Behavioral Aspects of Feeding

Basic and Applied Research in Mammals

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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 Nicolaides of the results of their joint explorations of prenatal influences on salt appetite in adult Norway rats. Galaverna and Nicolaides 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 Nicolaides 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 configurational 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 inges[illegible] 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 (CS_2), and experience of a food odor in conjunction with 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 Altbacker 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

water and young subjects exposed to an adult exhibiting washing behaviour were no more likely to wash fruit than were subjects simply exposed to pieces of fruit in water. In general, Visalberghi sees little in the evidence consistent with the view that naive monkeys learn food processing skills by observing the behaviour of skilled conspecifics.

Celia Heyes' chapter is concerned with the interaction of social learning and imitation (which Heyes defines as learning through direct observation of the behaviour of conspecifics) with individual experience of the consequences of behaviour. Heyes raises the interesting general question (critical to our interpretation of the impact on feeding behaviour of the social learning discussed by other authors whose work is described in the present and preceding sections) of whether behaviours which are learned socially or by imitation will be maintained without differential reinforcement by the environment.

Heyes makes the strong claim that although both social learning and learning by imitation allow information about behaviour to be transmitted, neither will produce stable behavioural traditions in the absence of environmental support. In Heyes's view, information acquired from a demonstrator by a social learner is as likely to be quickly lost as is individually acquired behaviour, if the environment does not differentially reward the socially learned behaviour. If Heyes is correct, and there is reason to expect that she may be, we must look to differences between environments, rather than to "tradition," to explain stable differences between populations of animals in feeding behaviours and food choices.

Studies in semi-natural enclosures. Observation of the feeding behaviour of animals held in large, semi-natural enclosures is an exciting, though relatively recent development in the study of the feeding behaviour. Such studies provide an important empirical link between laboratory investigations and field research. In the past, essentially all work on food intake, especially in rodents, was carried out on subjects confined in small individual cages. Results were extrapolated to the behaviour of animals living in social groups in large areas that provide both challenges and opportunities denied to their fellows serving as laboratory subjects. While such extrapolations from cage to field may prove accurate, we are only beginning to test their validity.

Manuel Berdoy's studies the feeding behaviour of rats within the general framework provided by foraging theory. He treats rat ingestive activities as shaped by conflicting demands arising from the need not only to eat but also to engage in other life-sustaining and reproductive activities.

Berdoy studied a colony of 30 to 50 wild rats housed in a 266 m^2 enclosure. Selected members of the colony were radio tagged, and the feeding behaviour of these individuals was automatically recorded, permitting precise

description of their eating patterns as well as broader measures of intake by the rest of the colony members.

Berdoy begins his discussion of his results with consideration of circadian and circannual rhythms of feeding in rats, the effects of the brevity of summer nights on rats' time budgets and the effects of such variables as sex and social status on distribution of meals. He ends by discussing the effects of scenting some members of a colony with cinnamon oil on the food preferences of other colony members offered a choice between two novel foods, one scented with peppermint, the other with cinnamon. Berdoy found, as have a number of investigators studying analogous situations in the laboratory (whose work is described in chapters by Galef and Valsecchi et al.), that his colony exhibited a long-lasting preference for the cinnamon-scented food.

The similarity of many of the results reported by Berdoy in a seminatural situation to findings of investigators studying rats in small laboratory cages is encouraging. Perhaps laboratory results can be extrapolated with confidence to the more complex conditions prevailing in the larger world.

Singleton and Valsecchi discuss the importance of laboratory research for an understanding of the factors leading to mouse plagues in Australia and the development of means of plague prediction and control. When plagues occur in grain-growing regions of Australia, they cause both substantial damage to crops and great inconvenience to those living in affected areas. By the time the problem is apparent, control measures are largely ineffective, so prediction of plagues and the ability to reduce mouse populations before they explode in numbers is critical.

Versatility in feeding behaviour, in particular an ability to switch rapidly from one food source to another is critical to mouse plague outbreaks. Consequently, understanding of the behavioural processes involved in diet choice may play a role in plague control. In a pair of studies of social transmission of food selection carried out in populations of 15 wild mice confined in 225 m^2 enclosures on a farm in central Australia, Singleton and Valsecchi found that mice given a choice between two novel foods when in the presence of demonstrator mice that had been fed one of those foods ate significantly more of the novel food to which their respective demonstrators had been exposed. On the other hand, mice in the same situation, given a choice between a novel food and their staple diet and exposed to demonstrators that had eaten the novel food, failed to consume more of the novel food. The authors suggest possible ways in which knowledge of the behavioural mechanisms guiding choice of foods in mice might prove useful in controlling mouse plagues, though there is obviously still a gap between what we know and what we need to know in order to be effective in the field.

Rodent control. Discussion of pest control begins with Russ Mason's chapter on differences in response of omnivores and of herbivores to volatile sulfur-bearing compounds. Omnivores seem to be attracted by compounds such as carbon disulfide, which when added to a bait increases bait consumption by both rats and mice. On the other hand, the evidence suggests that similar sulfur-containing compounds repel herbivores. For example, beaver, deer and rabbits are deterred from eating potential foods that have been scented with urine of predatory species such as coyote and lion.

In one case, that of lion dung (which is a "universal repellent" for deer), sulfur-bearing compounds found in the natural repellent have been demonstrated to themselves repel herbivores. As Mason points out, sulfur-containing odorants show promise as components of integrated pest management programs, and the study of the attractive and repellent properties of such compounds should provide fertile ground for the application of laboratory findings to practical problems of rodent control.

Next, Fan Zhiqin and his coauthors describe the results of their research on Brandt's vole, one of the more important agricultural pest species of Central Asia. In a series of laboratory and field studies, Fan and his colleagues have explored: (1) the importance of olfactory cues in food identification by Brandt's voles, (2) the role of the spatial location of foods relative to the burrow entrances and paths voles are using in determining food intake, (3) the importance familiarity in food preference, and (4) the importance of dominance hierarchies in determining both access to preferred foods and acceptance of novel foods. Fan et al.'s data indicate that: (1) the odor of plants is an important cue in food selection by Brandt's voles, (2) voles are more likely to eat foods close to their burrows and established paths than foods more distant from them, (3) adult voles prefer familiar foods to novel ones, while weaning voles prefer the foods that their parents are eating to others, and (4) dominant voles eat more of preferred foods, even when such foods are present in great excess, than do their subordinates; subordinate animals are most likely to ingest unfamiliar foods, even when familiar foods are abundant. The authors intend their observations to contribute not only to understanding of animal social behaviour, but also to the development of optimal control strategies for control of this major pest species.

Luciano Santini is explicit in his insistence that programs of integrated pest control, designed to reduce the quantities of toxic compounds introduced into the environment to control rodent pests, will require ecological and ethological studies of target species. Drawing on his 25 years of experience as an applied zoologist, Santini describes the importance of etho-ecological studies in the control of three rodent pest species (*Microtus savii*, *Apodemus sylvaticus* and *Glis glis*), each of which is of economic importance to Italian agriculture. For example, the Italian vole (*Microtus savii*) has become particularly destructive in the citrus orchards of southern Italy. Careful study of the annual

chapter makes clear, in a few instances we may be on the verge of being able to use information concerning chemicals attractive and repellent to animals to reduce the impact of pest species on human health and commerce. However, as other contributors to the section on pest control made equally clear, the complexities of managing pests over whole continents are addressed in only a limited way by findings in foot-square cages. Pest management involves more than designing baits that attract animals; it involves designing baits that are acceptable to Indian and Chinese rice farmers and baits that are easy and cheap to employ. As Santini showed, successful past management involves learning enough about the life cycle of a target species in natural environments to ensure employment of control measures at the proper time, in the proper place and in the proper way.

Personally, I was surprised by the currency of knowledge of laboratory investigations of food choice on the part of those involved in the practical business of controlling vertebrate pests. I was also surprised by my own ignorance of the complexities of pest control in the real world. We basic researchers can help our colleagues in the field by discovering better attractants or repellents or more effective poisons or traps. But criteria for better and effective are multidimensional in ways that laboratory studies are unlikely to capture. Those with the opportunity to work in seminatural enclosures can provide situations that incorporate some dimensions of success that are lacking in usual laboratory environments, but it will only be through recurrent feedback between those doing basic research relevant to pest control and those who work directly to control rodent pests that real progress is likely to be made. The editors of this volume hope that it is a useful first step in the appropriate direction.

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