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Social Influences on Fluid Intake: Laboratory Experiments with Rats, Field Observations of Primates

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Introduction

To undertake a review of research in the area of social influences on mammalian fluid intake is a daunting prospect. Little work has been done on social influences on drinking (at least of the non-alcoholic sort) in mammals and the results of much of what has been done are negative. Consequently, a straightforward review of social influences on mammalian fluid intake is not yet possible. I propose, instead, to proceed indirectly, first by reviewing processes known to support social influences on mammalian feeding behaviour (an area where there are many positive findings), then by considering whether the social processes that influence food selection or food intake might also influence fluid selection or fluid intake.

In the Laboratory

Effects of the Presence of Adult Rats at an Ingestion Site

Adult rats can influence weanling young to eat one food in preference to others by simply eating at one location rather than at another. The presence of adults at a potential feeding site attracts weanlings from a distance to that site and markedly increases the probability that weanlings will begin to eat whatever food is located there (Galef and Clark 1971; Galef 1981). In both laboratory (Galef and Clark 1971) and field situations (Steiniger 1950), maturing wild rat pups will, for weeks, eat only those foods to which the adults of their colony have introduced them.

Such local enhancement (Thorpe 1963) of a foraging site also has the potential to induce young rats to drink from one water source rather than from another. However, the only experiments undertaken to examine directly effects of drinking site utilization by adult rats on pups' choice of drinking site (Galef 1978) revealed little if any adult influence on rat pups' drinking site selection. In general, rat pups seeking food appeared more strongly motivated to affiliate with conspecifics than did rat pups seeking water (Galef 1978).

Effects of Residual Olfactory Cues at an Ingestion Site

Adult rats mark both foods that they are eating and the area around those foods with residual olfactory cues that make marked foods and marked feeding sites more attractive to juveniles seeking food than are unmarked foods or unmarked feeding sites (Galef and Heiber 1976; Galef and Beck 1985). There is no apparent reason why rats should not mark drinking sites in the same way that they mark feeding sites. However, that possibility has not yet been examined.

Flavour Cues in the Milk of Rat Dams

The results of several studies (Galef and Henderson 1972; Galef and Sherry 1973) are consistent with the hypothesis that (a) the milk of a lactating rat contains cues reflecting the flavour of her diet and (b) such flavour cues in mother's milk can influence pups' selection of foods at weaning. Although it has not been investigated, there is reason to expect that learned preferences for orally ingested, flavoured fluids, like preferences for intraperitoneally injected, flavoured fluids (Le Magnen and Tallon 1968, Martin and Alberts 1979) could be readily transmitted from mothers to their young via flavour cues incorporated in mother's milk. However, mother's milk may not provide an efficient medium for communication between dams and their young about relatively flavourless fluids, such as water. The effects of flavour cues in mother's milk on fluid selection by weanling pups will be limited to induction of enhanced preferences for substances the flavours of which pups can detect in mothers' milk.

Whether such enhanced preferences for flavoured substances would be useful to weanlings attempting to maintain fluid balance in natural settings depends on circumstance. If the main source of fluids for a population was widely separated water holes, flavour cues in mother's milk would probably not be of much use to juveniles in maintaining fluid balance. If on the other hand a population were garnering most of its water from flavoured fruit, then enhanced preference for the flavour of fruit, contingent upon experience of its flavour in mother's milk, might be a factor in maintenance of fluid balance by pups.

Olfactory Cues on the Breath of Rats

Galef and Wigmore (1983) and Posadas-Andrews and Roper (1983) discovered independently that after a naive rat (an observer) interacted for a few minutes with a recently fed conspecific (a demonstrator) the observer exhibited an enhanced preference for the diet its demonstrator had eaten (see also Strupp and Levitsky 1984; Galef 1989). Both olfactory cues escaping from the digestive tract of demonstrators and the smell of bits of food clinging to the fur and vibrissae of recently fed demonstrators permit observers to identify foods that their respective demonstrators have eaten (Galef and Stein 1985). However, simple exposure to the smell or taste of a food does not suffice to enhance an observer's preference for that food (Galef et al. 1985; Galef 1989; Heyes and Durlach 1990). Observers' preferences for foods are enhanced only by smelling a food in contiguity with rat-produced odours (Galef and Stein 1985) emitted by demonstrators. These demonstrator-produced odours are probably volatile sulphur compounds, like carbon disulphide (Galef et al. 1988), a chemical constituent of rat breath that, when added to a food, increases the

preferences of both rats and mice for that food (Bean et al. 1988; Mason et al. 1989). Social influences acting via rat breath can (a) facilitate identification by the naive of foods containing needed nutrients (Beck and Galef 1989), (b) facilitate identification and avoidance of toxins (Galef 1986a, b), and (c) act as aids in deciding where to search for foods (Galef and Wigmore 1983; Galef et al. 1987).

Interaction of observer rats with demonstrators that have drunk a flavoured liquid enhances an observer's preference for the flavoured liquid, just as exposure to a demonstrator that ate a flavoured food enhances an observer's preference for the flavoured food (Galef et al. 1985, Galef and Stein 1985). Thus, as with flavour cues in the milk, cues on rat breath might be important in directing fluid selection by populations of rats that obtain fluids from fruits or other plant materials, but probably not in populations that subsist on free water.

Socially Induced Aversions

A naive rat (a subject) that ingests an unfamiliar food and then interacts with an ill rat (a "poison partner") develops an aversion to the unfamiliar food it ate prior to interacting with its poison partner (Coombes et al. 1980; Lavin et al. 1980). It is, however, not obvious how this "poison-partner effect" might enhance avoidance of either toxic foods or toxic, flavoured fluids in natural circumstances. If an unfamiliar food eaten by an individual before it interacted with a poison partner were safe, then subsequent avoidance of that food would be counterproductive. If, on the other hand, an unfamiliar food ingested before interaction with a poison partner were toxic, then information received from the ill individual would be redundant; aversion learning would occur even in the absence of a poison partner (Galef et al. 1983).

Gemberling (1984) examined the situation in which the rat ingesting an unfamiliar, flavoured solution was a lactating female and the poison partners with which the dam then interacted were infants. It is possible for a lactating dam to eat something that has no ill effects on her, but causes distress to her suckling young and it would clearly be adaptive for dams to avoid eating foods that distressed their offspring. Gemberling found that lactating dams that had ingested a novel saccharin solution shortly before they interacted with young that had been injected with an illness-inducing agent subsequently showed an aversion to saccharin.

Competitive Enhancement of Intake

Harlow (1932) reported that rats would both eat more food and show greater weight gain when fed for 1 h/day in pairs than when fed for 1 h/day in isolation. He suggested that such social facilitation of food intake depended on interacting subjects engaging in unrestrained, active competition for food (see Clayton 1978, for a review). Whether socially enhanced water intake would also be observed in rats competing for fluids is not known.

Summary

Results of laboratory studies indicate (a) that the feeding behaviour and food choices of rats can be modified by social interactions among rats and (b) that a number of different behavioural processes can play a role in such social modification of feeding

behaviour. Although there are not a great deal of relevant data, social influences on feeding-site selection seem more robust than social influences on drinking-site selection. The fact that all foods have smells and flavours associated with them, whereas free water, possibly the most important source of fluids for many mammals, probably does not have a readily detected volatile component may result in social influence being less important in directing fluid intake than in directing food intake in natural circumstances.

In the Field

Unobtrusive observations in natural situations rarely permit analysis of behavioural mechanisms underlying food or fluid choice. However, field studies do provide evidence of possible social influences on ingestive behaviour that need to be analysed under controlled conditions (Galef 1984). The literature contains many observations of differences in the food preferences of different social groups of conspecific animals living in natural circumstances. However, we have only the crudest understanding of how these locale-specific behaviours develop, though there is reason to suspect that some may be the result of social learning (Galef 1990).

Examples of Locale-Specific Differences in Food Selection by Primates

Nishida (1987, see also Goodall 1986) has catalogued differences in food selection by chimpanzees at Mahale and Gombe, two field sites a few tens of miles apart along the east shore of Lake Tanganyika in Tanzania. For example, unripe seeds of *Saba florida* are neglected by Mahale chimpanzees, whereas those at Gombe eat them often (Nishida et al. 1983). Gombe chimpanzees eat *Dorylus* ants, rarely eat *Crematogaster* ants, and totally avoid *Camponotus* ants. Mahale chimpanzees eat the last two frequently and reject the first completely.

Although such differences between local populations in diet selection are well established, there are many possible explanations for the development of such locale-specific feeding habits. Differences in the relative availability of foods (Galef 1990; Nishida 1987), differences in the details of the characteristics of foods themselves in different areas (Nishida 1987), differences in alternatives to particular items (Gaulin and Kurland 1976), as well as differences between populations in socially transmitted food preferences could all produce locale-specific differences in food choice.

Field Observations of Apparent Social Learning About Foods by Primates

Occasionally, observations of the behaviour of free-living animals are sufficient to suggest that social learning may truly be involved in the development of a unique pattern of ingestive behaviour. One of the more convincing cases is Whitehead's (1986) observations of infant howling monkeys (*Alouatta palliata*) feeding for the first time on seasonally available leaves and fruits in the forests of Costa Rica. When feeding on leaves, infant howling monkeys (a) looked at a parent before eating, (b) fed only when a parent fed, (c) ate only what a parent ate, and (d) were subject to parental intervention if they chose to eat an "incorrect" leaf.

Although it seems likely that such interactions between adults and young would result in social transmission of food selection patterns between generations, there is

no evidence that the consequences of mother–young interaction on the food choices of young last for more than a few minutes (Galef 1990). It is known both that there are differences among troops of primates in the foods they eat and that social interactions occur between mothers and young that could produce differences in later food selection by the young; however it is not known if the two observations are related.

Hauser's (1988) observations of vervet monkeys at Amboseli, Kenya provide some of the most convincing evidence of social transmission of a feeding pattern available in the field literature. During a period of drought, the vervets were forced to subsist on *Acacia*, a plant they normally avoided. In September 1983, an adult female (BA) was observed to dip dry *Acacia* pods into the well of an *Acacia* tree containing a viscous exudate. Eating of exudate and the use of pods to secure exudate had not been observed during six preceding years of observations. Eight days after BA began pod-dipping, BA's two juvenile sons exhibited the behaviour; a day later two other troop members joined in, etc. The behaviour of dipping pods in *Acacia* exudate disappeared in 1984 when the drought broke and both free surface water and a diversity of plant material were again available to the troop. It is not known whether troop members had been eating or drinking *Acacia* exudate previously.

In Conclusion

Finding safe, adequate foods and sufficient liquids to sustain life are challenges facing all mammals. Although individuals can learn independently where and what to eat or drink, each young mammal interacts for an extended period with an adult caretaker whose survival and successful reproduction indicate that the caretaker has had access to adequate food and drink. There is every reason to expect the naive to exploit the knowledgeable as sources of information about the nature and location of needed nutrients. The evidence suggests that they do.

Both field observations of social interactions surrounding ingestive behaviour and experimental analyses of social influences on choice of ingesta indicate that study of conspecific influences on eating and drinking can provide insight into the development of adaptive ingestive repertoires by mammals (Galef and Beck 1990). Although to date most such observations and experiments directly involve feeding behaviours, they may also be relevant to understanding the ways in which animals come to locate free-standing sources of water and to select items to ingest that provide water for the maintenance of fluid balance.

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Commentary

de Castro: Social factors profoundly influence fluid intake in humans but do so secondarily as a result of a marked facilitation of food intake. The number of other people present strongly correlates with the amount of fluid ingested and also with the amount of food ingested. When both the number of people present and the amount of food ingested are used as predictors of fluid intake in a multiple linear regression, then the effect of the number of people vanishes while the effect of solids ingested remains. This implies that the social effect of fluid intake occurs secondarily to the influence of food intake. (see chapter 21.)