects and the mammals (plus fish). Where chemistry and technology intrude, the paucity of the behavioral research is merely emphasized. This book will have served its purpose if it can indicate where research on pheromone mediated behavior is weak and can indicate and stimulate research into new or weak areas.

The editor is very grateful to Barbara Barr, Linda Birch, Stanley Caveney, Charles David, Lewis Edson, Dorothy van Emden, Doug Light, Henry Moeck, David

Moscioni, Curtis Pantle and Susie Wong for their help in various ways with editing many of the chapters, to H. A. Bern, H. van Emden and J. C. Young for valuable help with the introduction, and to R. van den Bosch and J. Diekman for reading the introductory section to Ch. 22. The book could never have been put together without Professor David Wood's support during the time I was with his research group at the University of California, Berkeley; I am very grateful to him. Marian Merrill provided excellent administrative help throughout the organization and editing. The editor is particularly indebted to Barbara Zelwer for typing the entire final draft and to Linda Birch for the arduous task of compiling the index.



Pheromones emanating from the queen honey bee stimulate approaching, feeding and 'grooming' behavior by worker bees. (Photo by N. Gary, see ch. 11.)



An adult female marmoset (Callithrix j. jacchus) (left) marks her mate. (Photo by G. Epple, see ch. 19.)

List of contributors

- William D. Bedard Pacific Southwest Forest and Range Experiment Station, United States Department of Agriculture, Forest Service, Berkeley, California 94701, U.S.A. (ch. 22)
- Martin Birch Department of Entomology, University of California, Davis, California 95616, U.S.A. (chs. 1, 7, 22)
- Murray S. Blum Department of Entomology, University of Georgia, Athens, Georgia 30601, U.S.A. (chs. 10, 12)
- John H. Borden Department of Biological Sciences, Simon Frazer University, Burnaby 2, British Columbia, Canada (ch. 8)
- F. H. Bronson Department of Zoology, The University of Texas at Austin, Austin, Texas 78712, U.S.A. (ch. 18)
- Wendell E. Burkholder Stored Product and Household Insects Laboratory, Agricultural Research Service, U.S.D.A., Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706, U.S.A. (chs. 9, 22)
- E. Alan Cameron Department of Entomology, The Pennsylvania State University, University Park, Pennsylvania 16802, U.S.A. (ch. 22)
- Ring T. Cardé New York State Agricultural Experiment Station, Cornell University, Geneva, New York 14456, U.S.A. (ch. 6)
- Alex Comfort Department of Zoology, University College, Gower Street, London WC1, England (ch. 20)

- Gisela Epple Monell Chemical Senses Center, University of Pennsylvania, Philadelphia, Pennsylvania 19104, U.S.A. (ch. 19)
- S. R. Farkas Division of Toxicology and Physiology, Department of Entomology, University of California, Riverside, California 92502, U.S.A. (ch. 5)
- Norman E. Gary Department of Entomology, University of California, Davis, California 95616, U.S.A. (ch. 11)
- Lyle K. Gaston Division of Toxicology and Physiology, Department of Entomology, University of California, Riverside, California 92502, U.S.A. (ch. 22)
- D. D. Hardee Boll Weevil Research Laboratory, Southern Region, Agricultural Research Service, U.S.D.A., Mississippi State, Mississippi 39762, U.S.A. (ch. 22)
- Gerald H. Lanier Department of Entomology, College of Environmental Science and Forestry, State University of New York, Syracuse, New York 13210, U.S.A. (ch. 9)
- B. P. Moore Division of Entomology, C.S.I.R.O., P. O. Box 1700, Canberra City, A.C.T. 2601, Australia (ch. 13)
- Dietland Müller-Schwarze Department of Zoology, College of Environmental Science and Forestry, State University of New York, Syracuse, New York 13210, U.S.A. (chs. 16, 22)
- R. Mykytowycz C.S.I.R.O., Division of Wildlife Research, P. O. Box 84, Lyneham, Canberra, A.C.T. 2602, Australia (ch. 17)
- Thomas L. Payne Department of Entomology, Texas A & M University, College Station, Texas 77843, U.S.A. (ch. 3)
- Wolfgang Pfeiffer Zoophysiologisches Institut der Universität Tübingen, 74 Tübingen, Hölderlinstrasse 12, Western Germany (ch. 14)
- J. E. Percy Canadian Forestry Service, Insect Pathology Research Institute,
 P. O. Box 490, Sault Ste. Marie, Ontario P6A 5M7, Canada (ch. 2)
- Wendell L. Roelofs New York State Agricultural Experiment Station, Cornell University, Geneva, New York 14456, U.S.A. (ch. 6)

- C. J. Sanders Canadian Forestry Service, Great Lakes Forest Research Centre, P. O. Box 490, Sault Ste. Marie, Ontario P6A 5M7, Canada (ch. 22)
- H. H. Shorey Division of Toxicology and Physiology, Department of Entomology, University of California, Riverside, California 92502, U.S.A. (chs. 4, 5, 22)
- D. Michael Stoddart Department of Zoology, University of London, King's College, The Strand, London WC2R 2LS, England (ch. 15)
- James P. Tette Pheromone Field Research and Development, Zoëcon Corporation, Palo Alto, California 94304, U.S.A. (present address: Pheromone Systems, Box 260 D, R.D. 1, Stanley, New York 14561, U.S.A. (ch. 21)
- Kenneth Trammel New York State Agricultural Experiment Station, Cornell University, Geneva, New York 14456, U.S.A. (ch. 22)
- J. Weatherston Canadian Forestry Service, Insect Pathology Research Institute,
 P. O. Box 490, Sault Ste.Marie, Ontario P6A 5M7, Canada (ch. 2)
- David L. Wood Department of Entomological Sciences, University of California, Berkeley, California 94720, U.S.A. (ch. 22)

Contents

General preface	V
Preface	VI.
List of contributors	IX
Chapter 1. Introduction, by Martin Birch	1
Section I. Insect pheromone systems	
Chapter 2. Gland structure and pheromone production in insects, by J. E. Percy and J. Weatherston	11
2.1. Introduction	11
2.2. Individual secretory cells irregularly dispersed throughout the epidermis	11
2.3. Modified intersegmental membranes	12
2.3.1. Ductless cells	12
2.3.2. Cells associated with ducts	15
2.4. Modified abdominal sternites	17
2.4.1. Sternal glands with ductless cells	17
2.4.2. Sternal glands in which the cells are associated with ducts	18
2.5. Modification of abdominal tergites	19
2.6. Localized integumentary modifications with disseminating mechanisms	20
2.6.1. Secretory cells associated with ducts	20
2.6.2. Secretory units are hypertrophied trichogen cells	21
2.7. Internally located glands with cuticular lined reservoirs	25
2.7.1. Gland cells form part of the reservoir wall	26
2.7.2. Glands in which the cells form a secretory aggregate distinct from but	
connected to the reservoir	27
2.8. Glandular source associated with internal organs whose prime function is not	
pheromone production	28
2.9. Conclusion	29
References	29

XIV Contents

Chapt	r 3. Pheromone perception, by Thomas L. Payne	35
3.1.	Introduction	3.5
3.2.	Methods of investigation	35
3.3.	Structures used for pheromone perception	38
	3.3.1. The antennae	38
	3.3.2. The sensilla	39
3.4.	Events in pheromone perception	42
	3.4.1. Transduction	42
	3.4.2. Receptor and whole organism response thresholds	44
	3.4.3. Specificity	44
	3.4.4. Attractant mixtures	51
	3.4.5. Inhibitors and synergists	52
	3.4.6. Environmental influences	53
	2.4.7. 0.1. 1:	55
3.5.		
	Concluding remarks	56
	ledgments	56
Referen	es	57
Chapte	4. Environmental and physiological control of insect sex phero-	
	mone behavior, by H. H. Shorey	62
		02
4.1	To have described	
4.1.	Introduction	62
4.2.	Environmental variables	63
	4.2.1. Light intensity	63
	4.2.2. Temperature	64
	4.2.3. Air velocity	65
	4.2.4. Host substrate	66
4.3.	Physiological variables	66
	4.3.1. Time of day and circadian rhythms	67
	4.3.2. Age	68
	4.3.3. Mating history	69
	4.3.4. Previous exposure to pheromone	70
	4.3.5. Population density	71
	4.3.6. Nutrition	71
	4.3.7. Laboratory strains	71
	4.3.8. Hormones	73
	4.3.9. Sterilization	74
	4.3.10. Insecticides	74
	4.3.11. Anesthetization	75
4.4.	Interrelation of variables	75
Referen		76
ROTOTOL	es	76
-		
Chapte	5. Mechanisms of orientation to a distant pheromone source, by	
	S. R. Farkas and H. H. Shorey	81
	ser in nice papara application and	01
5.1.	ntroduction	01
5.2.	Neurical material C. L.	81 81
	rhysical nature of chemical trails	QI

	Contents	X
	5.2.1. Aerial trails	8:
	5.2.2. Terrestrial trails	8
5.3.	Mechanisms	8
0.0.	5.3.1. Initiation of flight	8
	5.3.2. Locomotion toward the source	8
	5.3.3. Arrestment of locomotion	8
5.4.	Effective distances for chemical communication	9
5.5.	An integrated system	9
	ices	9:
Chant	or 6 Sax pharamonas in the reproductive isolation of lanidanterous	
Cnapie	er 6. Sex pheromones in the reproductive isolation of lepidopterous	0
	species, by Wendell L. Roelofs and Ring T. Cardé	96
6.1.	Introduction	90
6.2.	Reproductive isolation with one compound systems	9
	6.2.1. Release rates	100
		102
6.3.	THE PROPERTY OF THE PROPERTY O	103
6.4.		109
6.5.	The second state of the se	109
6.6.		110
Referen	ces	110
Chapte	r 7. Aphrodisiac pheromones in insects, by Martin Birch	115
7.1.	Introduction	11:
7.2.		110
7.3.		119
7.4.		120
		12
		122
		12
7.5.		13:
	32/20/00/00/20/20/20/20/20 5 7 NO D 0 95 NO D 0 10 NO D 0 NO D	13
		13:
Chant	r 8. Aggregation pheromones in the Scolytidae, by John H. Borden	135
Cnapie	r 8. Aggregation pheromones in the Scotytidae, by John H. Borden	13.
		10 (22)
8.1.		135
8.2.		136
	mirriana i D ii	136
		138
8.3.		139
		139
		143
8.4.		143
	8.4.1. Concentration	143
	8.4.2. Establishment	149