WHY WE EAT
WHAT WE EAT

The Psychology of Eating

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ELIZABETH D. CAPALDI

Social Influences on Food Preferences and Feeding Behaviors of Vertebrates

Bennett G. Galef, Jr.

T o survive and reproduce in natural environments, animals not only must eat foods that provide all of the various nutrients necessary for self-maintenance and reproduction, they also must avoid eating lethal amounts of any toxic plants or animals that they encounter. Selecting a nutritionally adequate diet is no simple task, and physiologists, biologists, and psychologists have spent decades trying to understand how animals manage to discriminate foods containing needed nutrients from ingestible substances that are either valueless or dangerous to eat.

At first, interest focused on the fundamental question of whether animals are, in fact, able to select a nutritionally balanced diet when choosing foods from a cafeteria of items that vary in nutritional content (Crichton-Browne, 1910; Jordan, 1906). Once that question appeared to have been resolved (Richter, 1942–43; but see Galef, 1991a), interest shifted, first, to the question of how animals learn to select foods containing needed nutrients (Harris, Clay, Hargreaves, & Ward, 1933; Rozin, 1967), and then to the issue of how animals learn to avoid ingesting deleterious quantities of any toxins they might encounter while sampling unfamiliar potential foods in the search for nutrients (Garcia & Hankins, 1977; Rozin & Kalat, 1971).

Given the immense contribution of social interactions to the development of patterns of food selection by members of our own species, it is

surprising that early students of food selection never looked for social influences on the ingestive behavior of the animals they studied. Perhaps the emphasis throughout the present century on understanding adaptive rather than maladaptive patterns of food selection (Galef, 1991a; Richter, 1942–43) and on describing neural and physiological substrates of ingestive behavior diverted attention from investigation of social influences on feeding.

Whether they are in the theoretical mainstream or not, social influences on food choice could not be ignored forever. The last 2 decades have seen a striking increase in the number of studies of the role of social interactions in shaping not only food selection but also a range of behaviors from predator avoidance (Cook, Mineka, Wolkenstein, & Laitsch, 1985); Curio, Ernst, &, Vieth, 1978) to choice of breeding site (Warner, 1988, 1990a, 1990b) and sexual partner (Dugatkin, 1992; Dugatkin & Godin, 1992, 1993; Schlupp, Marler, & Ryan, 1994). Studies of social influence on the food choices of animals have been particularly fruitful, at least in part because such studies have been able to take advantage of decades of earlier research describing nonsocial factors that influence food selection by animals.

In this chapter, I review research, almost all completed during the last 20 years, on the role of social factors in the development of food preferences, food aversions, and feeding behaviors in vertebrates. The evidence clearly demonstrates the importance of socially acquired information, particularly information extracted from adults by juveniles, in shaping the development of food preferences and feeding behaviors of both birds and mammals.

SOCIAL FACTORS IN THE ACQUISITION OF FOOD PREFERENCES

Prenatal Effects

Even before birth, a young mammal can acquire information from its female parent about at least some of the foods that she has eaten. Hepper (1988) fed garlic to pregnant rats late in gestation. Within an hour of birth of each of their litters, he gave the young to foster mothers that had never eaten garlic to rear. When the foster-reared pups were 12 days old, each was offered a choice between two dishes, one containing garlic, the other onion.

Hepper found that rat pups that had been delivered by mothers that ate garlic while pregnant stayed near the dish containing garlic, whereas pups from control litters (whose mothers had not eaten garlic during pregnancy) did not exhibit any preference between garlic and onion.

Although Hepper's data demonstrate only that young rats can become familiar with the taste or odor of a food that their mother has eaten during pregnancy, it seems likely that pups with an enhanced preference for the odor of garlic when 12 days of age would have exhibited enhanced intake of either garlic or garlic-flavored food if their food preferences had been examined at weaning. Clearly, a potentially informative experiment remains to be done.

Effects While Nursing

Direct evidence is available that (a) flavors of foods that a dam eats while lactating can affect the flavor of her milk and (b) exposure to milk flavored by foods a lactating dam has eaten can affect food preferences of her nurslings at weaning. For example, at weaning, infant rat pups that had been made ill immediately after they were fed milk expressed manually from a lactating rat eating a distinctively flavored diet exhibited an aversion to the diet eaten by the lactating rat whose milk they had received (Galef & Sherry, 1973). Similarly, weaning rat pups exhibited enhanced preferences for foods eaten by a lactating female from whom the pups had suckled for several hours, but not for the same food if it had been eaten by a female rat that acted in a maternal way but did not give milk during the hours the pups spent with her (Bronstein, Levine, & Marcus, 1975; Galef & Henderson, 1972; Martin & Alberts, 1979).

Effects During Weaning

Presence of an Adult at a Feeding Site

Galef and Clark (1971b) used closed-circuit television and time-lapse video recorders to observe nine wild rat pups from three different litters each take its very first meal of solid food. All nine pups were observed to eat for the first time under exactly the same circumstances: Each ate while an adult was eating, and each ate at the site where the adult was eating, not at a nearby feeding site where no adult was feeding. Weaning mice also

exhibit a strong tendency both to approach an adult feeding at a distance from the nest and to initiate their first bouts of feeding on solid food near the place where the adult is eating (Valsecchi, Mainardi, Sgoifo, & Taticcchi, 1989).

In fact, simply anesthetizing a rat and placing it near a feeding site makes that site significantly more attractive to weaning rat pups than alternative sites that have no rat placed near them (Galef, 1981). Apparently, the simple physical presence of an adult rat at a feeding site makes that site attractive to young rats and markedly increases the probability that they will wean to whatever food is to be found there (Galef & Clark, 1971b).

In a methodologically innovative series of experiments on the role of maternal interaction on the development of food preferences in kittens, Wyrwicka (1978; 1981) used rewarding electrical stimulation of the hypothalamus to train mother cats to eat unusual foods such as banana. She then let weanling kittens (4–10 weeks of age) interact with their dam while she was eating the unusual food. After a few test sessions during which the kittens became habituated to the experimental setting, most started to lick and eat the food their mother was eating, often attempting to eat from exactly the same spot in the food dish where she had been feeding. Four months after eating banana with their mothers, many kittens continued to accept banana, whereas almost no kittens of the same age that had never before eaten bananas would do so.

Sheep can also induce their young to begin feeding on unfamiliar foods. Weaning lambs offered wheat for the first time ate much less wheat if exposed to wheat while alone than if offered wheat in the presence of their respective mothers, who had been trained to eat wheat (Lynch, Keogh, Elwin, Green, & Mottershead, 1983). In a similar experiment, Thorhallsdottir, Provenza, and Balph (1990) found that lambs exposed to a novel food while alone ate far less of that food than did lambs exposed to the same novel food while in the presence of their feeding dam.

It is not clear in either of the studies in which sheep served as subjects whether presence of a ewe simply provided an environment in which the probability of a lamb eating was enhanced (a social facilitation effect; Clayton, 1978) or the adult sheep were in some way directly influencing their young to eat the foods that they were eating. However, regardless of the mechanism involved, lambs exposed to an unfamiliar food while their

mothers ate it were more likely to eat and learn to accept that food than were lambs offered the same unfamiliar food while alone.

In sheep, as in kittens, the effects of eating a food on its later acceptance were long lasting. Lambs that ate wheat with their dams when 12 weeks of age ate considerably more wheat when 3 years old than did sheep of a like age that had never before eaten wheat (Green Elwin, Mottershead, Keogh, & Lynch, 1984).

Feeding hens (*Gallus gallus*) can also influence choices of foods and feeding sites of their chicks. Observation of a mechanical pointer "pecking" at a visually distinctive foodlike object caused newly hatched chicks to peck at matching objects (Suboski, 1989; Turner, 1964). Such social orientation of pecking may be a means for transmission of food preferences from hen to chick, allowing a hen to designate edible objects for her young (Suboski & Bartashunas, 1984).

In more natural circumstances, when a mother hen finds food, she emits a special "food call," which attracts her chicks. The hen then pecks at the food, picking up bits of it in her beak and then dropping them in front of her chicks. The hen's activity causes the chicks to eat the food she has been manipulating (Roper, 1986; Stokes, 1971). Presumably, the experiments of Suboski and of Turner described here tapped into these species-typical behaviors of mother hens and their young.

Older chickens are also able to learn to select particular feeding sites by observing the behavior of conspecifics. The sight of either an adolescent chicken or its television image feeding from a visually distinctive feeding site caused observing birds to feed from similar feeding sites when tested 2 days later (McQuoid & Galef, 1992, 1993).

Residual Olfactory Cues

In the examples described in the preceding section, the presence or activities of adults at a feeding site affected the feeding behavior of younger individuals. However, adults need not be physically present at a feeding site to guide their young to that site. While eating, adult rats deposit residual olfactory cues both in the vicinity of a food source (Galef & Heiber, 1976; Laland & Plotkin, 1990, 1993) and on any food that they are eating (Galef & Beck, 1985). These odorants are attractive to rat pups and cause them to feed at

marked sites in preference to unmarked ones (Galef & Heiber, 1976; Laland & Plotkin, 1990, 1993).

Exposure to Foods and Food Related Cues

The young of many species seem particularly attentive to the food objects that they see adults manipulating. For example, infant chimpanzees actively solicit food from their mothers, and chimpanzee mothers share the food items they are eating with their offspring (Silk, 1978). The young of other primate species, although often less active in soliciting scraps from adults than are young chimpanzees, still manage to focus their ingestion on the same items of food that adults of their troop are eating (e.g., chacma baboon [Hall, 1962, 1963a, 1963b], ringtailed lemur [Sussman, 1977], anubis baboon [Ransom & Rowell, 1972], Japanese macaque, [Kawai, 1965]). Hall's account of feeding interactions between adult baboons and their young is typical: "Dark-phase [chacma baboon] infants, prior to their actually eating food-plants, watch the feeding of their mothers or of other mature animals near them, and tend to direct their exploratory movements upon the same plants, chewing them or putting parts of them in their mouths (1963a, p. 220)."

In a systematic study of the interaction of infant monkeys and adults in feeding situations in the wild, Whitehead (1986) observed the feeding interactions of 4- to 12-month-old infant mantled howler monkeys (*Alouatta palliata*) and their mothers in the forests of western Costa Rica. Infants ate leaves only from species of plant on which they had observed adult group members feed, and the infants often fed from the same branch from which their mother was eating. On the other hand, infants frequently began to ingest unfamiliar fruits before adult group members did and, when eating fruit, seldom attempted to feed from the same branch from which an adult was feeding.

Although there is presently no direct evidence that such social introduction of young primates to food items that adults are eating shapes the later dietary repertoire of the young, it is difficult to imagine that eating foods that adults are eating has no effect on development of food preferences of young primates.

Primates are not the only animals that attend closely to foods that adults eat. McFadyen-Ketchum and Porter (1989) reported frequent investigations of the nose and mouth of lactating female spiny mice (*Acomys*

cahirinus) by their weanling young. After weanling spiny mice were returned to their mother (who, in their absence, had been given an unfamiliar food to eat), these young spent more than twice as long in nose-to-mouth and nose-to-head interactions with their dam as did pups assigned to a control condition and returned to a home cage containing a dam that had eaten a familiar food. In a subsequent choice test, weanlings that interacted with a mother that was fed a new food ate significantly more of that food than did pups whose mothers had not eaten it.

Other investigators (Ewer, 1963, 1969; Leyhausen, 1956; Liers, 1951; Schaller, 1967) have described a multitude of ways in which mothers of several predatory species (meerkat, otter, domestic cats, tiger; see Ewer, 1968, for a review) bring prey to their weaning young, which may either facilitate development of predatory behavior in their offspring or cause their young to prefer certain types of prey. For example, in an anecdotal report, Ewer (1963) described a maternal meerkat (*Suricata suricata*) inducing her young to eat banana, a food that they would not normally eat, by holding a piece of banana in her mouth and running to and fro in front of her offspring. Again, such informal observations are not sufficient to establish that the exposure to prey that a mother gives to her young either facilitates development of their predatory behavior or affects their later food preferences (Galef, 1990).

In a formal experiment, Caro (1980a, 1980b) found that kittens that had been exposed to a mother that killed mice in their presence were more likely to become mouse killers as adults than were cats that, as kittens, had been exposed to mice without their mother present. Unfortunately, Baerends-van Roon and Baerends (1979) found precisely the reverse. In several early experiments in which adult cats or rats that were not spontaneous killers of vertebrate prey were given repeated opportunities to observe conspecifics kill, the observers' probabilities of starting to kill were significantly enhanced (Johnson, DeSisto, & Koenig, 1972; Kuo, 1930; Pion, 1969). Clearly, effects of observation of predatory behavior on its expression are complex and have not yet been fully explored. Because of the change in public attitude toward experiments involving staged predatory encounters, however, studies of development of predatory behavior in vertebrates are no longer pursued, and many questions concerning the role of social learning in the development of predatory behavior remain unanswered.

Effects After Weaning

Transmission of Flavor Preferences in Rats

During the last decade, considerable attention has been focused on the ability of rats of all ages to determine which foods others of their species have been eating and on the surprising effectiveness of such socially acquired information in guiding its recipients' future food choices (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984).

Both olfactory cues escaping from the digestive tract of a recently fed rat and the smell of bits of food clinging to its fur and vibrissae allow other rats to identify foods eaten by an individual with whom they interact (Galef, Kennett, & Stein, 1985). Experience of the odor of a food together with rat-produced odors results in substantial enhancement of preferences for foods smelled on conspecifics. House mice show a similar (and probably homologous) enhancement of their preferences for foods experienced in contiguity with another of their species (Valsecchi & Galef, 1989).

Such socially enhanced preferences for foods experienced by a rat on the body or breath of a conspecific are not the result of simple exposure to the smell of a food that happens to be carried on a conspecific (Galef & Stein, 1985; Heyes & Durlach, 1990). For example, rats exposed to pieces of cotton batting dusted with an unfamiliar food do not develop a preference for it, whereas rats exposed to an anesthetized rat dusted with the same food exhibit a markedly increased preference for the food (Galef, Kennett, & Stein, 1985; Galef & Stein, 1985).

Surprisingly, changes in odor preference that result from exposure to the scent of a diet on the breath or fur of a conspecific are relatively specific to food odors. Rats that interact with a conspecific that has eaten cinnamon-flavored food subsequently show an enhanced preference for cinnamon-flavored food but not for cinnamon-scented nesting materials or cinnamon-scented nesting sites (Galef, Iliffe, & Whiskin, 1994).

Investigations of the nature of the rat-produced odor that increases preference for food odors experienced together with it indicate that the relevant chemical is carried on the breath of rats (Galef & Stein, 1985). Mass-spectrographic analyses of rat breath reveal the presence of carbon disulfide in the air taken from the noses but not from the mouths of rats. (Rats breathe only through their noses, not through their mouths.) Also,

rats exposed to pieces of cotton batting both dusted with a novel food and moistened with a dilute carbon disulfide solution subsequently exhibited an enhanced preference for that food, whereas rats exposed to pieces of cotton batting dusted with the same food and moistened with water did not (Galef, Mason, Pretti, & Bean, 1988).

Effects of exposure to a recently fed rat on the food choices of its fellows are surprisingly robust (Galef, Kennett, & Wigmore, 1985; Richard, Grover, & Davis, 1987). For example, rats that learned a profound aversion to an unfamiliar palatable diet and subsequently, interacted with other rats that had eaten that diet frequently abandoned their aversion (Galef, 1986; for similar data in hyena, see Yoerg, 1991). Many rats that had interacted with others that were eating a base diet to which cayenne pepper, a highly unpalatable adulterant, had been added exhibited a durable preference for the adulterated form of the diet (Galef, 1989).

Rats' olfactory communications about foods are also quite sophisticated. Individuals are able to exchange useful information with conspecifics about three or four different foods that each has eaten (Galef & Whiskin, 1992) and to use socially acquired information to determine which potential food sites to visit when foraging in an environment where several different foods are intermittently available at specific locations (Galef & Wigmore, 1983).

Social Transmission of Flavor Aversions in Rats

There is one way in which rats do not seem to be able to use socially acquired information about foods when such information would appear to be potentially useful. Unexpectedly, after a naive rat interacts with a conspecific that has eaten a novel food and become either violently ill or unconscious, the naive individual subsequently exhibits a preference for the food that the sick individual ate, not an aversion to it (Galef, McQuoid, & Whiskin, 1990; Galef, Wigmore & Kennett, 1983; Grover, Kixmiller, Erickson, Becker, & Davis, 1988). The finding that rats are not capable of direct social transmission of avoidance of toxins was completely unexpected.

After the fact, it could be argued that because wild Norway rats are exceedingly hesitant to eat any foods they have not previously eaten, biasing a rat to eat one food effectively prevents that rat from eating other foods (Galef & Clark, 1971a). A wild rat may wait for as long as 5 days before sampling a novel food available to it, even if it does not have access to any

familiar foods and hesitancy to eat the unfamiliar food results in several days of self-starvation (Barnett, 1958; Galef, 1970). Consequently, any behavioral processes that direct rats to a safe food would result in their avoiding ingestion of any toxic alternatives; therefore, avoidance of poisons may be transmitted among rats indirectly rather than directly (Galef, 1985).

Social Transmission of Flavor Preferences and Aversions in Other Animals

Compelling evidence of direct transmission of poison avoidance, as well as of food preference, has been reported in species other than Norway rats. Mason, Arzt, and Reidinger (1984) trained "model" red-winged blackbirds either to eat or to avoid food presented in a yellow cup while "observer" conspecifics watched the training of the models. After training was completed, both models and observers were given a choice between yellow and green cups containing the same food. Observer birds that had watched conspecifics learn to eat from a yellow cup preferred the food in the yellow cup, whereas observer birds that had watched conspecifics become ill after feeding from a yellow cup avoided the yellow cup almost completely.

It is not clear why blackbirds should be able to learn to avoid a toxic food by watching their fellows eat the food and become ill, whereas rats are unable to learn the same thing; however, that seems to be the case.

In an early laboratory experiment on social learning of food preference, adult baboons (*Mandrillus sphinx*) were offered slices of banana that had been both colored blue and adulterated with quinine to make them unpalatable as well as slices of banana that had simply been colored red. Five infant baboons that watched an experienced adult select palatable, red slices of banana and ignore unpalatable, blue ones were then offered a choice between equal numbers of red, palatable slices and blue, unpalatable slices of banana. Four of the five infants readily ate red slices of banana and hesitated before tasting blue ones (Jouventin, Pasteur, & Cambeferd, 1976). Jouventin and his coworkers interpreted these data as providing evidence of an ability of young baboons to learn to avoid a food that they had seen adults avoid, although their data are equally consistent with the hypothesis that young baboons learn to eat the foods that they see adults eat.

Local Enhancement

A review of social influences on feeding behavior in adult vertebrates would surely be incomplete without explicit mention of the important role of local enhancement (Thorpe, 1963) in the foraging behavior of a wide range of species; for example, the sight of vultures descending on a carcass draws others of their kind to a recent kill (Houston, 1979; Schaller, 1972). The distinctive rasping sound made by an agouti gnawing on a fallen nut carries dozens of meters through the rain forest and attracts other agouti to a newly discovered feeding site (Smythe, 1970). The "feeding buzzes" made by bats (*Lasiurus borealis*) as they home in on their insect prey informs others of their species both of the location of a potentially rich source of food and of possible opportunities to steal food from successful foragers (Balcombe & Fenton, 1988). There are many such examples in the literature describing situations in which the activities of an individual at a food source attract others of its species to the location where it is eating and biases them to begin eating there. The work of Krebs and his colleagues on social foraging by flocks of small birds (Krebs, 1973; Krebs, MacRoberts, & Cullen, 1972) is prototypical of the more informative of such studies.

Krebs et al. (1972) established small flocks, each consisting of four birds, in an indoor aviary and compared the success of these flocks in finding seed concealed in one of many food cups scattered about the branches of treelike constructions in the aviary with the success of both individual birds and pairs of birds foraging in the same enclosure. Krebs and his colleagues found that an individual bird foraging in a flock of four was significantly more likely to find concealed food during a 15-minute test period than it was when foraging either alone or as a member of a pair. The greater success in finding food exhibited by flocks of four birds than by individual or paired birds was the result of two factors. First, the greater the number of birds searching for the concealed food, the more likely one of the searchers was to find food during a 15-minute test period. Second, once one bird in a flock found food, the other members of the flock took advantage of the find by flying to and searching in the place where food had been found. In a later experiment in the same series, Krebs et al. (1972) examined the effects on foraging by flock members of observing one of their fellows find

food in one of four different types of food container. When one bird found food in a particular type of food cup, others in its flock increased their frequency of searching for food in other containers of that type.

Such local, or stimulus, enhancement (Galef, 1988; Spence, 1937) of one potential feeding site at the expense of others can, at least in principle, have important effects on the food choices of individuals that use social information to select locations in which to forage. By attracting conspecifics to one food source rather than another, local enhancement can indirectly determine which prey species foragers will encounter; the experience of feeding on one prey species or of foraging success in one microhabitat could have important effects on subsequent food choices (Galef, 1988).

SOCIAL FACTORS IN THE ACQUISITION OF FEEDING BEHAVIORS

Although great progress has been made in analyzing social interactions that affect food preferences, less is known about the ways in which social learning influences acquisition of motor patterns used in feeding.

Field Observations

In recent years, field workers have described a number of behaviors that are used to acquire food by only some of the many social groups that make up a species. Chimpanzees seem particularly likely to exhibit such population-specific patterns of behavior (Galef, 1992; McGrew, 1992). For example, chimps at Gombe National Park in Tanzania use twigs as probes to fish for termites (Goodall, 1986); their fellows in Tai National Park in Ivory Coast do not (McGrew, 1992). Chimpanzees in Tai National Park use hammers and anvils to crack open kola nuts (Boesch, 1991; Boesch & Boesch, 1990); chimps in East Africa do not (McGrew, 1992). Four chimpanzees at Bossou in the Republic of Guinea extracted sap from palm oil trees by using a palm stalk as a pestle to pound at the center of the top of the trees and a wad of vegetable fiber as a sponge to absorb sap. No other chimpanzees have ever been reported to be engaging in the behavior (Sugiyama, 1994).

Although essentially nothing is known either about how such idiosyncratic feeding behaviors develop in individuals or why they are found in some populations but not in others, it is not improbable (even if not proven)

that social learning plays an important role in the development and diffusion of population-specific patterns of feeding behavior.

Some observations by Hauser (1988) of a free-ranging troop of vervet monkeys at Amboseli National Park in Kenya that, like chimps at Tai National Park (Sugiyama, 1994) and at Gombe (Goodall, 1986), learned to use plant material as sponges to acquire liquids that were otherwise inaccessible; the report may provide some hint as to how such behaviors originate and spread. Vervets' use of a dry pod as a sponge to extract exudate from a tree during a period of drought was first seen when only one troop member was engaging in the behavior. Over a period of 22 days, diffusion of the behavior from its inventor to six other troop members was observed. Details of the conditions under which transmission of the behavior occurred are consistent with the hypothesis that some of the animals learned to use dry pods to acquire exudate by imitating a troop mate, though in uncontrolled environments it is impossible to know with certainty how any individual acquired the behavior.

Laboratory Analyses

There are only a few cases in which it has been clearly demonstrated, under controlled conditions, that social interactions contribute directly to the development of the kinds of idiosyncratic feeding behaviors that are exhibited by free-living animals.

Roof rats in the pine forests of Israel

Aisner discovered some years ago that the pine forests of Israel were inhabited by roof rats (*Rattus rattus*) that subsisted on a diet consisting solely of pine seeds and water (Aisner & Terkel, 1992). Extraction of pine seeds has been a stable tradition in these forest-dwelling rodents for many generations, and there is every reason to expect persistence of this unique feeding behavior, enabling rats to survive in an otherwise sterile habitat where pine seeds are the sole food available in sufficient quantity to sustain a population of mammals.

Laboratory studies have revealed that there is only one energetically efficient way for rats to remove the tough scales from pine cones and gain access to the energy-rich seeds they conceal. If rats are to realize a net energy gain while feeding on pine cones, they must take advantage of the

structure of the cone, first removing scales from the base of the cone and then removing, one after another, the spiral of scales running around the cone's shaft to its apex. Laboratory investigations of development of the energetically efficient spiral pattern of scale removal (necessary if rats are to realize a net energy gain while feeding from pine cones) have shown that only 6 of 222 adult rats maintained in the presence of pine cones for several weeks at 85% of normal body weight were able to learn the efficient pattern of pine cone opening by individual, trial-and-error learning. The remaining 216 subjects either ignored the pine cones or gnawed at them randomly in a way that did not lead to acquisition of more energy from pine seeds than was expended in their extraction and ingestion. On the other hand, essentially all young rats came to exhibit the efficient method of opening pine cones if they were reared by a dam that, in the presence of her young, stripped scales from pine cones efficiently. Rats learned to be efficient strippers of pine cones even if they were gestated and delivered by mothers that did not strip pine cones efficiently but were reared by a foster mother that exhibited the efficient means of cone stripping in the presence of her adopted young. Rat pups failed to learn to strip cones efficiently if they were born to mothers that stripped pine cones efficiently but were foster-reared by dams that didn't exhibit the behavior. Clearly, some aspect of the postnatal interaction between mothers that strip pine cones and the young they rear is necessary for the transmission of the behavior from one generation to another (Aisner & Terkel, 1992; Zohar & Terkel, 1992).

Further experiments demonstrated that the experience of young rats in completing the stripping of pine cones that had been started appropriately by an experienced adult rat (or by an experimenter using a pair of pliers to imitate the pattern of scale removal used by experienced cone-stripping rats) enabled more than 70% of young rats to become efficient strippers (Aisner & Terkel, 1992).

The behavior needed to strip pine cones efficiently is transmitted from one generation of roof rats living in Israel's forests to the next, but that tradition does not appear to be transmitted or maintained either by imitation or by any other complex social learning process. Rather, practitioners of the tradition of cone stripping alter the environment in which their young develop by allowing them access to partially stripped pine cones and thus markedly increase the probability that the young rats will acquire the traditional pattern of behavior.

Milk-Bottle Opening by British Birds

A similar social learning process is implicated in the spread of the traditional habit exhibited by several species of British birds that open the foil covers of milk bottles and feed on the bottles' contents. In a laboratory study of the processes responsible for the spread of milk-bottle opening in populations of wild birds (first described by Fisher & Hinde, 1949), Sherry and Galef (1984) took into account the fact that the presence in an area of a bird that opened milk bottles and fed from them provided naive birds not only with demonstrations of opening behavior to imitate, but also with open milk bottles from which the naive birds could feed.

In the laboratory, wild-caught black-capped chickadees (*Parus atricapillus*) that had experience feeding from milk bottles that were opened by a human experimenter were likely to open closed milk bottles, as were chickadees that had the opportunity to observe other chickadees opening milk bottles (Sherry & Galef, 1984, 1990). However, a chickadee that watched a conspecific opening milk bottles was no more likely to open a closed milk bottle in its own cage than was a chickadee that had a closed milk bottle in its cage and a view of a conspecific in a cage with no milk bottle. Apparently, the simple presence of a conspecific facilitates exploration in chickadees (birds that in natural circumstances often feed as members of flocks) and thus increases the probability that they will open milk bottles for themselves.

Hickory-Nut Opening by Red Squirrels

Weigl and Hanson (1980) measured both the time required and energy expended by two groups of red squirrels (*Tamiasciurus hudsonicus*) opening hickory nuts for the first time. One group of squirrels had been allowed to observe an experienced squirrel feeding on hickory nuts; the other had not. In a subsequent test, members of the group that had observed an experienced conspecific opening hickory nuts took only half as long and used only half as much energy to open hickory nuts as did members of the group that had not observed a model open hickory nuts. Again, social learning of some

kind had a major impact on thsition of a behavior of importance in the acquisition of food.

SOCIAL INFLUENCN HUMAN FEEDING BHOR

The experimental literature on sœcts on human eating (for examples see Birch, 1980a, 1980b; Pliner tat, 1986; Rozin, Fallon & Mandell, 1984) is relatively sparse (for reviRozin, 1988a, 1988b). Much remains to be done before researchers cdk with authority about the various roles that social interaction actuys in development of both adaptive and maladaptive patterns of foœe in members of our own species. There can be little question that nfluences on human food selection can be immense; response to repdhe media of a possible link between human disease and ingestion of beef (a front-page story as I write the final draft of this manuscript one of many examples bearing witness to the great impact that' acquired information can have on human food choices. Whether unding mechanisms of social influence on diet selection in our vertebrsins will eventually provide experimental paradigms and theoretictions of real use in understanding analogous processes in *Homo sœ*mains to be seen. I am optimistic.

COISION

Two decades of study of social ins on ingestive behavior have repeatedly demonstrated profound imf social interactions on the development of both the food prefererd feeding behaviors of animals. In simple cases of social influencerelopment of food preferences, the physical presence of one individuocation attracts others and increases the probability that they will eœever food is to be found there. In more complex instances, one anærns either to eat or to avoid eating some food by observing the behf another of its species when it eats the food and either does or doeecome ill.

Like social learning of food pces, social learning of feeding behaviors can proceed along routes œng complexity. In simple cases, the feeding behavior of one memberpulation alters the physical environ-

ment in a way that increases the probability that its fellows will acquire that behavior. In more complex instances, a naive individual might learn a complex feeding behavior by observing and then imitating a knowledgeable conspecific, or a knowledgeable animal might actively teach one of its fellows to engage in some feeding behavior, although convincing evidence of either imitation learning or teaching by animals is not yet available (Galef, 1990, 1992; but see Boesch, 1991; Caro & Hauser, 1992).

Even the simplest of social processes known to contribute to establishment and maintenance of traditional patterns of either food preference or feeding behavior should facilitate naive young animals' acquisition of those responses to environmental challenges that others of their social group have found rewarding. Social learning can reduce the time, energy, and risk associated with acquiring food preferences and feeding behaviors that are useful in the specific locale where each juvenile must overcome impressive odds if it is to achieve metabolic independence. The same processes that allow juveniles to exploit the knowledge their elders have acquired as a result of extensive experience in a particular area can also help adult animals to monitor the ebb and flow of resources in changing environments (Galef, 1993).

Members of our own species are not unique in exhibiting profound effects of social interactions on the development of their feeding habits and food preferences. The tardiness of scientists in starting to investigate social influences on feeding behavior is unfortunate, but the relatively brief history of such investigations should not interfere with our recognition of the importance of social learning in the development of feeding behavior in animals. Social interactions play a major role in facilitating development of patterns of ingestive behavior that allow animals to overcome the multitude of metabolic challenges provided by natural environments.

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