

Animal
Communication
by Pheromones

This page intentionally left blank

Animal Communication by Pheromones

H. H. Shorey

Department of Entomology University of California Riverside, California



ACADEMIC PRESS New York San Francisco London 1976

A Subsidiary of Harcourt Brace Jovanovich, Publishers

COPYRIGHT © 1976, BY ACADEMIC PRESS, INC. ALL RIGHTS RESERVED.

NO PART OF THIS PUBLICATION MAY BE REPRODUCED OR TRANSMITTED IN ANY FORM OR BY ANY MEANS, ELECTRONIC OR MECHANICAL, INCLUDING PHOTOCOPY, RECORDING, OR ANY INFORMATION STORAGE AND RETRIEVAL SYSTEM, WITHOUT PERMISSION IN WRITING FROM THE PUBLISHER.

ACADEMIC PRESS, INC.
111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by ACADEMIC PRESS, INC. (LONDON) LTD. 24/28 Oval Road, London NW1

Library of Congress Cataloging in Publication Data

Shorey, Harry H

Animal communication by pheromones.

Bibliography: p. Includes index.

1. Animal communication. 2. Pheromones. I. Title.

QL776.S54 591.5'9 75-44765

ISBN 0-12-640450-X

PRINTED IN THE UNITED STATES OF AMERICA

Contents

	Pre	face	vi	
1	Introduction			
	Tex	:t	1	
2	The Pheromonal Communication System			
	2.1	Emission of Pheromone	7	
	2.2	Transport of Pheromone	14	
	2.3	Reception of Pheromone	16	
3	Mech	anisms of Movement and		
	Orientation to Pheromone Sources			
	3.1	Orientation with Respect to a Pheromone Gradient	19	
	3.2	Terrestrial Odor-Trail Following	20	
	3.3	Aerial Odor-Trail Following	22	
	3.4	Distances of Pheromone Communication	27	
4	Recognition Pheromone Behavior			
	4.1	Recognition of Individuals	37	
	4.2	Recognition of Status	38	
	4.3	Recognition of Group	40	
	4.4	Recognition of Home	41	
	4.5	Recognition of Home Range	48	
5	Aggregation Pheromone Behavior			
	5.1	Exploitation of Sources of Food	45	
	5.2	Aggregation prior to Sexual Behavior	50	
	5.3	Aggregation prior to Aggressive Behavior	52	
		Maintenance of Societal and Family Groups	52	
		Colonization of Habitats	55	
	5.6	Other Aggregation Behavior	60	

			CONTENTS		
6	Dispersion Pheromone Behavior				
	-	Maintenance of Optimal Interindividual Spacing	65		
	6.2	Maintenance of Territories	67		
	6.3	Dispersion in Response to Alarm Pheromones	68		
	6.4	Antiaggregation	71		
7	Aggression Pheromone Behavior				
	7.1	Stimulation of Aggression toward an Individual of			
		Another Species	75		
	7.2	Stimulation of Aggression toward a Conspecific	80		
	7.3	Inhibition of Aggression toward a Conspecific	82		
		Release of Pheromone as an Aggressive Act	83		
8	Sex Pheromone Behavior				
	8.1	Stimulation of Aggregation	85		
		Stimulation of Courtship and Copulation	93		
	8.3	Hierarchies of Sex Pheromone Behavior	98		
	8.4	Human Sex Pheromones	101		
9	Environmental and Physiological				
	Control of Sex Pheromone Behavior				
	9.1	Environmental Control	105		
	9.2	Physiological Control	108		
10	Sex	Pheromones and Reproductive Isolation			
	Тех	•	113		
11	Evo	lution of Pheromonal Communication			
	Тех	•	117		
	Bib	liography	123		
	Ta	159			
	Sub	ject Index	163		
		J			

Preface

Pheromones are chemicals, either odors or taste substances, that are released by organisms into the environment, where they serve as messages to others of the same species. Although humans exude a great variety of chemicals, they make little conscious use of this potential means for communication with one another. On the other hand, pheromones are widely used within much of the rest of the animal kingdom in a great variety of species, ranging from primitive protozoans to higher primates, as a primary means for transmitting information. Depending on the particular species involved and the situation in which it finds itself at the time, pheromones may be used for attracting a mating partner or for stimulating that partner to copulate, for directing others to suitable food or resting sites, for causing others to stay away when staying away is appropriate, or for a variety of other behavioral functions.

The scientific literature dealing with pheromones has expanded enormously during recent years as have the number of reviews which have proliferated in symposium volumes and in collections of chapters prepared by individual contributors. Although most of the review articles have dealt with insect pheromones, the importance of mammalian pheromones has received increased recognition in recent years, and a number of reviews concerning this group have also been published. However, with the exception of a book by Martin Jacobson entitled "Insect Sex Pheromones" (published by Academic Press in 1972), no single-authored monograph concerning pheromones has appeared.

I have felt for some time that the information concerning pheromone communication within the entire animal kingdom should be reviewed, digested, and presented in a cohesive manner. This book represents my attempt to perform this task. It is mainly directed toward an assessment of how the behavior of animals is controlled and influenced by pheromone communication. Attention to individual taxa, such as worms, in-

sects, or fish, is minimized. Instead, an attempt has been made to generalize the diverse behaviors exhibited by animals when they are engaged in pheromone communication and to group together discussions of both primitive and advanced animals when they are using pheromone communication in a similar manner for such behavioral functions as sex, aggression, feeding, and recognition of other individuals. I have also attempted to draw attention to some of the interesting and specific pheromone behaviors that have evolved in particular animal species in relation to their particular ways of life.

Placing relatively simple invertebrates and complex vertebrates in the same generalized scheme involves the risk of making all these greatly diverse types of animals seem too much alike. However, despite this possibility, I felt this type of scheme of presentation valuable in achieving a mainly behavioral view of pheromone communication in the animal kingdom.

I wish to acknowledge a number of my colleagues who assisted me during the preparation of this book. J. S. Gaston prepared Figures 6, 8, 9, 10, 17, 18, and 26, and L. B. Bjostad prepared the schematic drawings of chemical molecules. P. A. Murray assisted in library research and in cataloging the literature. A. E. Colwell, J. F. Bollinger, and L. K. Gaston offered valuable advice concerning the substance of the manuscript. H. R. Bowman did all of the typing and the laborious collating of material. Finally, my children, Tom, Russell, Diane, and Hal, provided patience and encouragement during the years before and during preparation of this work; this book is dedicated to them.

H. H. Shorey