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Ethoexperimental Approaches to the Study of Behavior

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LABORATORY STUDIES OF NATURALLY-OCCURRING FEEDING BEHAVIORS: PITFALLS, PROGRESS AND PROBLEMS IN ETHOEXPERIMENTAL ANALYSIS

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1. INTRODUCTION

Nineteenth-century naturalists, the intellectual forebears of today's ethologists and experimental, animal psychologists, worked in one of two very different settings. Field naturalists, as the name implies, studied the behavior of free-living animals in natural habitat. Closet naturalists, working within the walls of the museum or 'closet', dissected dead organisms and attempted to find order in similarities and differences in the morphologies of the specimens they examined.

Although those laboring indoors depended on field workers to forward new material for dissection and analysis, there was little additional contact between field and closet. Because field workers wrote largely for lay audiences, closet naturalists, often suspicious of the public acclaim some field workers enjoyed, paid almost no attention to field publications. Unhappily for field workers, closet naturalists controlled the academic positions and prestigious scientific posts of the day. In consequence, many field naturalists came to resent "the tyranny of the closet", the domination of biology by practitioners of a "science of dead things" (Gosse, 1851, p.v).

The near-complete separation of laboratory and field research in biology that occurred in Nineteenth-century England was detrimental to both endeavors. There was little lasting value in the work of field naturalists unable (or unwilling) to identify scientifically the species they were observing. For example, the eccentric, explorer-naturalist Charles Waterton (1825) provided idiosyncratic transcriptions of local Arawak names, rather than Linnean names, of the mammals and birds whose behavior he described in his journal of South America travels. Consequently, many of Waterton's otherwise-informative observations proved of little scientific worth; the various animals and plants that Waterton discussed often could not be identified by later workers (Matthews, 1973).

On the other hand, lack of experience of animals in nature led closet naturalists, sometimes unable even to recognize living examples of animals they knew only as specimens for dissection, into embarrassing errors. The first straw-stuffed specimens of birds of paradise sent by field naturalists to England from New Guinea had had their legs removed to facilitate packing. Leglessness was assumed by closet men to be characteristic of the Paradiseidae and led some to conclude that birds of paradise spent their entire lives airborne. Only subsequent shipments of specimens complete with legs brought the misunderstanding to an end.[1]

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[1] I have depended heavily on Barber's (1980) characterization of natural history during the period 1820-1870 in preceding paragraphs.

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During the first 70 years of the present century, the situation in North American study of animal learning was little better than it had been in English naturalism of the preceding century. Although there were, in the late 1800's, those who, like Willard Small (1900a, 1900b) and Linus Kline (1898, 1899), strongly advocated integration of field and laboratory studies of animal learning, those thinking in ethological terms failed to carry the day. For half a century and more, study of animal learning by experimental psychologists was dominated by others (Hull, 1943; Thorndike, 1898; Tolman, 1938; Watson, 1914) who felt strongly that animal learning or, perhaps more precisely, "the nature of the process of association in the animal mind" (Thorndike, 1911, p. 20) was best studied in situations as different as possible from those one might expect members of each species of animal to encounter in their respective, ecological situations. As Seligman (1970, p. 406) accurately observed many years later, "What captured the interest of the psychological world was the possibility that laws of behavior deduced from the study of animals in arbitrary situations might describe the general characteristics of behavior acquired as the result of pairing one event with another."

The behavior of a rat at the junction of a T-maze and of the eyelid of a rabbit in response to a puff of air were to serve learning theorists (as the inheritance of traits in fruit flies served geneticists) as model systems where association formation could be easily explored and quantified. Knowledge of special abilities to learn, exhibited by members of particular species in their respective natural habitats, was useful only as a guide to situations to avoid studying in the laboratory. What was of interest was the formation of associations "free from the helping hand of instinct" (Thorndike, 1911, p.30), not specialized associative abilities exhibited by members of particular species.

During the past decade, it has become fashionable to question the usefulness of such 'closet', psychological studies of learning processes. It should, however, be kept in mind that one of the more-exciting, contemporary developments at the interface between psychology and biology, exploration of the cellular and molecular processes responsible for behavioral plasticity in animals with simple nervous systems (Hawkins & Kandel, 1984), has as its basis just this closet approach to animal learning, currently out of favor among behavioral scientists.

Hence, the point at which I would like to begin discussion of ethological and experimental contributions to the study of feeding behavior in animals, the main topic of the present chapter, is with the understanding that there is nothing intellectually inherently good or bad about the integration of 'field' and 'closet' approaches to the study of behavior. All depends on the questions one is trying to answer.

2. THE STUDY OF FEEDING BEHAVIOR

In one sense, the history of the study of feeding behavior is relatively unusual among areas of closet, behavioral research; study of feeding behavior has been characterized since its very inception by the attempt to capture, in the laboratory, behaviors presumed to occur in nature. However, in other important ways, the history of the study of feeding behavior has much in common with more typical areas of closet, behavioral research. In study of feeding behavior, as in many other areas, no one has looked to see how similar the behavior of animals outside the laboratory is to that of their captive brethren.

It is, I suppose, reasonable to assume that feeding in the field, like feeding in the laboratory, tends to occur in bouts interspersed with periods of other activities (Le Magnen, 1985) or that the signals, external and internal, that cause an animal to initiate, sustain, and terminate each of its feeding bouts are the same in field and closet. However, it is probably equally reasonable to speculate that the details of meal patterns in the laboratory reflect, at least in part, the ease with which food is acquired by captive animals and the absence of a need for caged animals to engage in many of the activities required for survival outside the laboratory. Similarly, satiety signals may be far more commonly experienced by those animals whose feeding schedules are controlled by the dictates of animal care committees than by those animals exposed to the vagaries of the natural world.

In general, the details of feeding probably depend on the circumstances in which it is observed. Thus, although animals outside the laboratory, like captive individuals, are probably selective feeders, eagerly ingesting some substances and avoiding others, it is not obvious that individuals that have had to compete for limited food resources throughout their lives would be so finicky as those used to life in cages providing <u>ad lib</u> access to food. Body weight regulation in free-living animals may depend more on variation in energy expenditure than is the case in relatively-immobile, caged animals (See Keesey, 1986, for relevant discussion). In sum, although closet study of the processes - neural, hormonal, physiological and behavioral - that control feeding behavior has been influenced for more than 50 years by a desire to understand feeding and body weight regulation as they occur in nature, there is little evidence that would convince the cynical that one can extrapolate with confidence from laboratory analogues of feeding behavior in the field to feeding behavior in natural habitat.

Study of food intake is, of course, much too large a field to be reviewed, even in cursory fashion, in a single chapter. Therefore instead of attempting a general review of the history of the study of feeding behavior, I have elected to discuss below the interplay of field and laboratory research in the development of two relatively-small areas of investigation -- self-selection of nutrients and poison avoidance -- chosen from within the broader area of feeding behavior. I have two reasons for choosing these particular areas to discuss. First, neither area is particularly technical and, consequently, both are relatively accessible to non-specialists. Second, studies of both self-selection of diet and poison avoidance provide clear object lessons in the difficulty of successfully integrating ethological and experimental analyses of feeding behavior.

2.1 <u>Self-selection of diet by animals</u>

The outcomes of early studies of the ability of animals (usually Norway rats or domesticated chickens) to select a balanced diet from among an array of foods, each of which contained different nutrients, were contradictory. Some rats or chickens faced with a cafeteria of foods to choose among ate a mix of foods that promoted rapid growth. Others elected to eat foods in proportions that led to abnormally slow growth and vitamin deficiency diseases (see for example, Dove, 1935; Harris, Clay Hargreaves & Ward, 1933).

It became clear early in the study of food selection that the success of subjects in selecting an adequate diet from an array of foods depended on the parameters of the test situation: the number of foods offered for choice (Harris <u>et al.</u>, 1933), the relative palatabilities of the particular foods available (Kon, 1931), the sensory discriminability of a food that contained a nutrient that would redress a dietary deficiency, and the rapidity with which the nutrients in various foods relieved symptoms of deficiency (Harris et al., 1933). It also became obvious early on that differences among individuals in both flavor preferences and sampling strategies influenced their relative success in self-selecting adequate diets in cafeteria-feeding situations (Dove, 1935). Indeed, by 1935, understanding of the processes involved in self-selection of foods by animals was not markedly different from modern interpretations (Rozin, 1976).

Five years later, in 1938, both interpretation of the abilities of animals to construct a balanced diet and speculation as to how they did so had been radically altered. These changes, not all desirable, had occurred as the direct result of introduction of ecological considerations into discussions of diet choice by animals.

It was proposed by Curt Richter, the major figure in the early study of behavioral homeostasis, that;

> "The survival of animals and humans in the wild state in which the diet has to be selected from a great variety of beneficial, useless, and even harmful substances is proof of this ability [..."To make dietary selections which are conducive to normal growth and reproduction"]... In the wild state, quantitative studies of the food intake of animals and humans would be impractical. It is necessary, therefore, to try to reproduce the essential features of field conditions in the laboratory. "(Richter, Holt, & Barelare, 1938, p.734).

To Richter and his co-workers, reproduction "of the essential features of field conditions in the laboratory" meant offering rats in captivity a choice among eleven 'purified' dietary constituents (Casein, yeast, sucrose, olive oil, cod liver oil, wheat germ oil, NaCl, KCl, Na_2 HPO_4, Ca-lactate) and H_2O. The success of subjects feeding from this particular array of foods was consistent with Richter's expectations based on his interpretation of the behavior of animals in the 'wild state'. Rats offered Richter's selection of purified dietary constituents selected substances to eat and drink with remarkable efficiency; they grew both faster and with lower caloric intake than did control subjects eating the McCullom Diet, compounded by nutritionists.

As already mentioned, there were, even in the 1930's and 40's, clear indications in the literature that rats (and chickens) did not always do so well when self-selecting a diet (Dove, 1935; Harris et al, 1933; Kon, 1931; Scott, 1946; Pilgrim & Patton, 1947; see Epstein, 1967; and Lát, 1967 for reviews). Such failures to self-select adequately among foods, found in the majority of studies of self-selection in cafeteria situations (Lát, 1967), were explained away by Richter and his associates as the result of one kind of laboratory artifact or another: (a) the use of complex, natural foods in choice tests (Richter, 1942-1943; Richter, Holt, & Barelare, 1938), (b) inherited defects in the sensory systems of some subjects, (c) breakdown in subjects' homeostatic systems due to aging or environmental stress, and (d) the effects, in humans, of perverse cultural influences on behavior (Richter, 1942-1943).

In retrospect, these explanations are obviously inadequate. They offer no compelling rationale for why subjects in Richter's laboratory selected an adequate diet, while those in the laboratory of Kon or of Scott or of Tribe, etc. failed to do so. The first of the four explanations even places Richter in the awkward position of arguing that the "use of natural foods instead of purified chemical substances will certainly frequently confuse the choices" (Richter, 1942-1943, p.223), when all researchers in the area were trying to capture in the laboratory processes analogous to those permitting "animals and humans to make dietary selection... conducive to normal growth and reproduction...in the wild state." (Richter, Holt, & Barelare, 1938, p. 734).

Richter's success in demonstrating total self-selection of diets by rats, when many others failed to do so, was probably the result both of his idiosyncratic method for selecting the particular macronutrients in his cafeteria (Richter, Holt & Barelare, 1938) and of chance. Richter's method for selecting macronutrients guaranteed that he would chose the least pure carbohydrate, fat, and protein from among those he considered for use. Happenstantially, his choices also resulted in a cafeteria with both multiple sources of protein and a relatively-unpalatable carbohydrate, a combination that seems to promote success by rats when self-selecting diets (Epstein, 1967).

Why devote so much attention to an unsatisfactory, 50-year-old approach to the study of self-selection of diet? Because, even today, Richter's proposition that the simple existence of omnivores in natural environments provides evidence of their very considerable ability to self-select balanced diets influences both design of experiments and interpretation of data.

Everyone in the field of psychobiology knows that Richter's rats thrived in his cafeteria-feeding situation. Most believe that Clara Davis (during the 1930's, a student of self-selection of diet by children) showed that human children, like Richter's rats, can self-select balanced, nutritious diets. Only relative experts in the area of diet selection know that Richter's cafeteria was unusual in allowing rats to self-select adequate diets and that Davis neither showed, nor claimed to show, that children were particularly clever at selecting foods to eat (Rozin, 1976; Story & Brown, 1987). Indeed, Davis (1939, p.261) concluded her classic paper on self-selection of foods by children with the statement "the results of the experiment...leave the selection of foods to be made available to young children in the hands of their elders, where everyone has always known it belongs."

Richter's overdrawn, ecologically-derived conclusion, that the survival of animals and humans in nature provides evidence of their abilities to self-select adequate diets in the laboratory, distorted the field for a half-century. Results of laboratory studies that showed that animals could self-select adequate diets were widely cited. Experiments that failed to produce the desired result were either ignored or treated as unnatural laboratory artifacts. Researchers were led to ask how omnivores self-select balanced diets before they knew much about whether (or under what conditions) omnivores were able to self-select balanced diets. The result was a failure to appreciate the complexity of natural environments and the insurmountable challenge that some natural situations may pose.

Rather than assume that animals can compose an adequate diet under any circumstance where it is theoretically possible to do so, it seems more reasonable to consider the possibility that members of any species, even those as cosmopolitan in distribution as Norway rats or 'primitive' H. sapiens are not able to survive everywhere within their respective species' ranges. By definition, individuals can survive only in those portions of the environment that both provide all resources necessary for life and lack insurmountable threats. An area would be devoid of rats if it contained either lethal substances that rats could no learn to avoid eating or a necessary nutrient that was available only in a form that rats could not learn to eat.

Contrary to Richter's assertion, existence of an omnivorous species in nature tells us little about the range of environments in which species members have the ability to self-select nutritionally-adequate, safe diets. Persistence of omnivores outside the laboratory shows only that there exist portions of the environment where the behavioral capacities of species members are sufficient to permit them to develop dietary repertoires adequate for self-maintenance, growth, and reproduction. Both those laboratory situations in which rats self-select foods adequately and those in which they fail to do so are probably informative analogues of situations in the real world. Armchair naturalism, of the sort practiced by Richter, though often powerful in its historical effects on the development of an area of laboratory research, is not necessarily beneficial.

2.2 Poison avoidance by animals

Like laboratory study of diet-selection by animals, laboratory investigation of the learning of aversions to toxic substances has been profoundly influenced by reference to ecological scenarios. For the past two decades, interpretation of taste-aversion learning by rats as a form of adaptively-specialized learning, evolved in response to selective pressures provided by naturally-occurring toxins, has served as a paradigmatic case of the utility of ecological perspectives in discussion of ingestive behavior. Following Rozin and Kalat's (1971) forceful presentation of taste-aversion learning as a major factor in the ability of rats to select nutrients when vitamin deficient, it became easy to forget that the ability of rats to learn association between tastes and toxicosis is not necessarily an important component of their response to naturally-occurring toxins.

John Garcia did not come to the study of taste-aversion learning as the result of field observations indicating that rats in nature learn to avoid ingesting naturally-occurring, palatable-but-toxic foods that induce illness some hours after they are ingested. Rather, the ability to learn taste-aversions over long delays was a serendipitous discovery in the course of explorations of the unconditioned effects of X-irradiation. Adaptive functions of the special properties of taste aversion learning were proposed *post hoc*.

2.2.1. *Long-delay learning*. Rats tolerate very long intervals between experience of a novel flavor and subsequent illness and still learn an aversion to the novel flavor (Garcia, Ervin & Koelling, 1966). In the laboratory, the novel flavorants used as conditional stimuli in taste-aversion-learning experiments are usually palatable substances such as sodium saccharin. If unpalatable flavorants, like quinine hydrochloride, were used as conditional stimuli, even naive subjects would be reluctant to ingest them and evidence of aversion learning would be more difficult to produce. Although it is convenient to study the acquisition of aversions to palatable foods by rats, it is not obvious that rats need to learn such aversions outside the laboratory. There is no evidence of which I know either that rats encounter palatable, toxic foods in their natural habitats or that such palatable, toxic foods have effects delayed by many minutes or hours. There are reasons to believe, to the contrary, that palatable toxins with delayed effects are less likely to exist tha vile-tasting, fast-acting poisons.

Prey species that evolve means to manufacture or sequester toxins do so at least in part, to deter potential predators. Immediately perceive unpalatability and rapid induction of pain or illness, are more reliabl deterrents to ingestion than is palatabilty coupled with long-delayed, negative after-effects (Domjan & Galef, 1983). The burden of proof of th existence of palatable toxins with delayed postingestional consequence that rats in natural ecosystems have had to learn to avoid for millenni rests with those who hypothesize the existence of such "cryptic toxins" Surely, human progress in the control of commensal rodent pests woul benefit immensely from discovery and use of cryptic toxins in concentrate form in poison baits.

It has become standard practice to accept as demonstrated an unprove (in fact, an unexamined) hypothesis about the properties of naturally-occurring toxins and their impact, via natural selection, on the learnin of flavor aversions. If there were palatable, toxic foods in th environment in which rats evolved and if the onset of illness resultin from the ingestion of such toxins was delayed by many hours, then th ability to learn aversions to palatable flavors over long delays migh have evolved in response to the selective pressures exerted by such toxi foods. However, we do not know that such cryptic toxins are present i the natural environments of rats. Hence, appeal to the selective pressur they would provide to explain the evolution of rat behavior is pur speculation. It is, for example, possible that a system permitting th association of tastes with long-delayed consequences of ingestion evolve to permit rats to identify beneficial foods, not toxic substances. O this hypothesis, the capacity of a system shaped by natural selection t permit rats to identify nutrients to respond to the negativ postingestional consequences of toxins would be largely epiphenomenal.

2.2.2. *Cue-to-consequence specificity*. It is frequently asserted (Rozi & Kalat, 1971) that the tendency of rats to learn to avoid the taste rather than the visual or auditory properties of the things that they ea (Garcia & Koelling, 1966) is adaptive. However, if, as has also bee argued (Wilcoxon, Dragoin, & Kral, 1971), it is adaptive for birds to b able to learn to avoid foods that cause illness on the basis of the visua properties of those foods, it is hard to understand why it would b disadvantageous for rats to do so as well (Galef & Osborne, 1978).

The assertion that organisms more readily learn aversions to foods usin the sensory modalities that dominate in their selection of substances t eat and drink (Rozin & Kalat, 1971) has not held up well as evidence ha accumulated. Buteo hawks, surely at least as visually guided in thei food selection as chickens or quail (species that tend to form aversion to the visual properties of foods), develop stronger aversions to th taste than to the visual properties of toxic prey (Brett, Hankins, & Garcia, 1976). The guinea pig, like the rat crepuscular in its dail activity rhythm, forms aversions to both the tastes and the visual properties of fluids (Braveman, 1974). Chickens tend to learn aversion to the tastes of fluids and to the visual properties of foods (Gillette, Martin, & Bellingham, 1980). While I do not doubt that it is possible, after the fact, to compose adaptive explanations for the tendencies o members of each of these species to form aversions to one or anothe sensory characteristic of the solids or fluids they ingest, I do not believe that such explanations could have been constructed before th facts were known.

The *post hoc* development of adaptive explanations for each feature of poison-avoidance learning is not only intellectually irritating. Once such explanations are widely accepted, they can come to serve as "filters", determining whether new findings are treated as important. Data compatible with a prevailing functional interpretation are accepted; data incompatible with an accepted functional explanation are either ignored or explained away. If such functional explanations of laboratory phenomena are based on field data, rather than on extrapolations from the results of the laboratory experiments themselves, then the functional explanations can be valuable in understanding laboratory findings. However, when field data are lacking, the influence of functional speculations can be pernicious.

2.2.3. *Adaptive patterns of diet sampling*. As discussed above, Richter's assertions about the ability of individual omnivores to self-select balanced diets in the wild led the unwary to ignore situations in which omnivores failed to select foods wisely. Similarly, *post hoc* functional explanations of the special features of taste-aversion learning may have persuaded some to ignore data that are inconsistent with the prevailing interpretation. For example, as Zahorik and Houpt (1981) have made clear, the usefulness of the ability of rats to form aversions to the taste of unfamiliar, toxic foods, when adverse effects of ingesting those foods are delayed for hours, depends on the sampling strategy that rats employ when they encounter unfamiliar, potentially-dangerous foods.

Rats should eat relatively-small, initial meals of unfamiliar foods. They should also eat only one unfamiliar food at a time. If a rat gorged on each unfamiliar food that it encountered, the ability to learn rapidly to associate the taste of an unfamiliar food with toxicosis would sometimes be of little use; at least some unfamiliar, toxic substances would prove fatal following a first, large meal. Obviously, if a rat were to sample several unfamiliar foods in rapid succession and become ill, it would have difficulty identifying the particular unfamiliar food that was toxic. The sick individual might develop a strong aversion to the most salient (Kalat & Rozin, 1970) or, perhaps, the last-eaten, unfamiliar food, but, unfortunately, neither salience nor order of ingestion are reliable guides to toxicity. Cautious ingestion of one unfamiliar food at a time would appear to maximize an individual's chances of both surviving initial encounters with unfamiliar foods and associating a poisonous food with its consequences.

Rozin and Kalat (1971, p.465), in discussing the acquisition of learned preferences, proposed that "The rat's feeding pattern maximizes the possibility of associating each diet with its appropriate consequences, since meals tend to be isolated in time and consist of a single food." Similar assertions have been made subsequently by others (Shettleworth, 1984; Zahorik & Houpt, 1981). Although there is general agreement in the published literature concerning the behavior of rats sampling among unfamiliar foods, the evidence contradicts the consensus. Adaptive sampling among novel foods by rats, leading to ready identification of toxins is accepted as true, not because there is adequate evidence of such sampling, but because it appears to be required by prevailing functional interpretations of the results of laboratory studies of taste-aversion learning.

Many investigators have described the hesitancy of wild rats to begin eating unfamiliar foods (Barnett, 1958; Barnett & Cowan, 1975; Galef, 1970; Mitchell, 1976; Rozin, 1968; Rzoska, 1953; Chitty & Shorten, 1946). However, evidence of reluctance to start eating an unfamiliar food or foods does not bear directly on the issue of whether rats sample among several unfamiliar foods so as to be able to associate each food with its postingestive consequences. Hesitancy to begin eating unfamiliar foods only delays the moment of truth.

Rozin (1969) is most frequently cited as having provided evidence that rats sample unfamiliar foods one at a time so as to facilitate identification of any toxins they ingest. However, Rozin demonstrated only that, over a period of several days, 4 of 10 thiamine-deficient, rats came to prefer the thiamine-rich alternative as a result of their sampling behavior. Rozin's (1969) data do not show (and Rozin has not claimed that they do show) that rats encountering several unfamiliar, potentially-dangerous foods sample among them so as to facilitate identification of a toxic food should one be present. To the contrary, Rozin's (1969) data indicated that most of his subjects ate two or three unfamiliar foods during the first 1/2 hour that those foods were available.

Promiscuous sampling of unfamiliar foods is not restricted to domesticated rats. Barnett (1956, p.30) found that when four unfamiliar foods were offered to first-generation, laboratory-bred, wild rats for the first time "It was usual for all four foods to be eaten within the first feeding period." Absence of sampling of one unfamiliar food at a time is obvious in each of several descriptions of the behavior of individual wild rats facing a choice among four unfamiliar foods (flour, sugar, liver, and wheat). For instance,

> "Eating begins with 15 minutes' intermittent consumption of flour with some sniffing of the other foods. Liver is eaten for 2 min., then still holding a piece of liver, leans into sugar box and eats sugar, leaves piece of liver at back of cage, returns to liver tin and eats liver for 1 min. Eats sugar for 5 min. Restless interval of 4 min. followed by picking up bits of liver and dropping them; eats wheat for 1 min, then sniffles in the wheat tin. Followed by 42 min of restlessness with some sampling of wheat, flour and sugar, before settling to sleep..." (Barnett, 1956, p.32).

It is difficult to see how a rat that suffered toxicosis after sampling mong four unfamiliar foods in this way would know which food to avoid in future. Similarly, in a more recent study of sampling among unfamiliar foods, Beck, Hitchcock, and Galef (1988) found that wild rats did not tend to eat one unfamiliar food at a time and did not wait an unusually long time after eating one unfamiliar food before eating another.

2.2.4. *Summary*. My reason for discussing at some length the use of functional arguments to provide frameworks for discussion both of dietary self-selection and poison avoidance is that review of both these bodies of literature suggests that an ethological approach to the discussion and interpretation of laboratory data can have costs as well as benefits. The benefits are obvious. A functional framework provides means both of integrating diverse findings into a coherent story and of identifying significant findings. Indeed, when an explanation of the function of some havior is based on data, it is likely to be helpful. When functional planation is based on speculation, it is likely to be costly.

Coherent stories about the functions of behavior take on a life of their m and become filters, determining which facts will be incorporated into organized knowledge and which facts will be rejected. In the case of self-selection of diet, data indicating that omnivores can have difficulty in composing balanced diets were ignored and data on diet choice were sometimes stretched to be consistent with the prevailing functional story, when they were, in fact, neutral or even negative (Brown & Story, 1987). Similarly, in discussion of poison avoidance, evidence that rats and other omnivores are not particularly adept at learning to avoid toxins (Chitty, 1954) was overlooked and data on diet sampling was assumed to be consistent with the prevailing ecological interpretation, when it was not. The message in all this is that functional interpretation is not necessarily the golden road to success. There are pitfalls as well as opportunities in using ethological perspectives to provide a framework to interpret data collected in laboratory situations.

3. SOCIAL INFLUENCES ON FOOD CHOICE AND FORAGING

The problems discussed in the preceding section should come as no surprise to those familiar with the history of the study of behavior. Field naturalists and closet naturalists have both made substantial contributions to our understanding of the biosphere. On the other hand, armchair naturalists, no matter how well-intentioned, have been a constant source of trouble. Guesses about the functional significance of laboratory findings, originally intended as working hypotheses or tentative explanations, become reified and exert an undeserved influence on research. In the absence of relevant field observations, visions of the natural world that make ecological sense of laboratory findings take a tenacious hold on the scientific imagination and distort interpretation of data.

On the other hand, without controlled experiments, field workers propose unlikely behavioral processes to explain the occurrence of behaviors they have observed in the field (Sherry & Galef, 1984). There is abroad in the land an unwillingness to confess ignorance as to whether or how an ability demonstrated in the laboratory enhances survival or reproduction in the field or to admit to lack of knowledge about how, in a mechanistic sense, an organism might be able to achieve the impressive performances it exhibits in its natural habitat. In such a climate, Just so stories about mechanism or function can come to pass for synthesis of field and closet approaches.

The present section is, I hope, about alternatives to Just so stories in integrating field and laboratory approaches to the study of feeding behavior. The two general strategies discussed below are surely not new. Each has been used countless times, by countless investigators, for more than 100 years. Each involves collection of data in both laboratory and field so as to be able to provide mechanistic analyses of behavioral phenomena observed in the uncontrolled world outside the confines of the closet where mechanistic analyses are often impractical. The examples I will discuss in detail are taken from my own studies of social influences on feeding behavior, both because it is the research with which I am most familiar and because it is the work that I am most free to criticize.

3.1 Using field data to pose questions for laboratory analyses of feeding behaviors

One of the more important grounds on which ethologists rejected the approach of experimental psychologists to the analysis of behavior was the failure of psychologists to observe the behavior of members of their subject species in the environments in which they normally lived.

Description of behavior in the natural environment was to Lorenz, Tinbergen, and other classic ethologists the obvious starting point for analyses of the causes of behavior. It is surely reasonable to find out what an animal does before you try to figure out how it does it.

Althoug the logic of the ethological approach to problem definition appears compelling to those with an evolutionary or ecological background, it has been slow to penetrate fields dominated by closet workers. Johnston (1981) proposed, for example, that the study of association formation in the abstract be abandoned in favor of an ethological strategy for the study of animal learning that began with a "task description" of naturally-occurring instances of learning that could then be analyzed in the laboratory. There has, however, been little movement in the direction Johnston suggested. More often, those laboratory workers interested in an ethological approach to behavior, instead of initiating their own field studies, have taken advantage of field descriptions of behavior already in the literature as starting points for analyses. It is this latter strategy, recourse to the literature, that my students and I have employed in the 20-year study of social influences on feeding behavior in Norway rats with which I will be concerned in the present section. My coworkers and I started with field observations that suggested that some aspect of the feeding behavior of our subject species might be socially mediated, brought the phenomenon into the laboratory, and then attempted to analyze the behavior under controlled conditions.

3.1.1. Field observation. Some years ago, Fritz Steiniger, an ecologist working in the field of rodent control, discovered that, if a poison bait were employed in an area for an extended period of time, despite initial success, with the rats eating lots of poison and dying in large numbers, later acceptance of the poison bait was very poor. Steiniger (1950) noted, in particular, that young rats, born to those adults that had survived poisoning, rejected the poison bait without ever even tasting it themselves. Steiniger attributed such poison avoidance by the young to the effects of urine and feces deposited on poison baits as a warning signal by surviving adults that had learned to avoid eating the poison.

3.1.2. Laboratory analogue. The phenomenon described by Steiniger, avoidance by young rats of a food that the adults of their colony have learned to avoid, is easily observed in small colonies of wild rats living in captivity (Galef & Clark, 1971a). My coworker, Mertice Clark, and I introduced nausea-inducing concentrations of poison (Lithium chloride) into one of the two very different foods (Diets A and B) that we presented to each of our colonies for 3 hr/day. Soon, colony members would not eat the poisoned food even when we offered them uncontaminated samples of it. We then had to wait until one of the females in each colony became pregnant, gave birth to a litter, and reared her litter to weaning age. Finally, we could observe the pattern of diet selection exhibited by those weanlings reared in colonies whose adult members had learned to eat either only Diet A or only Diet B when uncontaminated samples of both diets were available to them.

Just as Steiniger had observed in free-living colonies of wild Norway rats, young wild rats weaned in our captive colonies totally avoided whichever of the two foods the adults of their colony had learned to avoid. They ate only the food that the adults were eating. Over the years, we have observed 247 wild rat pups in our laboratory situation during their first 10 days of eating solid food and only one ate so much as a single bite of whichever food the adults of its colony had been trained to avoid.

As the result of his field observations, Steiniger proposed that urine and feces deposited by adult rats in or near a poisoned food dissuaded young rats from eating that food. In the laboratory, we found that wild rat pups, reared by adults fed only Diet B and never exposed o Diet A, preferred Diet B as strongly as did those wild rat pups reared by adults that had learned to avoid Diet A and, therefore, ate only Diet B (Galef & Clark, 1971a). These data suggest that the 247 rat pups in our first experiments were not avoiding a diet because the adults of their colony were marking that diet. Rather, pups raised by colonies trained to avoid Diet A were learning to eat Diet B, the food that adults of their colony were eating, and were avoiding Diet A for reasons that had nothing to do with the fact that adults were avoiding that food.

It is well known that wild Norway rats are very hesitant to eat a food that they haven't previously eaten (Barnett, 1958; Galef, 1970). Consequently, biasing young rats to start feeding on one diet could greatly reduce the probability they would feed on available alternatives. In fact, the results of a number of experiments have been consistent with the hypothesis that young wild rats learn from adults only about what foods to eat and avoid alternatives as a result of their tendency to avoid unfamiliar foods (Galef & Clark, 1971a; Galef & Clark, 1972; see Galef, 1985a for review).

3.1.3. Interpretation. At this point, it might be worth considering some conclusions that can be reached from the two laboratory studies described above considered together with Steiniger's (1950) field work. First, Steiniger's (1950) observation, that adult wild rats in uncontrolled environments can lead their offspring to eat only safe foods when a food that the adults have learned is toxic is present, is repeatable under controlled conditions. In the laboratory, rats behave as Steiniger observed them behave in a variety of natural circumstances. Second, Steiniger's attempt to deduce mechanism from simple observation in the field was unsuccessful. Not only have controlled experiments repeatedly failed to confirm Steiniger's suggestion that rats that have learned to avoid a food mark that food so as to make it unattractive to conspecifics (Galef & Clark, 1971a; Galef & Beck, 1985), 20 years of study in the laboratory have failed to reveal any way in which rats can directly lead their colleagues away from a food. One rat can induce others to eat one of several available foods and, thus, lower the probability that they will eat available alternatives, but the avoidance of alternatives is an indirect, not a direct result of social interaction (Galef, 1985a).

In retrospect, it is not difficult to understand both the failure of rats to directly dissuade conspecifics from eating a known toxin and their ability to lead conspecifics directly to a safe food. After all, for one rat to mark a food that it has learned to avoid so as to reduce the probability that others would eat that food involves a complex of behaviors that would evolve only if close relatives of a knowledgeable rat benefited more from the warning than did the knowledgeable rat's evolutionary competitors. Once an individual has learned to avoid a food, that individual has no reason to approach the noxious food again. It surely has no interest in making the food unattractive to unrelated conspecifics.

On the other hand, an individual that has learned that a food is safe has reason to continue to exploit the safe food. Exploitation of a food requires returning to the place where that food is to be found. Exploitation of a food also requires introduction of the exploited food into one's own digestive tract. Pursuing one's own interests may, thus, provide sources of useful information to others as to where and what one is eating, without the evolution of patterns of behavior specifically evolved for purposes of communication (Galef, 1986a). For example, hungry rats might follow a successful forager to food (Galef, Mischinger & Malenfant, 1987) or learn what a successful forager has eaten by smelling its breath (Galef & Wigmore, 1983). Hence, communication of information among rats about what foods they are eating seems, a priori, more likely than communication of information about potential foods they are not eating.

3.1.4. Redundant processes. Over the years, analyses of the behavioral processes involved in social influence on diet selection by rats has revealed a number of redundant, possibly-mutually-reinforcing ways in which a young rat can be influenced in its choice of diet by an adult. First, the simple physical presence of adults at a potential feeding site attracts pups to that site and greatly increases the probability that young rats will wean to the particular food located there. For example, in an experiment (Galef, 1981) in which an anesthetized, adult, female rat was draped across one of two bowls containing the same food and located less than a meter apart, pups took 80 to 90 percent of the food that they ate from the bowl draped with the female. Similarly, when Clark and I (Galef & Clark, 1971b) watched nine individually-marked pups from three litters take their very first meals of solid food, each of the nine ate its first meal from a food bowl at which an adult was eating and while the adult was eating there.

Second, adult rats deposit residual, olfactory cues both in the areas that they visit (Galef & Heiber, 1976) and in the foods that they eat (Galef & Beck, 1985). These residual cues are attractive to pups (not aversive as Steiniger, 1950, proposed) and can bias pups' choices both of areas to explore and feeding sites to exploit. Galef and Heiber (1976) found that individual rat pups preferred to eat and to explore in the end of an enclosure that had been soiled during its previous occupancy by conspecifics, rather than in the clean end of the enclosure. Galef and Beck (1985) found that rats offered two samples of a diet preferred the sample from which conspecifics had eaten to a previously-untouched sample.

Third, both Sherry (Galef & Sherry, 1973) and Henderson (Galef & Henderson, 1972) and I have provided evidence that the milk of a lactating female rat contains cues directly reflecting the flavor of her diet. Galef and Sherry (1973) took rat pups that were nursing from a female rat eating Diet A, hand-fed them a 1/2-cc of milk manually expressed from another lactating female rat eating Diet B, and then made the pups ill by injecting them with lithium chloride. At weaning, in comparison with a number of relevant controls, these experimental pups exhibited a strong aversion to Diet B. Cues in mother's milk allowed pups to identify their mother's diet. Comparison of the food preferences at weaning of rat pups raised by mothers eating Diet B and fostered daily (6 hr/day for 18 days) either to a lactating female eating Diet A or to a maternal, non-lactating female eating Diet A (Galef & Henderson, 1972) showed that cues in mother's milk influenced diet choice by pups. When tested for diet preference at weaning, pups fostered daily to lactating females eating Diet A, but not pups fostered daily to maternal, non-lactating females eating Diet A, showed an enhanced preference for Diet A, the diet eaten by their foster mothers.

3.1.5. Interpretation. Redundancy in the ways in which social influences can affect the diet preferences of rat pups at weaning, like redundancy in the processes underlying other behavioral capacities of