Paradoxical effects of experience with food size and flavour in golden hamsters, *Mesocricetus auratus*

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Abstract:
Young hamsters were reared until 35 days of age with access to food pellets of one of three sizes. They were then given a choice between the three sizes of pellets: the familiar size and two unfamiliar sizes, and the rate of energy gain from eating pellets of each size was established. Contrary to predictions from optimal foraging theory, the animals chose pellets of the most unfamiliar size, not the most profitable ones. A taste preference study was conducted to see whether hamsters respond to taste cues as do other rodents. The animals showed a preference for familiar flavours. The results of these studies suggest that the sorts of experiences animals have had with food must be considered in any account of food choice behaviour.

Article:
Early experience with specific food tastes can have long-lasting effects on later diet preferences. Galef and his colleagues (Galef 1977) have accumulated convincing evidence to show that food preferences in rats, *Rattus norvegicus*, are transmitted from dams to offspring. Galef & Clark (1971), using poison avoidance, induced a preference in adult rats for one of two nutritious and palatable foods. When the pups born to colony members first left the nest and ate solid food, they ate only the diet the adults ate, and even after being transferred to a new colony, the preference persisted. Bronstein et al. (1975) obtained a similar result by restricting pregnant dams to one food and measuring pups' preferences immediately after weaning.

These studies, among others, demonstrate that food preferences learned by young animals in the presence of adults, especially their dams, affect their feeding behaviour after the adult influence has been removed. The influence of social factors in diet preference is not limited to adult—young interactions; adult rats also influence the food choices of other adults. Posada-Andrews & Roper (1983) removed a rat from a social group, fed it a distinctively flavoured diet, and returned it to the group. Subsequently, the other animals in the group chose the diet the demonstrator had eaten. Similar results have been found by others (Galef & Wigmore 1983; Strupp & Levitsky 1984; Galef et al. 1985).

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The role of social experience in the diet selection of free-living adults seems clear. However, taste is not the only property of food to which animals respond when making foraging decisions. Research in optimal foraging theory (Pyke et al. 1977) has demonstrated that animals can choose between items within a food type and will choose those items that maximize profitability, that is, the net rate of energy intake. In many instances, this has been interpreted to mean that animals will take the largest available items of a particular food type.

The research of Werner & Hall (1974), on bluegill sunfish, *Lepomis macrochirus,* feeding on three sizes of *Daphnia,* and Barnard & Brown (1981), on common shrews, *Sorex araneus,* feeding on large and small pieces of mealworm, confirmed the prediction that animals choose larger prey preferentially when it is readily available. In both sets of experiments, however, profitability was not measured directly; a positive correlation between size and profitability was assumed. This can only be the case if the net energy gain per gram of food remains the same across item size so that bigger pieces provide more energy, and if the time it takes to search for, prepare and ingest the food is only negligibly different across sizes. Despite this limitation, the conclusion drawn from these studies, as well as others that have examined prey size, is that animals seem to use a rule of thumb when choosing prey items: lacking the ability to assess directly the net energetic value of food items, they use size as the most reliable index of value and select the largest prey items available.

How do animals come to use size as a heuristic to estimate profitability? The optimal diet model, optimal foraging theory applied to choices of food items to include in the diet, was developed to predict food choices of animals when energy maximization is the focus of concern. An assumption of the optimal diet model is that animals choose large food items because there is a genetic tendency to do so. In other words, animals possess some sort of innate recognition device that allows them to select the largest (and hence most profitable) food items. The assumption of innateness is not logically necessary to predict and obtain the results of these experiments and, indeed, is not well supported by contemporary developmental theory (Johnston 1987). While animals may not be able to assess profitability directly, they do have access to cues that depend on it, namely, internal feelings of hunger and satiation. Animals may come to associate the consequences of eating food with its physical characteristics. For example, Rozin (1976) demonstrated that rats that are restricted to a diet that is nutritionally deficient will subsequently avoid that diet and sample new diets until the deficiency is overcome, behaving like rats that have been poisoned. This response is mediated by taste.

It is likely that the size of food items may become associated with their profitability in the same way; for example, animals may learn that larger pieces of food will alleviate hunger more readily than small food items. As one would expect from such a model, diets do change as a result of experience. McNair (1981) showed that as few as one or two prey encounters can lead to changes in feeding behaviour. After a few encounters with a particular type of food, an animal may pursue, capture and eat items more quickly. Partridge (1981) demonstrated that experience can change an optimal diet. After establishing which of two foods, oats or wheat, was preferred, she restricted members of four species of wild-caught rodents to the non- preferred (non-optimal) food for 6 weeks. The animals preferred the food to which they had been restricted, showing that experience may play a role in determining diet. As Partridge wrote, 'if food preference changes

with experience, then either optimal food choice has changed, or food choice is sometimes not optimal' (page 215).

Although most studies of food preferences have examined the consequences of experience during foraging or social contact with another animal, some species hoard food. Their young contact food items in the hoard before individual foraging begins. Hoards are maintained to ensure against food shortages (Wong & Jones 1985), and contain samples of many of the food items available in the environment. By eating from the cache, the young may learn about the properties of food, such as profitability, from early experience with the stored food and this knowledge may affect later food choice. In the present study, we examined the effects of experience with food of different sizes both in the hoard and during early independent foraging in golden hamsters.

EXPERIMENT 1
Our aim in experiment 1 was to measure the profitability of three sizes of Noyes food pellets. All three had the same energetic content (16.33 kJ/g). However, it seemed possible that pellets of different sizes would have different handling times. If handling times are different for different sizes, then profitability may not be proportional to size, and pellet choice may be affected in free-foraging situation.

Methods
All subjects used in the studies reported here were golden hamsters born to animals in the breeding colony of the Psychology Department at the University of North Carolina, Greensboro. Three litters were used in experiment 1. Only litters with four or more pups were used in this study; litters with more than four pups were culled when the pups were 5 days old using halathane anaesthesia.

Until postpartum day 9, the dams of the litters used in this study were maintained on ad libitum Purina Laboratory Chow 5001 (Ralston-Purina Company) and water in polycarbonate breeding cages. On day 10, the dams and their litters were transferred to clean cages. Each litter was provided with one of three sizes of Noyes food pellets (Noyes Pharmaceutical Company, Formula A: Small Rodent Diet): 20, 45 or 94 mg. On day 10, dams and litters were provided with 24 g of food, and, thereafter, 12 g were added daily, an amount sufficient to maintain normal growth and development of the pups. On day 35, the pups were placed in individual cages, each containing 12 g of pellets of the size on which they had been fed.

On days 36, 37 and 38, each animals was presented with a plastic petri dish containing 12 g of either 20-, 45- or 94-mg pellets. We counterbalanced order of presentation across days, animals and rearing conditions. The hamsters were allowed one foraging trip for each pellet size. The experimenter determined the weight of the pellets remaining in the dish and the amount of food each animal took. The duration of a foraging trip was defined as beginning when an animal's nose touched the petri dish and ending when its body was completely outside the dish.

A 3 (rearing) x 3 (days) x 3 (size) Latin square split-plot ANOVA was performed on these data. Statistical values reported here are in mg/s.

The only significant source of variance in the ANOVA was the main effect for size $(F_{2,18}=$ 20.16, $P < 0.01)$. A Scheffe's post-hoc analysis showed that the means for all three sizes were different from one another $(P < 0.05)$: for 20-mg pellets, $X= 9.88$ mg/s; for 45-mg pellets, $X= 31.37$ mg/s; and for 94-mg pellets, $X=77.9$ mg/s. Analysis of the handling times showed that the mean number of pellets taken per second did not differ across sizes $(F_{269}= 0.29$, NS: for 20-mg pellets $X= 0.291$; for 45-mg pellets, $X= 0.298$; for 94-mg pellets, $X= 0.257)$. For these pellet sizes, size reflects profitability; 94-mg pellets are more profitable than are 45-mg pellets, and both 94- and 45-mg pellets are more profitable than are 20-mg pellets.

EXPERIMENT 2
Our aim in this experiment was to investigate the effect of early experience with only one size of food item on subsequent choice of pellets, when more than one size of pellets was available.

Methods
Subjects and procedure
The subjects in experiment 2 were nine litters (four animals per litter) of golden hamsters. Five days before their litters were due, each female hamster was placed in a rectangular wooden arena. Attached near one corner of the arena was a plastic tub that served as a nestbox. The nestbox was covered with hardware cloth and was connected to the arena by a metal tube, 5 cm in diameter. The floor of the nestbox and arena were covered with corn cob bedding and shredded newspaper was provided. Until the day the litters were delivered, the dams were fed Purina Laboratory Chow. The animals were kept on a reversed 14:10 h light:dark cycle for the duration of the experiment. As in the previous experiment, litters were culled to four pups, at 5 days of age.

On the day a litter was delivered (day 0), all chow was removed from the enclosure. A baking tray (33 x 20 cm) containing approximately 125 cm of sand was placed in the arena. Each day, 24 g of either 94-, 45- or 20-mg Noyes food pellets (depending on the group to which the litter was assigned) were spread across and pushed into the sand so that although the pellets were not completely covered, the animals had to dig the pellets out of the sand. On day 35, dams were removed from the arena and returned to the breeding colony. Littermates continued to live together in the arena until the end of testing.

Testing
Beginning on day 36 and continuing through to day 45, littermates were tested individually. For 5 min, the animals were kept blocked in their nest- box. The baking tray was emptied and the sand was sifted to remove bedding material and faeces that had accumulated. The sifted sand was returned to the baking tray and enough clean sand was added so that a depth of approximately 1.25 cm of sand remained in the tray.

Three hundred food pellets (100 of each of the three sizes) were spread randomly over the sand and pressed into it. Each animal was allowed one foraging trip, which was defined as the period of time between walking onto the tray and walking off the tray. The maximum time allowed for a foraging trip was 10 min. At the end of the foraging trip, we removed the animal from the arena. The tray was removed from the arena, the sand was sifted to remove any remaining pellets and

was returned to the tray. We repeated this procedure for each animal until all individually marked members of the litter had completed a foraging trip. At that point, the animals and sand tray were returned to the arena and the nestbox was opened.

Dependent measures
The pellets remaining in the tray after each animal had completed its foraging trip were sorted into
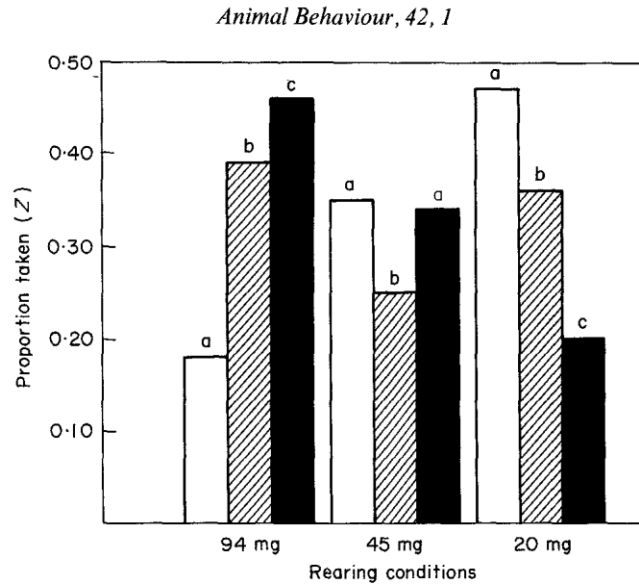
Figure 1. Mean proportion of 94-mg (❑), 45-mg (01) and 20-mg (■) pellets taken by hamsters within rearing Mean proportion of 94-mg (❑), 45-mg (01) and 20-mg (■) pellets taken by hamsters within rearing Mean proportion of 94-mg (❑), 45-mg (01) and 20-mg (■) pellets taken by hamsters within rearing conditions. Within rearing conditions, bars with different letters represent means that are significantly different $(P < 0.05)$.

sizes and counted. The value obtained from the count was subtracted from the original 100 to determine the number of pellets of each size the animal had taken. Once the number of pellets taken of each size had been determined, it was transformed into a proportion: $Z=$ (number of pellets taken of a given size)/(total number of pellets taken).

Analyses
 As recommended by Abbey & Howard (1973), litters were used as the unit of analysis. For each litter, a chi-squared analysis was performed on the number of pellets of each size taken each day. If the value of the daily chi-squared test was not significant, it meant that the animals were taking pellets as they encountered them. Of the 90 chi-squared values calculated, 79 (87%) were significant, indicating that the hamsters were not taking pellets randomly.

Analyses of variance were performed for each rearing condition (3 (litter) x 3 (size) x 10 (days)). Before the ANOVAs were calculated, the proportional data were arcsine transformed, as recommended by Kirk (1968).

Results

Examination of the ANOVAs showed that there were no significant effects of litter or of days nor were there any significant interactions. The only reliable effect was that of size. The pattern held true for all rearing conditions: for animals reared on 94- mg pellets, $F_{2,,}$ = 98.2; for animals reared on 45- mg pellets, $F_{2,,,}$ = 22.3; for animals reared on 20-mg pellets, $F_{2,27}$ = 599 (all Ps <0.01).

To analyse the size effect further, post-hoc analyses were performed using Scheffe's method (Kirk 1968). Animals reared on 94-mg pellets were found to prefer 20-mg pellets *(Z=0.46)* to 45-mg pellets *(Z=0.34)* and both 20- and 45-mg pellets to 94-mg pellets *(Z=0.20).* Animals reared on 45-mg pellets had an equal preference for 94- and 20-mg pellets *(Z=0.39* and 0.36, respectively) and both these sizes were prefered to 45-mg pellets *(Z= 0.25).* Animals reared on 20-mg pellets were found to prefer 94-mg pellets *(Z=0.47)* to 45-mg pellets *(Z 0.35)* and both these sizes to 20-mg pellets *(Z = 0.18).* The preference patterns persisted for the 10 days of testing. The results of experiment 2 are summarized in Figs 1 and 2.

Discussion
The results of experiment 2 showed that hamsters did not take food items as they were encountered, did not always take the most profitable food, and did show a preference that depended upon early experience with food items of a particular size.
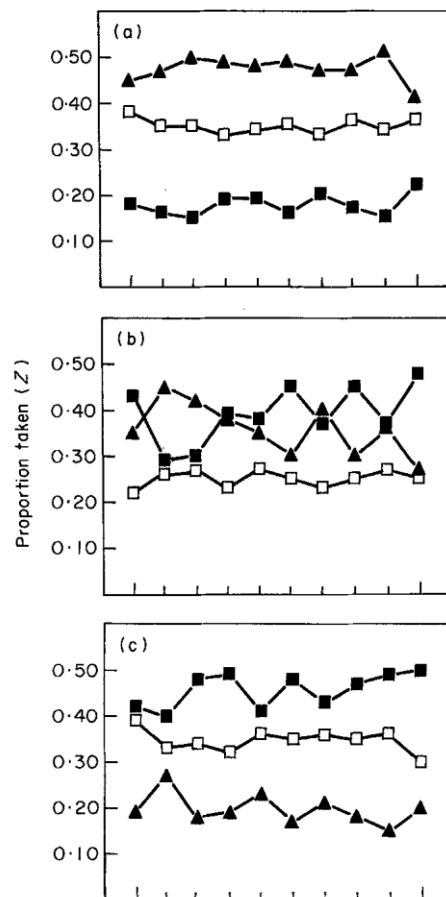
Figure 2. Mean proportion of 94-mg (•), 45-mg (D) and 20-mg (A) pellets taken by day. (a) 94-mg rearing condition; (b) 45-mg rearing condition; (c) 20-mg rearing condition.

Instead of preferring the most familiar size, animals took, from the first day of testing, the food size(s) most dissimilar from the size with which they were reared. The preference for novel size appears on the first day and persists throughout the 10-day testing period. The animals did not come to prefer the most profitable pellets. The preference for the most novel size (neophilia) is clearest in the 94- and 20-mg rearing conditions. The neophilia effect was unexpected and is consistent with none of the existing literature on food choice, with the exception of some of the research reviewed by Rozin (1976). This research showed that in situations in which animals are fed nutritionally incomplete diets, they will sample novel foods and select those that correct the deficiencies. However, the Noyes food pellets used in this study were a complete diet for small rodents so in this experiment it cannot be the case that the neophilia was mediated by nutritional deficiency.

EXPERIMENT 3
The results of experiment 2 could be explained if it were the case that hamsters do not form food- related preferences as do other rodents. Many researchers have found that early experience with food of a particular flavour induces a subsequent preference for that flavour. The preponderance of work in this area has been done with rats, and other rodents may behave differently. It is reasonable to assume that most rodents do respond to taste cues because they have been shown to be very dependent upon olfactory information when foraging (Langley 1985), and the olfactory and gustatory senses are highly related.

Our aim in this experiment was to determine whether hamsters are influenced by early restriction to one flavour as are other rodents.

Methods
Subjects and apparatus
The subjects used in experiment 3 were six litters of golden hamsters. As in the previous experiments, litters were culled to four pups, at 5 days of age.

Control animals. Two litters were reared on unflavoured food until they were 35 days of age. For the next 5 days (days 36-40) they were given two plastic petri dishes containing 15 g of granulated food (Noyes formula A), flavoured with either banana or coconut extract presented simultaneously in the home cage. We counterbalanced the position of the dishes (front and back) across animals and days. After 20 min, we removed the dishes, weighed the remaining food and calculated the amount taken from each dish.

Flavour-experienced animals. Four litters were reared on granulated food to which artificial flavours had been added. Two litters received banana-flavoured food and the other two received coconut-flavoured food. The dams began receiving the food the day they were mated, and the pups continued receiving it until they were 35 days of age. These litters were tested in the same manner as the control animals.

Food composition. The unflavoured food was made by mixing 50 ml of water with 0.24 litres of granulated Noyes food. The flavoured foods were made by mixing 45 ml of water with 5 ml of banana- or coconut-flavoured extract (Sauer Company) and then adding it to 0.24 litres of granulated food pellets. The mixtures were spread out on waxed paper and allowed to dry overnight. The foods were then kept in covered plastic containers. The finished product consisted of granulated food with a few small pieces, slightly moist. Pretesting indicated that hamsters will readily eat this food, although they do not pouch it.

The dependent variable used for analysis was the weight of food (in grams) taken from the Petri dishes. For all the rearing conditions, a 2 (flavour) x 5 (days) ANOVA was performed.

Results
Preferences of control animals
There were no significant sources of variance in this analysis. Animals reared on unflavoured food prefered neither banana nor coconut ($F_{1,70}= 1.37$, Ns). On average, these animals took 7.00 g of banana-flavoured food and 5.89 g of coconut- flavoured food per day.

Banana-reared animals
Animals who had experienced only banana- flavoured food until they were 35 days old preferred banana-flavoured food ($F_{1,70}=4.02$, $P < 0-05$). On average, these hamsters took 6.80g of banana-flavoured food per day and 5.06 g of coconut-flavoured food.

Coconut-reared animals
The animals that had experienced coconut- flavoured food also reliably preferred familiar food. The animals took a mean of 3.92 g of banana- flavoured food and 7.66 g of coconut-flavoured food per day ($F_{1,70}= 28.52$, $P < 0.01$). There was no effect for days and no days x flavour interaction.

Discussion
Hamsters, it appears, are like other rodents. They prefer familiar-tasting foods. Although the design of this experiment was somewhat different, the results replicated the findings of Capretta & Rawls (1974), Strupp & Levitsky (1984) and the work conducted by Galef and his colleagues (Galef 1982). Early experience with taste affects food choices made later in life.

It is clear from the results of these experiments that size and taste are food cues that have very different effects on foraging behaviour in hamsters. The foraging behaviour of hamsters differs from that of most of the species studied in experiments on food choice. They rarely eat as they are collecting food; their pouches are filled and then emptied into a hoard at the nest site. When these animals do eat, they select food items from their hoards, and the choices they make at that point are unknown. Perhaps it is the case that, for hamsters, pouching can be thought of as comprising two components, pouching and eating. While eating, hamsters may respond to certain properties of items that are in the hoard, such as taste and nutrient composition. When collecting food, they may respond to different properties of the available food items.

GENERAL DISCUSSION

The results of experiment 2, that neophilia in food choice was persistent and relatively long-lasting, are inconsistent with the findings of Galef (1982). It could be argued that 10 days was not long enough to show a shift in preference. Although this may be true, most studies on the development of food choice have shown a shift away from familiar tastes within 3 or 4 days (Galef 1977). In experiment 2, one litter, reared on 94-mg pellets, was inadvertently tested for 13 days instead of 10; animals in this litter continued to show the same pattern of preferences as other animals in their rearing conditions. While this is not conclusive evidence, it supports the conclusion that the effect is persistent.

Implications for the Optimal Diet Model

The results of these experiments do not refute the optimal diet model. The body of work on the optimal diet model is too large and too diverse and too many of its predictions have been confirmed experimentally for it to be rejected altogether. However, the findings of these studies should lead researchers to examine more carefully the assumptions of the model.

Optimality and choice

In the optimal diet model, the optimal diet is the one in which energy gain offsets energy loss. If handling and search times are kept constant, or nearly so, and energy content per gram and nutrient composition are the same across sizes, larger sizes should be more profitable than smaller sizes. According to the optimal diet model predictions, the largest size should be taken most often if all sizes are equally available. However, this did not happen; the results of experiment 1 revealed that animals do not automatically take the most profitable available food. Adult food choice is strongly influenced by the kinds of food to which animals are exposed while young. This is true for taste (Capretta & Rawls 1974; Neuringer & Neuringer 1974; Galef 1977; Partridge 1981) and, as these experiments have shown, for size. If animals do not always choose an optimal diet, why should the optimal diet model be considered at all? Under certain circumstances, adult animals do choose optimally, but the choice does not spring from a `phylogenetic tendency' to pick foods that meet the optimal diet model. Even when all the conditions under which animals should choose according to the optimal diet model are met, the animals may not do so. If an animal chooses an optimal diet, it does not mean that the animal is responding to profitability. Partridge (1981) suggested that, to predict the foods an animal will choose to eat, one should look at what they have eaten most recently, which is, in turn, influenced by food availability.

This is not to say, however, that animals cannot learn about the profitability of foods and respond in the way predicted by the optimal diet model. If animals have had a great deal of experience with a variety of foods that vary in profitability, they should be able to learn about the relationship between choice and energy gain, and act accordingly (Fantino & Abarca 1985). As Rozin (1976) established in his review of the literature on food choice, animals can change their diets in response to nutritional deficiencies as well as to unpleasant consequences that result from ingesting certain foods. Why should they not do so in response to profitability?

Development of optimal food choice

These considerations make it clear that, when studying foraging, whether one is concerned with the selection of a diet or of a search strategy, the behaviour patterns of interest are under developmental control. They are influenced by a complex set of environmental and organismic

events, which interact and influence the performance of the behaviour patterns. Partridge (1981) attributed the non-optimal diet choices shown by her mice to changes in digestive system efficiency brought about by restriction to one type of grain in their diets. Animals are not aware of these changes, of course, but their behaviour is affected none the less (Balagura & Harrell 1974). Animals can learn, with experience, to handle a specific food type more efficiently or to find it more easily (McNair 1980, 1981). Therefore, an animal's diet may contain nothing but items that a particular model predicts to be below the threshold of profitability as defined by optimal foraging theory criteria.

Recognition of food as food is often influenced by specific early experience. As Galef (1982) showed, rats do not eat every possible food item available to them, but are strongly influenced by the foods eaten by other conspecifics. Although the diets of their dams have the most profound effects, other animals can serve as demonstrators. Given a supply of new food, rats will sample it sparingly until they learn that it is safe; however, if an animal interacts with a conspecific that has eaten the unfamiliar food, the rat will eat much more of it. The effect is as strong with adults as it is with pups (Posada-Andrews & Roper 1983; Galef et al. 1985).

The results of the size preference study reported here lead to much the same conclusions. Before the hamster pups could forage on their own, they were exposed only to the pellets their dams collected and brought back to the nestbox. When they were old enough to forage independently, they followed their dams into the arena and found the same food size that they had encountered in the hoard. They did not, when given a choice between many different sizes of food, prefer the familiar size, but their preferences were systematically influenced by the early experience they had obtained. The preferences were consistent within rearing conditions and different between rearing conditions. Why the hamsters chose unfamiliar food item sizes is still open to investigation. What is clear is that the optimal diet model does not provide a complete explanation of food choice; it is a description of what happens when animals with certain kinds of experience with food are given a choice between different kinds of food. A more complete explanation of food choice behaviour, as well as other behaviour
displayed by animals, must include the examination of the factors that contribute to the preferences that are demonstrated. What experiences lead animals to choose food optimally? Are these likely to be the experiences they have had during early development? These are among the questions that need to be answered in order to reach an explanation of food choice behaviour.

REFERENCES
Abbey, H. & Howard, E. 1973. Statistical procedure in developmental studies on species with multiple offspring. Devl Psychobiol., 6, 329-335.

Balagura, S. & Harrell, L. E. 1974. Effect of size of food on food consumption: some neurophysiological concerns. J. comp. physiol. Psychol., 86, 658-663.

Barnard, C. J. & Brown, C. A. J. 1981. Prey size selection and competition in the common shrew (Sorex araneus L.). Behay. Ecol. Sociobiol., 8, 239-243.

Bronstein, P. M., Levine, M. J. & Marcus, M. 1975. A rat's first bite: the nongenetic, crossgenerational transfer of information. J. comp. physiol. Psychol, 89, 295-298.

Capretta, P. J. & Rawls, L. H. 1974. Establishment of a flavour preference in rats: importance of nursing and weaning experience. J. comp. physiol. Psychol., 86, 670-673.

Fantino, E. & Abarca, N. 1985. Choice, optimal foraging, and the delay-reduction hypothesis. Behay. Brain Sci., 8,315-330.

Galef, B. G., Jr. 1977. Mechanisms for the social transmission of food preferences from adult to weanling rats. In: Learning Mechanisms in Food Selection (Ed. by L. M. Barker, M. Best & M. Domjan), pp. 123-148. Waco, Texas: Baylor University Press.

Galef, B. G., Jr. 1982. Studies of social learning in Norway rats: a brief review. Devl Psychobiol., 15, 279-295.

Galef, B. G., Jr & Clark, M. M. 1971. Parent-offspring interactions determine time and place of first ingestion of solid food by wild rat pups. Psychonomic Sci., 25, 15-16.

Galef, B. G., Jr, Kennett, D. J. & Stein, M. 1985. Demonstrator influence on observer diet preference: effects of simple exposure and the presence of a demonstrator. Anim. Learn Behay., 13, 25-30
.
Galef, B. G., Jr & Wigmore, S. W. 1983. Transfer of information concerning distant foods: a laboratory investigation of the 'information-centre' hypothesis. Anim. Behav., 31, 748-758.

Johnston, T. D. 1987. The persistence of dichotomies in the study of behavioural development. Devl Rev., 7, 149-182.

Kirk, R. E. 1968. Experimental Design: Procedures for the Behavioural Sciences. Belmont, California: Brooks/ Cole.

Langley, W. M. 1985. Relative importance of distance senses in hamster predatory behaviour. Behay. Proc., 10, 229-239.

McNair, J. N. 1980. A stochastic foraging model with predator training effects. I. Functional response, switching, and run times. Theor. Pop. Biol., 17, 141-166.

McNair, J. N. 1981. A stochastic foraging model with predator training effects. II. Optimal diets. Theor. Pop. Biol., 19, 147-162.

Neuringer, A. & Neuringer, M. 1974. Learning by following a food source. Science, 184, 1005-1008.

Partridge, L. 1981. Increased preferences for familiar foods in small mammals. Anim. Behay., 29, 211-216.

Posada-Andrews, A. & Roper, T. J. 1983. Social transmission of food preferences in adult rats. Anim. Behay., 31,265-271.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol., 52, 137-154.

Rozin, P. 1976. The selection of food by rats, humans, and other animals. Adv. Study Behay., 6, 21-76.

Strupp, B. J. & Levitsky, D. A. 1984. Social transmission of food preferences in adult hooded rats (Rattus norvegicus). J. comp. Psychol., 98, 257-266.

Werner, E. E. & Hall, D. J. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology, 55, 1042-1052.

Wong, R. & Jones, C. H. 1985. A comparative analysis of feeding and hoarding in hamsters and gerbils. Behay. Proc., 11, 301-308.