

ETTORE MAJORANA  
INTERNATIONAL  
LIFE SCIENCES SERIES  
**Volume 12**

# **BEHAVIORAL ASPECTS OF FEEDING**

**Edited by  
B.G. Galef Jr.  
M. Mainardi  
and  
P. Valsecchi**

**harwood academic publishers**

# **Behavioral Aspects of Feeding**

## **Basic and Applied Research in Mammals**

6th Workshop of the International School of Ethology,  
Ettore Majorana Centre for Scientific Culture,  
Erice, Sicily, Italy, 8 – 14 June 1992

*Edited by*

**Bennet G. Galef, Jr.**  
*McMaster University, Canada*

**Marisa Mainardi**  
*University of Parma, Italy*

*and*

**Paola Valsecchi**  
*University of Parma, Italy*



harwood academic publishers

Switzerland • Australia • Belgium • France • Germany • Great Britain  
India • Japan • Malaysia • Netherlands • Russia • Singapore • USA

Copyright © 1994 by Harwood Academic Publishers GmbH, Poststrasse 22, 7000 Chur, Switzerland. All rights reserved.

### **Harwood Academic Publishers**

Private Bag 8  
Camberwell, Victoria 3124  
Australia

12 Cour Saint-Eloi  
75012 Paris  
France

Christburger Strasse 11  
10405 Berlin  
Germany

Post Office Box 90  
Reading, Berkshire RG1 8JL  
Great Britain

3-14-9, Okubo  
Shinjuku-ku, Tokyo 169  
Japan

Emmaplein 5  
1075 AW Amsterdam  
Netherlands

820 Town Center Drive  
Langhorne, Pennsylvania 19047  
United States of America

### **Library of Congress Cataloging-in-Publication Data**

Ettore Majorana International Centre for Scientific Culture.

International School of Ethology. Workshop (6th : 1992 : Erice,  
Italy)

Behavioral aspects of feeding : basic and applied research in  
mammals : 6th Workshop of the International School of Ethology,  
Ettore Majorana Centre for Scientific Culture, Erice, Sicily, Italy,  
8-14 June 1992 / edited by Bennett G. Galef, Jr., Marisa Mainardi,  
and Paola Valsecchi.

p. cm. -- (Ettore Majorana international life sciences series  
; 12)

Includes index.

ISBN 3-7186-5457-1

1. Mammals--Food--Congresses. 2. Mammals--Feeding and feeds--  
Congresses. 3. Rodents--Food--Congresses. 4. Rodents--Control--  
Congresses. I. Galef, Bennett G. II. Mainardi, Marisa.

III. Valsecchi, Paola. IV. Title. V. Series: Ettore Majorana  
international life sciences series ; v. 12.

QL737.3.E88 1994

599.053--dc20

93-38705

CIP

No part of this book may be reproduced or utilized in any form or by any means, electronic or mechanical, including photocopying and recording, or by any information storage or retrieval system, without permission in writing from the publisher. Printed in Singapore.

# **Behavioral Aspects of Feeding**

## **Ettore Majorana International Life Sciences Series**

Edited by A. Zichichi, Director, Ettore Majorana Centre for Scientific Culture.

A series of books from courses and workshops held at the Ettore Majorana Centre.

---

### **Volume 1**

#### **ADVANCES IN PERINATAL MEDICINE**

*Edited by E.V. Cosmi, G.C. Di Renzo  
and D.F. Hawkins*

### **Volume 2**

#### **THE STATE AND FUTURE DIRECTIONS OF ACUTE MYOCARDIAL INFARCTION**

*Edited by A. Raineri, R.D. Leachman  
and J.J. Kellerman*

### **Volume 3**

#### **ADVANCES IN ONCOLOGY**

*Edited by M. Ghione, A. Pellegrini  
and L. Rausa*

### **Volume 4**

#### **ONCOGENES IN PEDIATRIC TUMORS**

*Edited by G.P. Tonini, L. Massimo and  
P. Cornaglia-Ferraris*

### **Volume 5**

#### **BIOLOGY AND BIOCHEMISTRY OF NORMAL AND CANCER CELL GROWTH**

*Edited by L. Castagnetta and I. Nenci*

### **Volume 6**

#### **HOUSE MOUSE AGGRESSION**

*A Model for Understanding the  
Evolution of Social Behavior*

*Edited by P.F. Brain, D. Mainardi  
and S. Parmigiani*

### **Volume 7**

#### **RESISTANCE TO ANTITUMOR AGENTS**

*Laboratory and Clinical Studies*

*Edited by M. Ghione and L. Rausa*

### **Volume 8**

#### **FEAR AND DEFENCE**

*Edited by P.F. Brain, S. Parmigiani,  
R.J. Blanchard and D. Mainardi*

### **Volume 9**

#### **PROGRESS IN PERINATAL MEDICINE**

*Edited by D.F. Hawkins, G.C. Renzo  
and E.V. Cosmi*

### **Volume 10**

#### **RECENT ADVANCES IN PERINATAL MEDICINE**

*Edited by E.V. Cosmi, G.C. Di Renzo  
and D.F. Hawkins*

### **Volume 11**

#### **BEHAVIORAL ECOLOGY OF FISHES**

*Edited by F.A. Huntingford and  
P. Torricelli*

### **Volume 12**

#### **BEHAVIORAL ASPECTS OF FEEDING**

*Basic and Applied Research in  
Mammals*

*Edited by B.G. Galef Jr., M. Mainardi  
and P. Valsecchi*

This book is part of a series. The publisher will accept continuation orders which may be cancelled at any time and which provide for automatic billing and shipping of each title in the series upon publication. Please write for details.

# Introduction to the Series

The purpose of this Life Science series is to provide the latest information on the research and development taking place at institutions throughout the world.

The courses, held at the Ettore Majorana Centre for Scientific Culture in Erice, Sicily, are invaluable forums for direct communication between specialists.

It is hoped that the dissemination of information via this series will provide international reference works for researchers, practitioners and students.

Antonio Zichichi  
*Director of the Ettore Majorana Centre  
for Scientific Culture*

# Acknowledgements

The Editors are grateful to Dr Gianni Pavan (Centro Interdisciplinare di Bioacustica, Università degli Studi di Pavia, Italy) for his help in the editing and manuscript-handling, and to the Italian Ministry of Education, the Italian Ministry of University and Scientific Research, the Italian National Research Council, the Sicilian Regional Government and McMaster University (Canada) for financial sponsorship.

# List of Contributors

**VILMOS ALTBÄCKER**

Department of Ethology, Eötvös  
University, Jávorka S. u. 14,  
H-2131 Göd, Hungary

**MANUEL BERDOY**

Wildlife Conservation Research Unit,  
Department of Zoology, University of  
Oxford, Oxford OX1 3PS, UK

**DAVID A. BOOTH**

School of Psychology, University of  
Birmingham, Edgbaston, Birmingham  
B15 2TT, UK

**GISELA EPPLÉ**

Monell Chemical Senses Center, 3500  
Market Street, Philadelphia,  
Pennsylvania 19104 3308, USA

**ZHIQIN FAN**

Institute of Zoology, Academia Sinica,  
100080 Beijing, China

**OLIVIER GALAVERNA**

School of Arts and Sciences,  
Department of Biology, Leidy  
Laboratory of Biology, University of  
Pennsylvania, Philadelphia,  
Pennsylvania, USA

**BENNETT G. GALEF, JR.**

Department of Psychology, McMaster  
University, Hamilton, Ontario  
L8S 4K1, Canada

**WARREN G. HALL**

Department of Experimental Psychology  
and Neurobiology, Duke University,  
Durham, North Carolina 27706, USA

**MARC D. HAUSER**

Department of Biological Anthropology  
and Psychology, Harvard University,  
Cambridge, Massachusetts 02138, USA

**HAKON HEIMER**

Department of Experimental Psychology  
and Neurobiology, Duke University,  
Durham, North Carolina 27706, USA

**CECILIA M. HEYES**

Department of Psychology, University  
College London, Gower Street, London  
WC1E 6BT, UK

**ROBYN HUDSON**

Institute of Medical Psychology,  
University of Munich, Goethestrasse 31,  
D-8000 Munich 2, Germany

**DANILO MAINARDI**

Dipartimento di Scienze Ambientali,  
Università Cà Foscari, Dorsoduro 2137,  
30123 Venezia, Italy

**MARISA MAINARDI**

Dipartimento di Biologia e Fisiologia  
Generali, Università degli Studi di  
Parma, Viale delle Scienze,  
43100 Parma, Italy

**J. RUSSELL MASON**

U.S. Department of Agriculture,  
Animal and Plant Health Inspection  
Service, Animal Damage Control,  
Denver Wildlife Research Center,  
c/o Monell Chemical Senses Center,  
3500 Market Street, Philadelphia,  
Pennsylvania 19104 3308, USA

**ANNA MOLES**

Dipartimento di Biologia e Fisiologia  
Generali, Università degli Studi di  
Parma, Viale delle Scienze,  
43100 Parma, Italy

**STYLIANOS NICOLAIDIS**

Laboratoire de Neurobiologie des  
Régulations CNRS, Institut de Biologie  
du Collège de France,  
Paris 5e, France



**DALE L. NOLTE**

U.S. Department of Agriculture,  
Animal and Plant Health Inspection  
Service, Animal Damage Control,  
Denver Wildlife Research Center,  
c/o Monell Chemical Senses Center,  
3500 Market Street, Philadelphia,  
Pennsylvania 19104 3308, USA

**ISHWAR PRAKASH**

INSA Senior Scientist, Zoological  
Survey of India, Paota B Road,  
Jodhpur 342 006, India

**FREDERICK D. PROVENZA**

Range Science Department, Utah State  
University, Logan, Utah 84322 5230,  
USA

**PAUL ROZIN**

Department of Psychology, University  
of Pennsylvania, 3815 Walnut St.,  
Philadelphia, Pennsylvania 19104 6196,  
USA

**LUCIANO SANTINI**

Dipartimento di Coltivazione e Difesa  
delle Specie Legnose, Sezione di  
Entomologia Agraria, Università di  
Pisa, Via S. Michele 2, 56124 Pisa,  
Italy

**GRANT R. SINGLETON**

Division of Wildlife and Ecology,  
CSIRO, PO Box 84 Lyneham,  
A.C.T. 2602, Australia

**JOSEPH TERKEL**

Department of Zoology, The George S.  
Wise Faculty of Life Sciences, Tel Aviv  
University, Ramat Aviv 69978, Israel

**PAOLA VALSECCHI**

Dipartimento di Biologia e Fisiologia  
Generali, Università degli Studi di  
Parma, Viale delle Scienze,  
43100 Parma, Italy

**ELISABETTA VISALBERGHI**

Istituto di Psicologia, CNR, Via  
Aldrovandi 16B, 00197 Roma, Italy

**RUMEI XU**

Department of Biology, Beijing Normal  
University, 100875 Beijing, China

**YINLIE YANG**

Institute of Zoology, Academia Sinica,  
100080 Beijing, China

**QIAN ZHENG**

Institute of Zoology, Academia Sinica,  
100080 Beijing, China

# Contents

<i>Introduction to the Series</i>	vii
<i>Acknowledgements</i>	viii
<i>List of Contributors</i>	ix
<b>Preface</b>	1
<b>Individual Development of Flavour Preferences</b>	
Prenatal Induction of Natriophilia and Its Neuroendocrine Mechanism	13
<i>Olivier Galaverna and Stylianos Nicolaidis</i>	
Acquired Ingestive Motivation and the Structure of Food Recognition	37
<i>David A. Booth</i>	
Components of the Feeding Sequence, Their Development and Control	63
<i>Warren G. Hall and Hakon Heimer</i>	
<b>Social Learning of Food Preferences</b>	
Olfactory Communications about Foods among Rats: A Review of Recent Findings	83
<i>Bennett G. Galef, Jr.</i>	
Individual and Social Experiences in the Establishment of Food Preferences in Mice	103
<i>Paola Valsecchi, Anna Moles, Danilo Mainardi and Marisa Mainardi</i>	
Development of Feeding and Food Preference in the European Rabbit: Environmental and Maturational Determinants	125
<i>Robyn Hudson and Vilmos Altbäcker</i>	
Ontogeny and Social Transmission of Food Selection in Domesticated Ruminants	147
<i>Frederick D. Provenza</i>	
The Transition to Foraging Independence in Free-Ranging Vervet Monkeys	165
<i>Marc D. Hauser</i>	

Food Enculturation <i>Paul Rozin</i>	203
<b>Social Learning of Feeding Skills</b>	
Social Transmission of Pine Cone Feeding Behaviour in the Black Rat <i>Joseph Terkel</i>	229
Learning Processes and Feeding Behavior in Monkeys <i>Elisabetta Visalberghi</i>	257
Imitation and Culture: Longevity, Fecundity and Fidelity in Social Transmission <i>Cecilia M. Heyes</i>	271
<b>Studies in Semi-natural Enclosures</b>	
Making Decisions in the Wild: Constraints, Conflicts and Communication in Foraging Rats <i>Manuel Berdoy</i>	289
The Possible Role of Social Influences of Food Selection in the Formation and Control of Mouse Plagues <i>Grant R. Singleton and Paola Valsecchi</i>	315
<b>Rodent Control</b>	
Semiochemicals and Improvements in Rodent Control <i>J. Russell Mason, Gisela Epple and Dale L. Nolte</i>	327
The Impact of Social Factors on the Feeding Behavior of Brandt's Voles <i>Zhiqin Fan, Rumei Xu, Yinlie Yang and Qian Zheng</i>	347
Knowledge of Feeding Strategies as the Basis for Integrated Control of Wild Rodents in Agriculture and Forestry <i>Luciano Santini</i>	357
Rodent Management in India: Problems and New Perspectives <i>Ishwar Prakash</i>	369
<b>Index</b>	387

## PREFACE

### The Workshop

Early in June of 1992 a group of 46 scientists and students from around the world convened in Erice, Sicily to discuss the development of food preferences in animals and to explore the possible contribution of laboratory research on food choice to problems of vertebrate pest control.

The workshop, held at the Ettore Majorana Centre for Scientific Culture under the auspices of the International School of Ethology, was the result of two years of discussion and organization by the workshop directors, Marisa Mainardi of the Department of Biology and Physiology of the University of Parma (assisted by Paola Valsecchi) and Bennett Galef from the Department of Psychology at McMaster University in Canada.

The content both of the workshop and of this volume reflects the hope of the workshop directors that interaction between investigators involved in basic research on food preference development in animals and scientists interested in control of vertebrate pests might prove useful to workers in both fields. Those engaged in research under controlled conditions might gain some insight into the difficulties of applying basic knowledge to complex, real-world situations; those working in pest control could be brought up to date on recent advances in understanding of the factors making foods frequently used as baits in programs of pest control either attractive or repulsive to animals.

The directors were able to secure financial sponsorship from a variety of sources (the Italian Ministry of Education, the Italian Ministry of University and Scientific Research, the Italian National Research Council, the Sicilian Regional Government and McMaster University) sufficient to bring nineteen speakers from ten countries to the workshop venue at Erice.

Erice is a medieval town of paved streets, Norman battlements and medieval churches perched atop a 750-meter peak in northwestern Sicily. A place of strong winds, cool temperatures and magnificent vistas of the Sicilian coast and plains, Erice is close enough to the bustling city of Palermo and its modern airport to be readily accessible, yet sufficiently isolated to ensure that those attending meetings in Erice's unique conference center are continuously interacting throughout their stay.

Excursions, as well as group lunches and dinners at many of Erice's dozen restaurants, provided ample opportunity for informal discussion and as is so often the case at conferences, as much was learned outside as within the lecture theater.

### **The Book**

The organization of chapters in this volume follows roughly the order of papers presented at Erice, but changes have been made to reflect the fact that a participant's oral presentations did not always cover the same material as did the chapter he or she wrote. Logical development of topics has been given precedence over historical accuracy in organizing this collection of invited contributions.

**Individual development of flavour preferences.** The book opens with a recounting by Olivier Galaverna and Stelio Nicolaidis of the results of their joint explorations of prenatal influences on salt appetite in adult Norway rats. Galaverna and Nicolaidis have shown that the sons and daughters of rat dams that were exposed to episodes of extracellular dehydration while pregnant exhibit an exaggerated need-free appetite for salt when adult.

This demonstration of a change in flavour preference as a result of intrauterine experience is part of a growing literature indicating that events occurring before birth can effect responses to both flavours and odours during postnatal life (Hepper, 1988; Smotherman, 1982). The work described by Galaverna and Nicolaidis is unique both in its demonstration that prenatal experiences can affect flavour preferences of animals in adulthood and in its analyses of the physiological processes supporting the observed change in flavour preference. Fetal exposure to angiotensin II, which is released into a dam's bloodstream when she experiences extracellular dehydration and which crosses the placental barrier, appears to have an organizing effect on the neuronal substrate that subserves salt appetite in adulthood.

The second paper in the section on individual development of food choice was contributed by David Booth who reviews his extensive studies, both in animals and in humans, of the importance of positive consequences of eating on the development of food preferences. Booth emphasizes both the role of configural stimulus learning in the development of food recognition and the multidimensional nature of the discriminations involved in such learning. According to Booth, the postingestional consequences of eating a nutritive food change the behavioural valence of the entire situation in which feeding occurs, altering the desire both to eat a particular food and to eat at a particular site.

In a comprehensive series of experiments, Booth and his coworkers have shown that acquired preferences for foods can be induced by pairing flavors with carbohydrates and that such preference acquisition is modulated by the internal state of a subject at the time when carbohydrate is administered. Booth emphasizes the importance of such postingestive reinforcement in determining patterns of food preference in both animals and humans and the capacity of configural stimulus learning to completely suppress unlearned reflexive responses to both flavours and textures.

From Booth's perspective, social learning of food preferences (such as those discussed in later chapters by Galef, by Provenza, and by Valsecchi) is the result of social facilitation of intake of a particular substance followed by nutritional enhancement of the valence of that food, resulting in enhanced preference for it. In all cases, it is reinforcement contingent on ingestion which is central to future diet selection.

Ted Hall and Hakon Heimer next provide analyses of the development of both appetitive and consummatory components of the ingestive behaviour systems of rodents. Very young rats are born essentially without a hunger system; they do not increase their food intake in response to food deprivation. Stomach distention provides signals that terminate ingestion, as does habituation of flavor receptors in the oral cavity, but there is no nutrient-related control of initiation or maintenance of the consummatory components of eating. Because little is known of the development of appetitive responses to nutrient-related changes in physiological state, Hall and Heimer discuss the better-understood development of water intake in response to dehydration as a model system that may cast light on development of response to nutrient depletion. Both the ability to precisely specify the initiating stimuli for water ingestion and the considerable progress in identifying brain sites responding to both cellular and extracellular dehydration make possible analyses of the thirst system not yet feasible regarding hunger.

**Social learning of food preferences.** Social, rather than individual controls of ingestive behaviour in young rodents are the topic of the next group of chapters. First, Galef reviews recent studies of social influence on development of food preferences by Norway rats. The work of Galef and his coworkers provides evidence that exposure of naive observer rats to food odors carried on the breath of a recently-fed demonstrator rat produces a marked increase in observers' later preferences for whatever foods their respective demonstrators ate. This enhanced preference, on the part of observer rats, for demonstrators' diets is a result of simultaneous exposure of observers to both food odours and demonstrator-produced contextual cues that emanate from the mouths of demonstrators.

Rat breath contains traces of chemicals such as carbon disulfide ( $\text{CS}_2$ ), and experience of a food odor in conjunction with  $\text{CS}_2$  results in an enhancement of later preference for foods of that odour.

Effects of such social experiences on food preference are both profound and long lasting; social influence can reverse both inherent palatability preferences and learned aversions and can last for weeks. The data suggest that young, free-living rats may be able to determine where to eat and what to eat (but not what not to eat) as a result of interaction with adult numbers of their social group.

Paola Valsecchi and her colleagues, studying house mice, have demonstrated that both exposure to flavours in mother's milk and following mother to a feeding site can influence the food preferences of young mice. They have also found that odours of foods on the breath of adult demonstrator mice influenced the later food preferences of adult observer mice with whom the demonstrators interacted. They have thus extended the work of Galef and coworkers with Norway rats (Galef and Clark, 1971; Galef and Sherry, 1973; Galef and Wigmore, 1983) to another Murid species, indicating both that powerful social influences on food selection may be wide-spread in rodents and that the multiplicity of mechanisms for such social induction of food preference, previously observed in *Rattus norvegicus*, is not unique to that species. Indeed, similarities in details of the processes of social learning about foods in rats and mice are so great as to suggest that such social learning is homologous rather than analogous. If so, one might expect to find similar social learning about foods throughout the Muridae (the old world rats and mice).

Hudson and Altbacher extend the study of social influences on food preference to yet another mammalian species, this one not a rodent but a Lagomorph. Hudson and Altbacher start with observation of the food choices exhibited by wild rabbits living in the juniper forests of central Hungary, noting particularly the frequency of toxic plants in their environment. They then describe in detail the maternal care of rabbit does and the development of rabbit pups from birth to weaning. Finally, in a series of compelling experiments, Hudson and Altbacher demonstrate that either prenatal or postnatal exposure to a dam eating juniper are sufficient to increase her pups' ingestion of juniper at weaning. They provide evidence that: (1) exposure to smells either on the ventrum of a dam or in her milk and (2) ingestion of fecal pellets that dams deposit in the nest are each sufficient to enhance pups' preferences for foods that their dam has eaten. In concluding, Hudson and Altbacher call for a return to the field from the laboratory to determine whether the types of experiences that they have found influencing food choices in captive rabbits are equally effective changing food preference of their free-living fellows. These are questions for which answers are beginning to be provided in other species, as described in the next two chapters.

Fred Provenza's contribution describes the extensive research which he and his colleagues have carried out on the development of food choices by ruminants. Provenza discusses the development of food preferences in sheep and goats, focusing on the relationship between socially-acquired information and direct nutritional feedback in shaping food preferences. The chapter is striking in the parallels it reveals between factors influencing food choices by ruminants and by rodents: like rats, sheep and goats can acquire food preferences as a result of interaction with their dam or peers at weaning. Like rats, lambs develop preferences for foods that their dams are eating, not aversions to foods that she is avoiding. Like rats, ruminants will learn both to

increase intake of flavours paired with positive postingestional consequences and to reduce intake of flavours paired with negative postingestive consequences. On the other hand, there is evidence of a "sensitive period" for learning about foods in ruminants of a kind that appears to be rare in rodents (see Capretta, Petersik and Stewart, 1975).

Although research on the role of experience in development of food choices by ruminants is of relatively recent origins, such research promises to advance our understanding of food choice in natural circumstances more rapidly than does research with other animals because so much is already known about the nutritional value of the plants that ruminants normally ingest.

Marc Hauser's studies of the transition from dependence on mother's milk to foraging independence in troops of free-ranging vervet monkeys in Amboseli National Park in Kenya provide the first evidence of enhanced survival in unrestrained animals correlated with their degree of exposure to social influences on their food selection.

Hauser has found that the extent of synchrony in feeding between mother vervets and their young changes as infants mature. Very young vervets (those less than 2 months old) do not feed synchronously with their dam. By month three, most infants feed both at the same time and on the same food item as does their mother, and this synchrony persists until the end of the first year of life, when asynchronous feeding increases in frequency. In Hauser's study, those 4-month-old vervets that both synchronized their feeding bouts with those of their mothers and fed on the same food items that their mothers did had a higher probability of surviving to one year of age than did infants who either tended to feed independently of their mothers or fed together with their mothers, but on different food items than those that she selected to eat. The data are, thus, consistent with the hypothesis that social feeding contributes to survival by infant vervet monkeys foraging in natural habitat.

Paul Rozin's chapter deals with food selection by members of a species whose food choices are almost entirely accounted for by social learning. The foods that people eat are determined by social effects both indirect (culture wide practices that determine price and availability) and direct (observation of or teaching by adults that shapes food preferences of new recruits to a population). Rozin focuses on ideational motivations, probably unique to humans, that determine those items individuals and cultures view as appropriate for ingestion. While humans share with other animals susceptibility to both sensory/affective responses and anticipated consequences in selecting foods, humans are unique in the ideational component of their response to foods, the culturally determined value and belief systems surrounding eating.

Exploration of these belief systems is still in its infancy, but it is already clear that the contrast between the role of social factors in determining food choice in humans and in other animals is qualitative rather than quantitative. As Rozin points out, if you want to know about a person's food habits and attitudes



and can ask only a single question, "the best question by far is what is your culture or ethnic group." Culture and tradition in humans seem to outweigh individual learning as a source of variability in food selection. Such analyses have proven particularly fruitful in understanding development of human disgust reactions to contaminated or inappropriate foods, and it is this aspect of human responses to foods which Rozin emphasizes in his chapter.

**Social learning of feeding skills.** Nuts protected by hard shells, fruits guarded by spines or thorns, insects defended by poison stings--each may require sophisticated motor skills for their successful exploitation. The question of how such motor skills develop is an important area of inquiry for those interested in feeding behaviour in natural habitat. Terkel's chapter, the first in this section, provides a summary of his innovative analysis of development of the behaviour of stripping seeds from pine cones, exhibited by black rats (*Rattus rattus*) living in the forests of Israel. The ability to strip pine cones efficiently has allowed black rats to extend their species range, to live in mature pine forests where pine seeds provide the sole source of nutriment.

Terkel has found that only rats that are reared by dams exhibiting pine cone stripping behaviour develop an ability to open pine cones efficiently. The physical structure of pine cones, in particular the way in which the scales overlap one another, requires that stripping be started at the base of a cone and then continued up the cone in a spiral pattern. Young wild rats appear to learn the appropriate behaviour as a result of snatching partially opened cones from adults and finishing the job for themselves. Only young with experience finishing partially stripped cones develop an efficient method of cone opening and are able to survive on a diet of pine cones and water.

Elisabetta Visalberghi reviews literature on both the development of food preferences in monkeys and the possibility of social transmission of food processing techniques among nonhuman primates. In general, the picture that emerges of development of food preferences in monkeys and apes is similar to that found in other mammals: food preferences, but not food avoidance, are learned socially, while both food acceptance and food avoidance are learned as the result of experience of postingestional consequences of consuming various foods.

Visalberghi's analysis of the learning of food processing techniques by monkeys contains some surprises. Perhaps most interesting is the data Visalberghi provides relevant to the well known "food washing" behavior exhibited by Japanese macaques on Koshima Island in Japan. Her observations suggest, first, that food washing is probably not washing (perfectly clean food is washed) and, second, that the probability is high that washing behaviour is acquired independently by individual monkeys, when suitable environmental opportunities arise. Both capuchin monkeys and crab-eating macaques given the opportunity to interact with food and water rapidly came to dunk the food in the