SOME BEHAVIOURAL PRINCIPLES GOVERNING THE ACCEPTANCE OF SUPPLEMENTS BY SHEEP

J.J. LYNCH*

SUMMARY

The problems caused by sheep and cattle either not eating or being slow to eat a supplement are well known to animal producers and scientists. Some of the principles related to modification of food selection in vertebrates have been examined and in some cases their importance has been assessed in sheep.

Some inate preferences are genetic. The tastes of sweet, salt, sour and bitter are well developed in the newborn. These preferences are subject to modification by experience, age, and the diet selection of others of the same species.

It has been shown that sheep, like rats are neophobic to both troughs and novel food. Sheep when first introduced to wheat grain learn to eat it most rapidly either from mothers or other sheep experienced in eating wheat. They can learn in 15-30 min in some situations including temporary withdrawal of sight, smell or sound.

Field studies on sheep movement and social behaviour at troughs must now be studied before sheep management can be incorporated into other drought studies.

I. INTRODUCTION

Undernutrition or death can result from the failure of sheep to eat a supplement when it is first offered (Franklin, 1952; Arnold and Bush, 1968; Leng et al., 1977; Lobato et al., 1980). The reasons for the reluctance of sheep to eat foods known to be edible and adequate in energy or protein have received very little attention from research workers. The great gaps in our knowledge of feeding behaviour is not restricted to sheep. An examination of the literature shows that man and the domesticated rat are the only two species in which there is reasonable information concerning the principles of diet selection.

This review will briefly indicate some underlying behavioural factors related to diet selection and discuss in greater detail those factors which appear to be applicable to sheep.

*CSIRO, Division of Animal Production, Pastoral Research Laboratory, Armidale, New South Wales, 2350

2, DIET SELECTION

Diet selection has two major components. First there are

i) preferences which are determined by

(a) chemical stimuli impinging on the sense of taste

(b) genetic basis for food acceptance.

Then there can be modification of these preferences by

ii) experience. Experience will be considered under the following headings

(a) simple exposure, familiarity and sensitive periods

(b) taste aversion

(c) social interactions

A further modification in diet preference may be imposed by the liking or disliking of a substance when tasted by the animal (Cabanac, 1979). This is an area of speculation with few if any experiments being done on any species except humans.

The behavioural component in any consideration of dietary preferences is, of course, the approach to and acceptance of one of a group of foods or the avoidance or rejection of that food. Acceptance or rejection of a food can occur if only one food type is offered. In a sense acceptance could be considered a particular situation of dietary preference.

3. PREFERENCE

(a) Effect of Chemical Stimuli The sense of taste is present in the ovine foetus for the last third of pregnancy (Barcroft and Barron, 1939) but experiments testing preferences to stimuli of sweet, salt, sour and bitter solutions have generally been done on adult sheep. Sheep have a low sensitivity to sweet solutions and do not show the attraction to sweet-tasting substances which are said to be shown by higher mammals although there is a degree of individuality in this response (Goatcher and Church, 1970a). Goatcher and Church (1970b) tested glucose, sodium choride, acetic acid and quinine hydrochloride and showed in a series of experiments that for the sense of taste there was an increasing sensitivity or discrimination in the following order: sweet, salt, sour and bitter. This strong sensitivity to bitter solutions may provide some protection to those poisonous plants containing alkaloids or glycosides although the relation between herbivors and poisonous plants is likely to be more complicated. For example) Kingsbury (1964) suggested that sheep and cattle were susceptible to poisonous plants of Western USA because the herbivores and the plants did not experience co-evolution and the plants were palatable to the domestic animals. This was in contrast to those plants on the east coast which were far more similar to areas of Europe where the cattle were found originally.

In a series of experiments on sheep Arnold *et al.* (1980) examined the effect of a wide range of chemicals found in plants on food preference. The odour of 32 compounds was tested and two, butyric acid and amyl acetate, increased the voluntary food intake of hay while several other compounds reduced intake. Amy1 acetate strongly depressed wheat intake in another experiment (Lynch, unpublished). None of eight chemicals affecting taste increased intakes and five depressed it.

An experiment by Roe & Mottershead (1962) showed clearly that the ether extract of leaf from an unpalatable strain of Phalaris arundinacea sprayed onto a palatable strain resulted in sheep rejecting the latter strain. This finding may well result from the high sensitivity of sheep to bitter substances and non-acceptance of alkaloids.

(b) Genetic Effects In the animal kingdom, there is very little documented evidence of a genetic basis for the acceptance or rejection of foods. However, the research of Arnold (1981 a,b) on garter snakes shows the possibility that vertebrates have inate flavour preferences for other than simple chemical compounds which stimulate the taste system. Arnold worked with garter snakes of two populations, one of which lived on the coastal areas of California and the other over the ranges. Coastal snakes had a predominance of slugs in their stomach while the inland population mainly ate annelids, fishes and leeches. In laboratory tests on the progeny of the captured snakes, the predilection for slugs by coastal garter snakes was confirmed. Arnold showed that 73% of the laboratory-reared snakes from the coastal population attacked slugs but only 35% from the inland population did so. When tested a year later after both groups had been fed on fish the results were similar. In a long series of experiments with the progeny of these two populations this preference for slugs by the coastal population was found to be highly heritable.

Other evidence for innate preferences is more subjective as it is based on the facial expressions of human infants in response to concentrated solutions of sour, sweet and bitter solutions (Steiner, 1977).

Although the evidence of sheep preferring leaves to stems and new pasture growth to old has been well reviewed by Arnold (1964), very little is known about the genetic basis for the inate preferences of sheep seen when they are offered various pasture plants and shrubs.

4. MODIFICATION OF PREFERENCE BY EXPERIENCE

(a) Simple Exposure and Familiarity and Neophobia A simple exposure of rats and chickens to a particular flavour or colour of a diet can enhance consumption of that diet. In these species the enhanced intake is generally ephemeral although Siegel (1974) found that 30 minutes exposure of rats to either coffee or vinegar solutions resulted in an increased preference for the particular solution 24 days later.

The alteration in taste preference caused by familiarity is well illustrated in the Mexican population which gradually introduces chilli

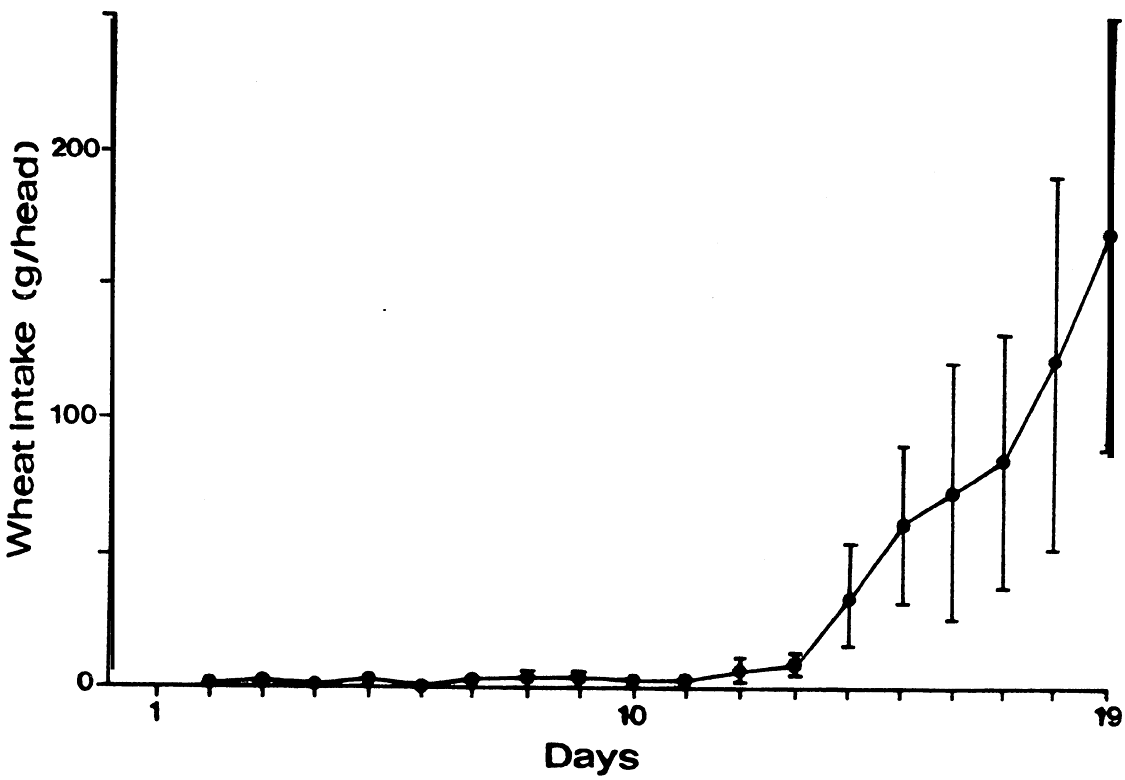


Fig. 1 Mean intake of wheat over 19 days (g/head/day ± SE)

pepper to the food of children until it is voluntarily added at the age of 5-7 (Rozin, 1979). Perhaps it is also due to familiarity that North Indian labourers, describe solutions of quinine sulphate as pleasant (Moskowitz et al., 1975). The behaviour of the North Indian labourers is perhaps analogous to the Englishman's ability to become used to gin and tonic!

Sheep show no subsequent increased intake of wheat after a simple exposure of one 15 minute period (Lynch 1983). There is, eventually, an effect of familiarity. In studies on acceptance of wheat by sheep a 15 min. daily exposure of the sheep to the grain was routinely used. The curve of intake (Fig. 1) shows that it took 13 days before the sheep ate 10 g of wheat in 15 min but after this time the quantity of grain consumed per day increased very rapidly (Chapple 1985). She also showed that part of the time delay before wheat was eaten was due to neophobia (fear of new things) of the trough containing the wheat. Sheep used to eating lucerne hay from the trough took only 6 days before they ate more than 10 g wheat in a 15 min period. Once sheep eat more than 10 g per day they will readily eat wheat even if they have not seen it for up to three years (Green et al., 1984).

Food neophobia has been recognised for many years by those attempting to kill pests by poisoned baits (Shortens, 1954) while Domjan (1979) has reviewed work showing the large number of vertebrate species which exhibited a neophobia for edible substances. Animals eat far less of a novel than of a familiar substance. Hence, neophobia of a novel but edible substance is almost certain to be a major component in the delay shown before sheep will eat wheat although there are almost no experiments other than Chapple's work specifically examining this point.

5. AGE OF EXPOSURE

For some reason most research workers have exposed animals to particular foods early in the animals life, often the exposure is within the first 14 days of life, There has been almost no work on offering mature animls new foods, In general Hill (1978) concluded there was little effect of age on modifying food preferences in rats.

Little is known about the effects of age at exposure on modification of diet in domestic animals, A wide experience of plant species early in life of sheep appeared to result in consumption of unfamiliar plants when offered them later in life (Arnold and Maller 1977). Lobato et al. (1980) found that lambs which were offered molasses-urea blocks before weaning ate none but blocks were eaten post-weaning. A suggestion was made that lambs may have become familiar with the sight and smell of the blocks in the pre-weaning phase.

There is some evidence that diet preference may be changed irreversibly by an animal being exposed to a food during a "sensitive period" of its life, Burghandt and Hess (1966) have shown an imprinting phenomenon for food in newborn turtles which prefer the food they were first given. Ferrets have been shown to become imprinted on the odour of prey when their age was between 2 and 4 months (Apfelbach, 1978). Imprinting may have occured in lambs which were exposed with their mothers to wheat when the former were less than 5 days old (Lynch , et al., 1983). The lambs subsequently ate large quantities of wheat when offered it again after weaning. It is by no means certain that the lambs were imprinted on wheat for though it is unlikely that 5 day old lambs would eat any grains of wheat they were not observed continuously to determine that they ate no wheat.

(b) Feed Aversion There is a rapid change in diet selection by rats which have eaten a diet and are then poisoned by X irradiation or an injection of lithium chloride. The food, even if it was highly palatable previously will be rejected (Garcia and Koelling, 1966). In many species of vetebrates, including cattle (Zahorick and Houpt, 1979), the pairing of food with a poison has resulted in the diet being not eaten. However, acidosis associated with consumption of large quantities of wheat does not stop subsequent ingestion of wheat by sheep (Green et al. 1984).

(c) Social Interactions Animals will learn to perform tasks more rapidly if they can watch conspecifics performing the task. This statement can be made for a range of species, including bats , birds, primates, rodents and cats.

For example, a group of red squirrels inexperienced in opening hickory nuts were able to observe a conspecific opening the nuts. Another group was not shown the demonstrator animal opening nuts. When both groups were offered hickory nuts the former opened the nuts in half the time of the latter (Weigl and Hanson, 1980).

Oyster-catchers, Haematopus ostralegus, have two distinct ways of opening mussels. The birds either put their bill through the slight opening of mussels bathed in sea water or take a mussel from the rocks over to an area of firm sand and hammer on the ventral surface until it breaks and they can eat the flesh. Norton-Griffiths (1967, 1969) described the two techniques and showed that:
(i) an individual bird always used the same method;
(ii) the method had been learnt by the young bird following its parents down to the mussel bed and gradually ‘acquiring the same technique as its parent.

Wyrwicka (1978) trained mother cats to eat banana or potato in the presence of meat pellets. Around the age the kittens were being weaned, the mothers and the kittens were offered meat pellets either with banana or mashed potato. After weaning the kittens were tested individually and almost all the 22 kittens ate the banana or potato. Later, at 9 and 27 weeks of age the kittens were again offered meat pellets and banana or potato and again ate the banana or potato and ignored the meat.

These three examples illustrate the way animals can modify their diet preferences after observing conspecifics. This phenomenon has been called observational learning although it has many synonyms such as imitation, cultural transmission, local enhancement and social transmission. The result of observational learning is that individuals of a social species do not always have to learn individually by the laborious process of trial and error learning what items to ingest. They can make use of acquired food patterns of others.

Mother young interactions Since young of most species are initally very dependent on their mothers, the assumption is often made that the young is strongly influenced in its diet selection by its mother.

In a cross fostering experiment (Key and MacIver 1980) showed that Clun Forest and Welsh Mountain lambs preferred the distinctly different improved pasture or tussock and heather eaten by their foster mothers. The authors state that "it would appear ... that sheep are not born with innate behavioural patterns determining their grazing habits but rather that the latter are acquired by copying the habits of their natural or foster mother".

Lobato et al (1980), Key and MacIver (1980) and Lynch et al (1983) have all assumed that lambs have been strongly influenced in their diet selection by their mothers. Since the mother and its lamb was not an isolated unit in these experiments but part of a flock it is quite possible that the lambs were being influenced by adults other than the lamb's mother.

It has been shown in rats that mothers can directly influence the diet of their young by the flavour cues which occur in the mother's milk (Galef and Sherry, 1973). This type of observation does not appear to have been reported in other species.

Adult Young Interactions The relation between the mother and its young can result in the young learning from its mother but in many species the young is equally capable of learning from other experienced animals.

In rats, the adult can influence the diet of a young animal in several ways (Galef, 1979).

(a) A rat can deposit olfactory cues near the feeding site (Galef & Heiber, 1976)
(b) If an adult rat is very near the feeding site young rats will eat there (Galef & Clark, 1971)
(c) A rat which has recently fed will have particles of food around its muzzle. If this rat is then placed with other rats at a site distant from the food the smell of the food will influence the diet of other rats (Galef and Wigmore, 1983).
(d) Even if the pelage of the "demonstrator rat" is thoroughly cleaned of food particles there is still evidence that the "observer rat" can have its food preferences altered, perhaps via odours on the demonstrators breath (Posadas - Andrews and Roper, 1983).
(e) Adult-young interactions were more important in determining the

diet selection of weanling than adult rats. (Galef, 1977).

Although these factors can modify the food preferences of rats the list of modifying factors may not be exhausted. Further there is no evidence that any of these factors are operating in a natural population of rats.

6. FACTORS AFFECTING LEARNING TO EAT NEW FOODS IN SHEEP

Until now, this review has concentrated on factors affecting diet selection. Some of these factors have been examined in sheep. The initial experiments were done to see if observational learning was important in shaping the diet selection of lambs. Later experiments examined the importance of age and the senses.

Observational Learning Over 100 lambs varying in age from newborn' to nine weeks were exposed to wheat during one hour a day for periods up to 45 days without adults being present. Another 45 lambs and their mothers were offered what for as short a period as the first three days of life up to four weeks old, The adults in this case had been fed a complete diet of wheat in the field during pregnancy and lactation (Lynch et al., 1983). There were two other groups of 20 animals. One group was removed from their mothers at birth and reared on reconstituted milk powder with wheat available in the pen while the other was reared with their mothers on a diet of wheat. (Lynch, unpubl. data). Both groups were weaned at 10 weeks. At 12 weeks lambs in all four treatments plus a control group which had never previously seen wheat were offered wheat for 30 min a day for 5 days and the intake was measured each day. The results (Fig. 2) show that if adults were present and ate when lambs were offered wheat the weaners subsequently ate substantial quantities of wheat. However, neither of the other two groups ate a significiant quality of wheat.

This experiment clearly showed that simple exposure to wheat' is not, by itself, a major factor in altering diet preferences since the group of artificially reared lambs with wheat available for 24 h per day for 10 weeks ate almost no wheat at testing.

The fact that lambs which were, on average, three days old when removed from wheat ate as much as other groups that were reared with their mothers suggests that food imprinting may have occurred. This result needs more rigorous observation of the lambs to see if lambs actually ate any wheat.

There must be other triggering factors. One of these may be that about 3% of sheep when offered wheat for the first time will eat it within a few days (Lynch, unpublished data). Results from other treatment groups suggest that observational learning is occurring i.e. it is generally necessary for one animal to watch another eating before the first animal starts to eat.

Long term memory After all lambs were tested to see if they ate wheat at weaning, the long term memory for wheat was examined by dividing

. Fig. 2 Mean intake of wheat (g/head/day) after weaning for groups exposed to wheat without mothers for 1 hour a day for up to 45 days, 10 weeks continuously and for groups exposed continuously for 4 or 10 weeks with their mothers.

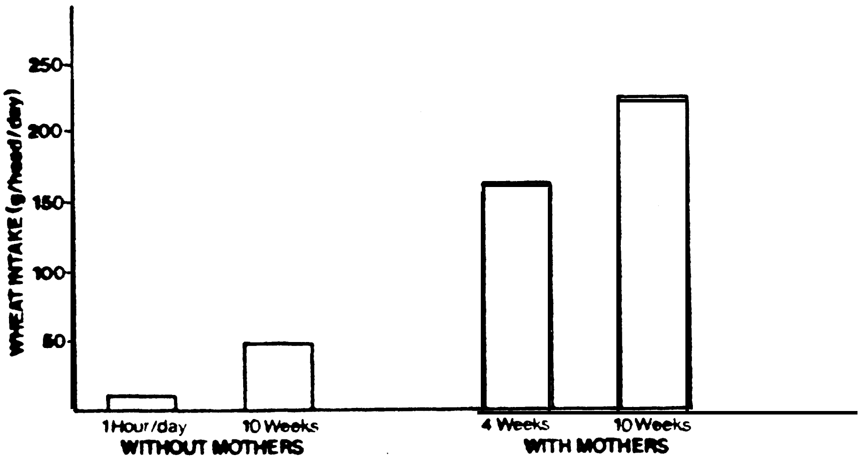
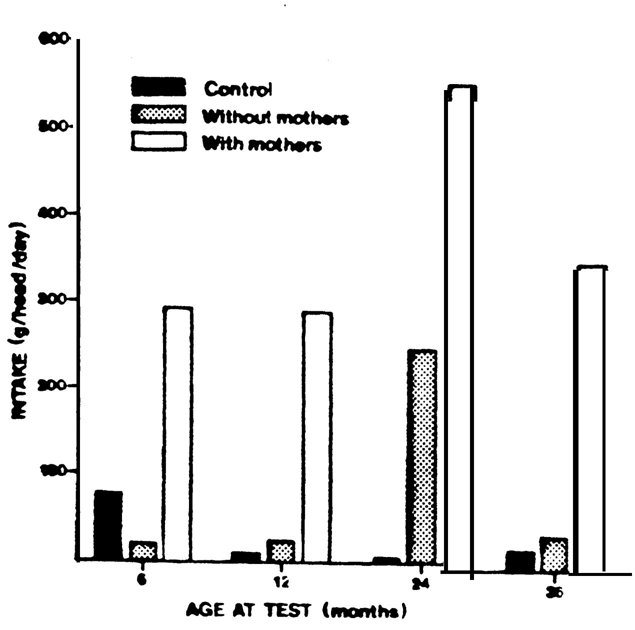


Fig. 3 Mean wheat intake (g/head/day of groups of sheep offered wheat at 6, 12, 24, or 36 months after having been exposed to wheat pre weaning without or with mothers. Controls had never previously seen wheat until the month of testing.



into four the group exposed with their mothers and the group exposed for one hour a day without their mothers. One quarter of each group was tested at 6, 12, 24 or 34 months. Controls were offered wheat for the first time at each testing. The results show clearly that sheep which ate wheat at 12 weeks of age will readily eat it almost three years later. Again, sheep exposed to wheat with their mothers ate significantly more than either those which were exposed without mothers or the controls (Fig. 3), (Green et al., 1984)

Sheep which had been exposed to wheat before weaning without their mothers ate substantial quantities of wheat when tested at 24 months during severe drought while the controls ate nothing. This raises the possibility that simple exposure of the sheep to wheat as lambs actually affected their diet selection under severe nutritional stress two years later. A similar explanation of early familiarisation could be interpreted from the work of Lobato et al. (1980) who showed that no urea-molasses blocks were eaten by lambs pre-weaning but the blocks were eaten post-weaning when herbage availability was restricted.

The results of these experiments are consistant with the idea that lambs learn to eat wheat grain by watching sheep experienced in eating wheat. This would provide an explanation for the controls aged 12 months eating wheat as they were accidently located next to a group of sheep which at 300 g/head/day. Subsequently, sheep in various groups were screened from one another.

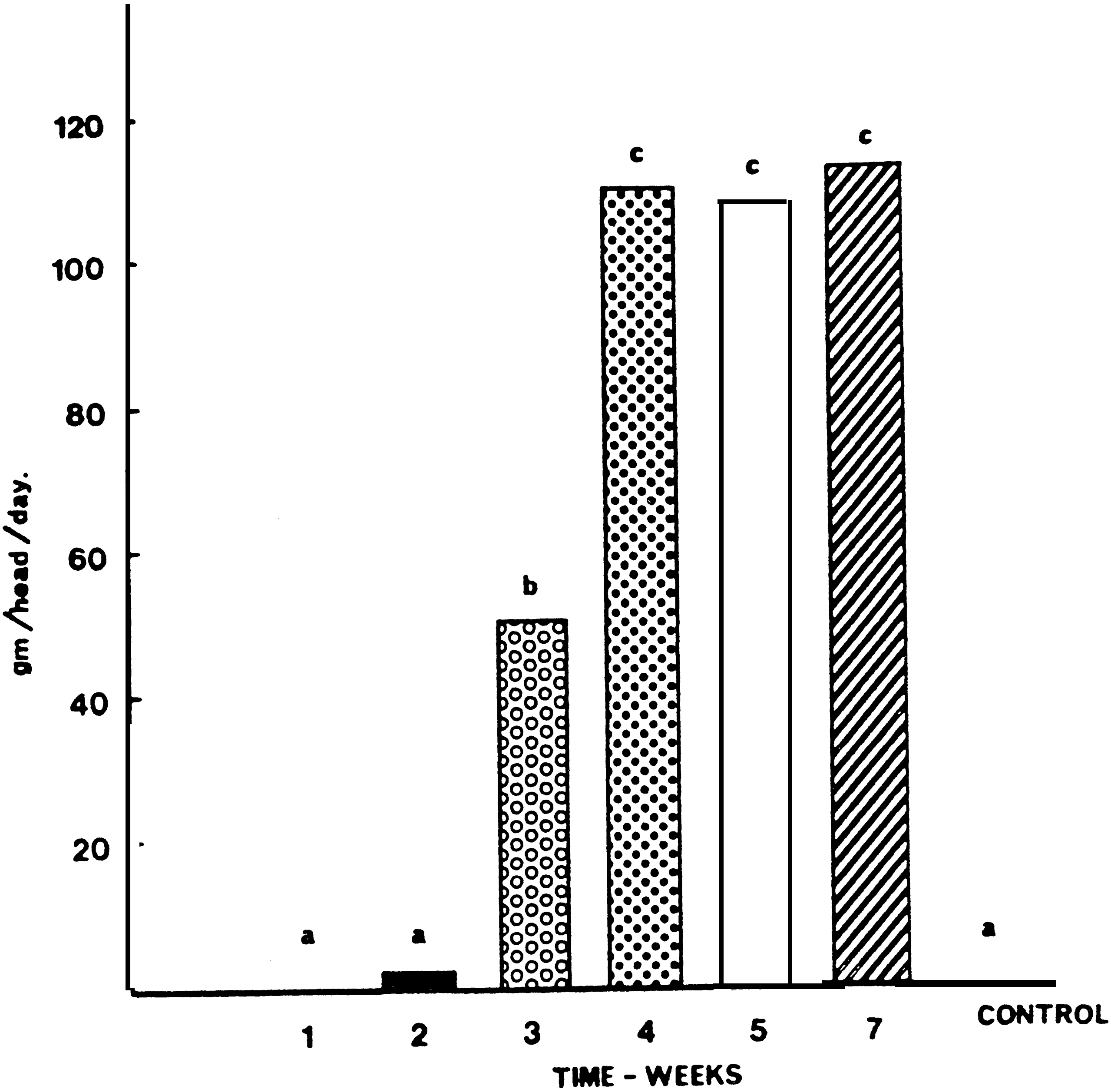
7. PEN EXPERIMENTS

A standard system is now used of offering sheep a novel food for 15 min per day for five consecutive days with suitable treatments, then in the future offering the food again for the same time period and weighing the food residue each day.

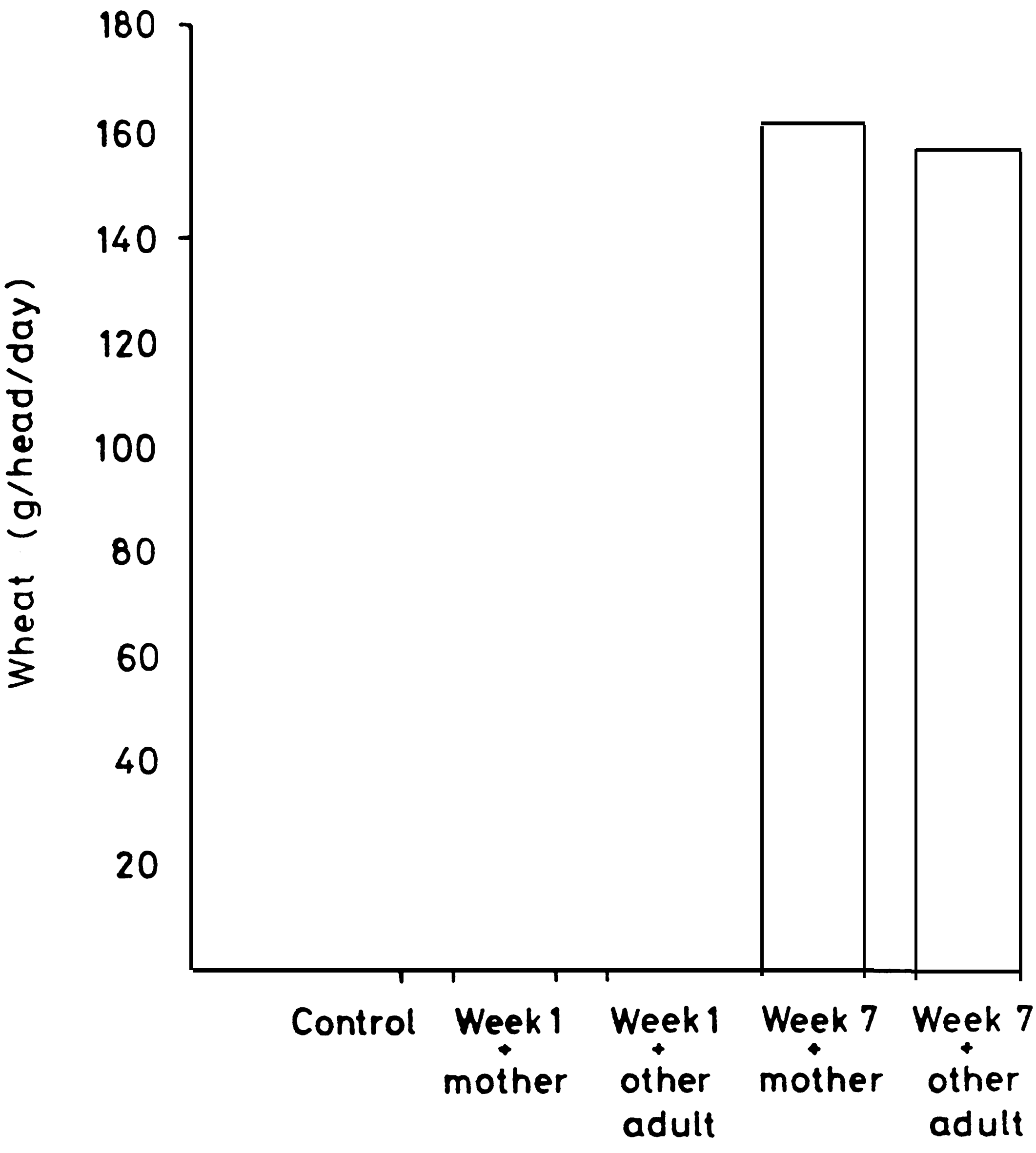
Mother or other adult An experiment was done to find out if other adults in a flock had a similar role to a lamb's mother in teaching the lamb to eat. Lambs one or seven weeks old were offered wheat either with their mothers or with adult wethers experienced in eating wheat. The results showed that provided the lambs were seven weeks old they can learn from any experienced adult (Fig. 4). Given the method of trail ing grain during a drought lambs are likely to learn how to eat grain from any animal that is already eating it.

Age of lambs Groups of lambs were offered wheat for five days with their mothers during the first to seventh week of life. Subsequently , the lambs ate an average of 120 g/head when tested after weaning if they were more than three weeks old (Fig. 5) when first offered wheat. Other research had shown that lambs exposed for two days when seven weeks old eventually ate less than half the amount of wheat of lambs exposed for five days. There seems to be evidence that there is an interaction between length of exposure and age of lamb and the standarised system described above is not necessarily optimal for lambs learning to eat novel foods.

Fig. 4 Mean wheat intake (g/head/day) after weaning of groups of sheep offered wheat with their mothers or other adult sheep at age one or seven weeks. The control group say wheat for the first time after weaning,



5Fig.   Mean wheat intake (g/head/day) after weaning of groups of sheep offered wheat with their mothers at 1,2,3,4,5 or 7 weeks of age. Control sheep say wheat for the first time after weaning.



In 1985, Chapple showed that weaners up to the age of nine months could learn to eat grain but there has been no research on the effect of age on the acceptance of wheat past this age. Lobato (1979) considered that sheep older than 9 months do not eat a urea-molasses block as readily in re-exposure as younger lambs.

The ability of adult sheep to learn how to eat a novel food needs study prior to considering management stragegies for drought feeding of sheep.

Neophobia Sheep have also shown to be neophobic both to the container holding food (in pens) and to the food itself (Chapple, 1985). Having learnt that wheat is food they must also learn how to prehend and chew the grain. (Lynch et al., 1983).

Senses There has been little work on the importance of the various senses in respect to sheep learning to eat novel foods. Arnold (1964) said that the senses of touch, taste and smell all played some role in determining preferences of pasture plants by sheep. In deer, taste and smell are said to play some part in the initial response of acceptance or rejection of a food (Longhurst et al., 1968).

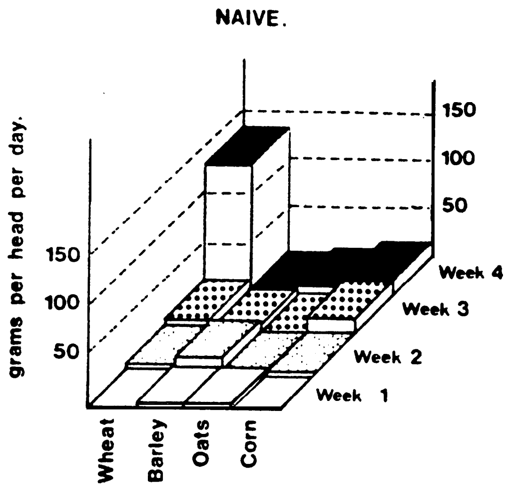
In one experiment (Lynch, unpublished), lambs 5 weeks old were exposed to wheat in the company of adults experienced in eating the grain. Post-weaning when the lambs were offered wheat grain, wheat flour and wheat pellets they ate similar quantities of each (160 g/h/day). In another experiment a group of control sheep and other adult sheep that ate wheat and were offered wheat, oats, barley and corn in a latin square design (Mottershead et al., 1985). Sheep that ate wheat took 6 daily exposures before they ate barley and at least 12 before they ate either corn and oats. The sheep unaccustomed to eating any grains ate wheat only towards the end of the experiment. (Fig. 6).

Taken together these two experiments suggest that if texture of wheat is altered or sheep are offered wheat and three other grains the sight of the food is not as important as its smell in determining if sheep will eat a food. Also, sheep which eat wheat must learn to eat other grains and the grain that wheat eaters learn to eat most rapidly is barley. The results from the second experiment are consistant with the two experiments (Hutson and van Mourik, 1981, Hutson & Wilson, 1984) which show that wheat and barley are preferred foods for sheep.

The volatile components of wheat to which the sheep might be responding have not yet been identified, although some of the constituents have been identified (Vit, unpublished). Once they are known it would be interesting to see if consumption of other grains could be enhanced by incorporating the wheat volatiles into the other supplements and offering the material to sheep which can eat wheat. This technique has been partially successful in increasing the consumption by rats of a granulated whole grain rice, which included zinc phosphide as a bait (Table 1) (Shumake, 1977).

Fig. 6

(a) Intake of 4 grains (g/head/day) by sheep which had never 'Previously seen wheat. Sheep were offered a grain for three days each week in a Latin Square design.



(b) Intake of 4 grains (g/head/day) by sheep which previously ate wheat. Sheep were offered a grain for three days each week in a Latin Square design.

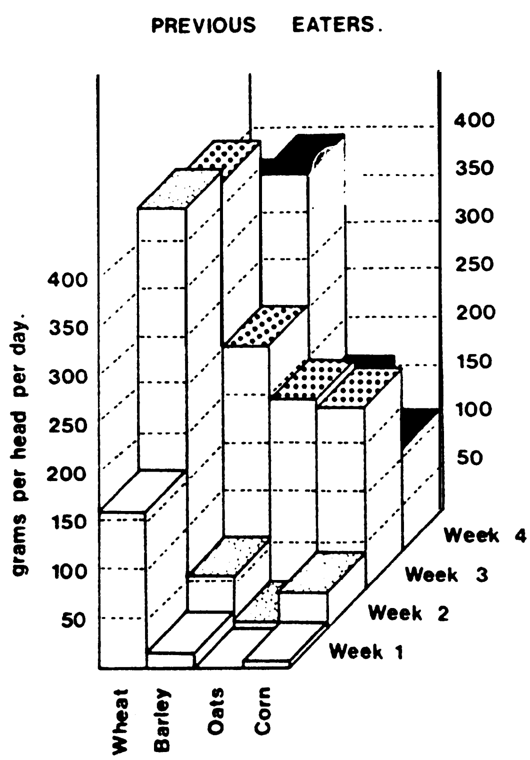


TABLE 1. GRAMS OF RICE BAIT CONSUMED BY FIVE RICEFIELD KATS EACH IN FOUR ENCLOSURES (MEAN $\pm$ SE)

	Bait			
	(A)	(B)	(C)	(D)
Day	Whole grain rice	Granulated whole grain rice	Granulated whole grain rice treated with 1.0% soybean oil	Granulated whole grain rice treated with trapped rice volatiles
1	8.1 $\pm$ 1.7	12.9 $\pm$ 2.7	22.8 $\pm$ 2.9	35.1 $\pm$ 3.2 **
2	6.6 $\pm$ 2.1	8.9 $\pm$ 1.6	21.9 $\pm$ 2.3	35.1 $\pm$ 3.2 *
3	5.3 $\pm$ 2.0	15.5 $\pm$ 2.7	25.9 $\pm$ 2.5	35.9 $\pm$ 3.3 **
4	6.4 $\pm$ 2.4	14.6 $\pm$ 2.9	16.4 $\pm$ 3.0	34.4 $\pm$ 2.8 **

* $P(D > A) < 0.10$
** $P(D > A) < 0.05$
*** $P(D > A) < 0.01$

(Abridged from Schumake 1977)

Although the sense of smell was thought to be more important than that of vision, the work of Chapple (1985) has clearly shown that sheep rapidly adapt if any or all of the senses of smell, sight and hearing were temporarily withdrawn when naive weaner sheep are offered wheat in close proximity to sheep which can eat wheat (Chapple,, 1985).

In an experiment, the naive sheep were surrounded by experienced wheat eaters and the experimental groups which were either controls or sense deprived ate an average of 250 g/head/day when offered wheat for 15 min per day over 5 days Table 2.

Table 2. The number (total of 16 per group) of sensory impaired sheep which accepted wheat over 5 days, and the mean wheat intake (grams) per head for 5 days.

TREATMENT	No. of Animals Feeding by Day 5	Mean Wheat Intake/head (g)
Blind	14	460
Deaf and anosmic	13	362
Deaf	14	316
Deaf and blind	9	305
Control	15	198
Deaf, blind and anosmic	6	177
Anosmic	14	165
Anosmic and blind	9	141

Chapple concluded that the sheep could rapidly adapt (in 15-30 min) to the loss of one or even the three senses and no one sense was more important than another in helping a sheep learn to eat a new food. The speed with which eating of wheat was learned was more rapid in the senses-deprived than in the control sheep.

The technique of using surgery or chemicals to destroy the sense of sight, smell or hearing may be of little benefit in trying to assess the relative importance of various senses in diet selection since the adaptation to loss of a sense can be so rapid.

8. CONCLUSIONS

There is some information concerning factors which can cause alteration in dietary preferences in rats but less information of a similar nature in ruminants. In comparision with rats) sheep are very conservative eaters and rarely show the phenomenon of small sampling of discrete parcels of food. Apart from observational learning which certainly occurs in sheep as well as in many other species, the different mechanisms discussed which may induce weaner rats use to change diet preference have not been studied in sheep.

The research on acceptance of a novel food in sheep has been done in pens but it is now time to start field studies on the dynamics of accpetance of novel feeds by sheep. This is likely to bring in a new dimension with dominance hierarchies and other social behaviour affecting observational learning. These factors and factors affecting the movement of sheep to supplementary feed must be considered before an integrated approach to the management of sheep is incorporated in other drought feeding strategies .

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