THE FUNCTIONAL RESPONSE OF THE BANK VOLE, CLETHRIONOMYS GLAREOLUS (SCHR.), TO FOOD DENSITY

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I hereby declare that this thesis has been composed by myself and the research presented in it is my own.

ABSTRACT

The aim of this work was to investigate the relationship between food consumption and food density in the bank vole, Clethrionomys glareolus (Schr.). This relation is known as the functional response, and has importance for the population dynamics of the food and the feeding populations, and for the pattern of energy and material flow through a community.

The first part of this work was to describe the response of the bank vole to changes in the density of a preferred food (groats, or huskless oat grains), in the presence of an abundant supply of a less-preferred food (wheat grains). A system (the "brushes" system) was devised which met the opposing requirements of ease of handling by the experimenter, and difficulty of searching by the vole. This system also made it possible to measure the distance travelled by the vole in search of its food. It was found that voles settled to the system in 2-3 days, though some subsequently showed long-term changes over the course of the experiment. Voles responded to a sudden removal of groats by a temporary increase in the daily distance travelled; thereafter, travelling through the area was maintained at a low level. Voles appeared less willing to search for groats when wheat was scattered with the groats, rather than separate. The data could be used to estimate the vole's reactive distance for groats, at 2-4 cm. The functional response curve showed four features, for some or all of the voles: a region of constant groat intake, and regions of a linear rise, a negatively-accelerated rise, and a positively-accelerated rise in the response curve. Distance travelled was depressed at low groat densities. The response during periods of falling groat density was higher than during periods of

rising groat density. At intermediate densities, differences were found between the first and last day at each density. Quantitative features of the response curve are also described.

To provide background information on the feeding mechanism, aspects of feeding behaviour are considered. Vole feeding and searching behaviour are described. Stability, regulation and temporal patterns on consumption and preference were investigated. Restriction to wheat was found to increase the subsequent relative preference for groats. Aspects of hoarding and drinking were studied. As a first step in analysing the functional response mechanism, the main components of the response were identified and investigated. Three intervening components (having an indirect effect on the feeding response) were considered - hunger, specific hunger and learning - and three direct components - speed-of-movement, handling time and reactive distance. A theoretical model of the hunger system was derived, and the component was investigated experimentally: at least two state variables were deemed necessary to represent this component. Fine-scale analysis of the pattern of selection following limitation to wheat led to the conclusion that specific hunger operates on the peripheral sensory as well as on the metabolic levels. The nature of the learning component was deduced from the functional response experiments, and the difference between extinction and forgetting of a learnt response is stressed. Speed-of-movement in the brushes system was found to be 2-4 cm/sec. Handling time for groats and for wheat was approximately 0.7 minutes and 2.0 minutes. The reactive distance for groats was measured experimentally as being approximately 4 cm. There was little evidence for a marked effect of the intervening components on the

direct components, though it was not always possible to test for this. Various possible qualitative explanations for the presence of particular regions on the functional response curve are discussed, and a speculative but plausible model to account for the positively-accelerated region is proposed. It is concluded that the inclusion of the three intervening components greatly increases the difficulty of modelling the functional response.

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Section 1. Introduction.

This study is concerned with the way that individual bank voles, Clethrionomys glareolus, respond to changes in the density of a preferred food when an alternative, less preferred food is in abundant supply. Solomon (1949) used the term "functional response" to describe this response, specifying that it be measured in terms of the number of food items consumed; the term "numerical response" was then used to describe the response of the population as a whole, in terms of its density as a function of food density. In this study the use of the term functional response will be extended to include other measurable aspects of the way that the vole responds to changes in the density of its preferred food, notably an index of the distance travelled per day over the feeding area.

As with any other process, the functional response can be considered at both the descriptive level and at the analytical level. At the descriptive level, the aim is to describe the relationship between the density of a particular food type and the amount eaten (or whatever other measurement is used). This description is usually in the form of a graph; this is adequate when only a single food type is involved or an alternative food is very abundant at all times, but this method cannot deal with more complicated situations.

The analytical approach involves determining the main behavioural and physiological factors underlying the functional response, and the relationships between them. These can then be expressed in the form of a mathematical relationship which should be capable of generating the functional response actually demonstrated by the individual animal.

The ecologist is usually in the position of asking simple questions about very complex systems. What happens to a deer population if its predators are removed? What regulates the population size of an insect pest? In some cases, an answer can be found by appropriate manipulation of the natural system, but in this case the answer is usually specific to the situation under study. In other cases, the complexity of the natural system may make it impossible to unravel the implications of a particular action. In either case, a fruitful approach can be the construction of an analogue, usually in the form of a mathematical model, of the natural system. The model can then be monitored to assist in understanding the workings of the natural system, or manipulated in order to determine the effects of particular actions.

Models of ecological systems usually take one of two forms. Population models represent the dynamics of population processes, using equations to incorporate the factors which tend to increase and to decrease the population size. The functional response is important here for two reasons. First, when considering the population dynamics of a food species, losses due to consumption will be determined by (amongst other things) the functional responses of the species which feed upon it. Second, the reproductive success and the survival of a feeding animal will be in part a function of its feeding success, both in terms of total intake and in terms of the quality or balance of the intake. Both these factors will be affected by the animal's functional response. Despite this, models of population processes usually incorporate the functional response in the most elementary of ways. Thus, Maynard-Smith (1974) considers models in which each feeding animal is assumed to eat a constant amount, or to eat an amount proportional to food density.

The other form of model of ecological systems deals with the flow of material or energy from one recognisable section, or compartment, of the system to another. These compartments usually correspond with trophic layers or smaller trophic groupings, though in the case of material flow the non-biotic sections of an ecosystem are included. Although many of the flows correspond with feeding relationships, and could thus be usefully described by the functional response, once again the simplest of mathematical expressions are used for determining the relationship, with flux usually being proportional to the value of the donor compartment, to the value of the recipient compartment, or to the product of both.

In both types of model, these very simple forms of the functional response have been used mainly because of lack of information on actual functional responses, and because it is easier to manipulate and obtain analytical solutions of models based on these relatively simple solutions. There is now a variety of cases for which the functional response has been determined, so the basic forms of the response are known. And it is now well known that the advent of the modern digital computer has removed the obligation to formulate a model so that it is capable of analytical solution.

Knowledge of the functional response can be incorporated in one of two forms. It can be treated as a description, in which case the input to the model is the number of food items eaten as a function of its density. In more complicated situations, in which the functional response cannot be simply described, either because of a multi-food situation or because of time lag effects, it can be incorporated in the form of a model based on components of the searching and feeding process.

Quite apart from the need to develop explanatory as well as descriptive approaches to the functional response to improve whole-ecosystem models, a model of the functional response is an important exercise in its own right. First, such a study is a way of formalising one's understanding of an important ecological process; it provides the explanation behind the description of the functional response. Second, models of this type can be useful in situations such as the management of a grazing system, where the cost in time and in money of conducting sufficient experiments to describe the functional response may be prohibitive. In either case, there is a premium on expressing the model in the form of general relationships which apply to a large variety of situations: from the theoretical point of view, it is desirable to express ecological processes in different species in as economical way as possible; and from the practical point of view, the determination of common features of the functional response mechanisms can reduce the amount of work required in any one application to develop an adequate model.

Section 2 Background

2.1 The bank vole

A general description of the bank vole and its habits can be found in Southern (1964).

The bank vole, *Clethrionomys glareolus* (Schreber, 1780) belongs to the order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Microtinae. The Microtinae (voles and lemmings) have interested population ecologists because of the regular fluctuations, with a period of 3 to 4 years, in population size (Chitty and Chitty, 1962).

The bank vole is found from the Mediterranean to the Arctic, in several races. The vole has a characteristic reddish pelage, and typically has a head-and-body length of 9 to 10 cm. The voles used in the experiments were variable in weight, generally ranging between 12.0 and 22.0 gm.

The most characteristic habitat of the vole is an area with a well developed and varied ground vegetation: deciduous woodland, shrub vegetation and hedges. The size of the home range is approximately 2,000 to 4,000 m^2, is larger for males than females, and tends to be inversely related to population size (Mazurkiewicz, 1971). There is considerable overlap of home ranges, with any point including 10 to 20 home ranges, so that there should be little need to consider the problems of distinct home ranges in relation to food distribution.

Bank voles appear to represent an intermediate stage in the evolutionary sequence of the Muroidea from a protein-rich diet of for example the wood mouse, *Apodemus sylvaticus*, to more abundant cellulose foods used by the short-tailed vole, Microtus agrestis. The former are more active and lack the well-developed caecum of the latter (Vorontzov, 1962). There are even differences in the degree of development of the caecum between bank voles living in the south of Europe, and those living in the north, corresponding with an increase in the proportion of green plant material.

There have been several studies of the foods eaten by the voles (Miller, 1954; Watts, 1968; Drozdz, 1966, 1967, 1968; Eldridge, 1969). The two major components of the diet are seeds and green parts of plants. The proportion of seeds in the diet over a year range from 20% (Watts, 1968) to 50% (Drozdz, 1966), where the values are percentage of stomach volume of captured animals. In addition, Watts found a considerable amount of fruit and dead plant material, and Drozdz identified some fungi and invertebrates. These differences probably indicate differences in availability: the seasonal pattern of fruit, seed and green plant in the diet corresponds with seasonal availability, and heavy falls of beechmast are reflected in the diet. The diet has also been studied in the laboratory by feeding experiments in which the vole is presented with most of the items thought to be potential food (Drozdz, 1967). This study has indicated a large preference for seeds: seeds of trees were consumed most frequently, followed by fresh seeds and fruits, and green material, in similar proportions. Thus, it seems that voles would eat more seeds in nature if they were more abundant.

The activity of the bank vole has been studied under natural conditions by trapping at 2 hour intervals (Buchalczyk, 1964). No evidence of a diurnal cycle of activity was detected. Saint-Girons and Durup (1962) found that under laboratory conditions the bank vole may show a nocturnal cycle of activity, the extent of which depends on season. This finding has been confirmed by Harradine (1970) using simulated seasonal changes in light period. Grodzinski (1962) found that the bank voles only showed pronounced nocturnal cycles of activity when food was of poor quality.

2.2 The food

The food used in the studies was groats (de-husked oats, Arena sativa L.), and wheat (Triticum aestivum L.). This was the only food to which the voles were exposed once captured, and voles were able to survive well over a year on this diet. In addition, five voles were kept on groats alone, and five on wheat, for two months before being offered both foods, so it would appear that either food in isolation is satisfactory. The usual weight range for groats and wheat were respectively 25 - 30 mg and 45 - 55 mg, though the weight of individual seeds fell outside this range, and in certain experiments seeds were selected from one end of the weight range. Approximate nutrient composition of the two seeds is given in Table 2.2-1. These are based on two sets of published data (Stephens, 1891; Ingle, 1913) and include a correction for the groat values, which are derived from values for oats.

Table 2.2-1 Approximate nutrient composition of groats and wheat.

	Groats	Wheat
Moisture	13.8%	11.5%
Ash	3.3	1.7
Fibre	0.5	2.2
Carbohydrate	62.7	70.6
Protein	13.7	12.0
Fat	6.0	2.0
	100.0	100.0

2.3 The meaning of the term "functional response".

From the time of their original proposal (Solomon, 1949), the terms "functional response" and "numerical response" to food density have been used largely uncritically. Hassell (1966), in a largely ignored paper, has attempted a more rigorous definition of the terms, and it is the aim of this section to extend this approach and clarify the way in which these terms can be used.

Solomon states this of the functional response: "as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly." And of the numerical response: "an increase in the number of the enemy due to an increased rate of survival or reproduction, or both".

There are two problems in using the two terms as they stand.

First, the use of the term "attack" implies a rate, of number attacked per unit time, but this depends on whether the unit of time is minute, hour, day or week. The shorter time unit will only relate to time in which the animal is searching; the longest one could include movement by the animal into an area of higher food density. Second, the term "numerical response" has been used in relation to changes in the number of predators/ parasites which may or may not be due to the population processes of reproduction and mortality. An example of such an approach is found in Holling (1959a), where the numerical response is determined from differences in the density of small mammal predators of sawfly cocoons, in different areas without examining the reasons for these differences.

Hassell proposed three new terms to replace the above two. The first term, the "individual response", refers to the response of the individual animal to changing food density in a homogenous environment. The "aggregative response" refers to the non-random distribution of predators corresponding with spatial differences in food distribution. These two types are both considered as behavioural responses, since they are mediated through the behaviour of the individual in relation to food density. "Intergeneration relationships", on the other hand, depend on changes in the number of predators which take place from one generation to the next in response to food density, and are characterised by lag effects arising either from the time needed to produce offspring or from delays in the effect of changes in consumption on survival.

The advantage with this alternative method is that it emphasises the underlying mechanisms to a greater extent, and makes it easier to determine which aspects of the response operate in a subproportional or superproportional manner.

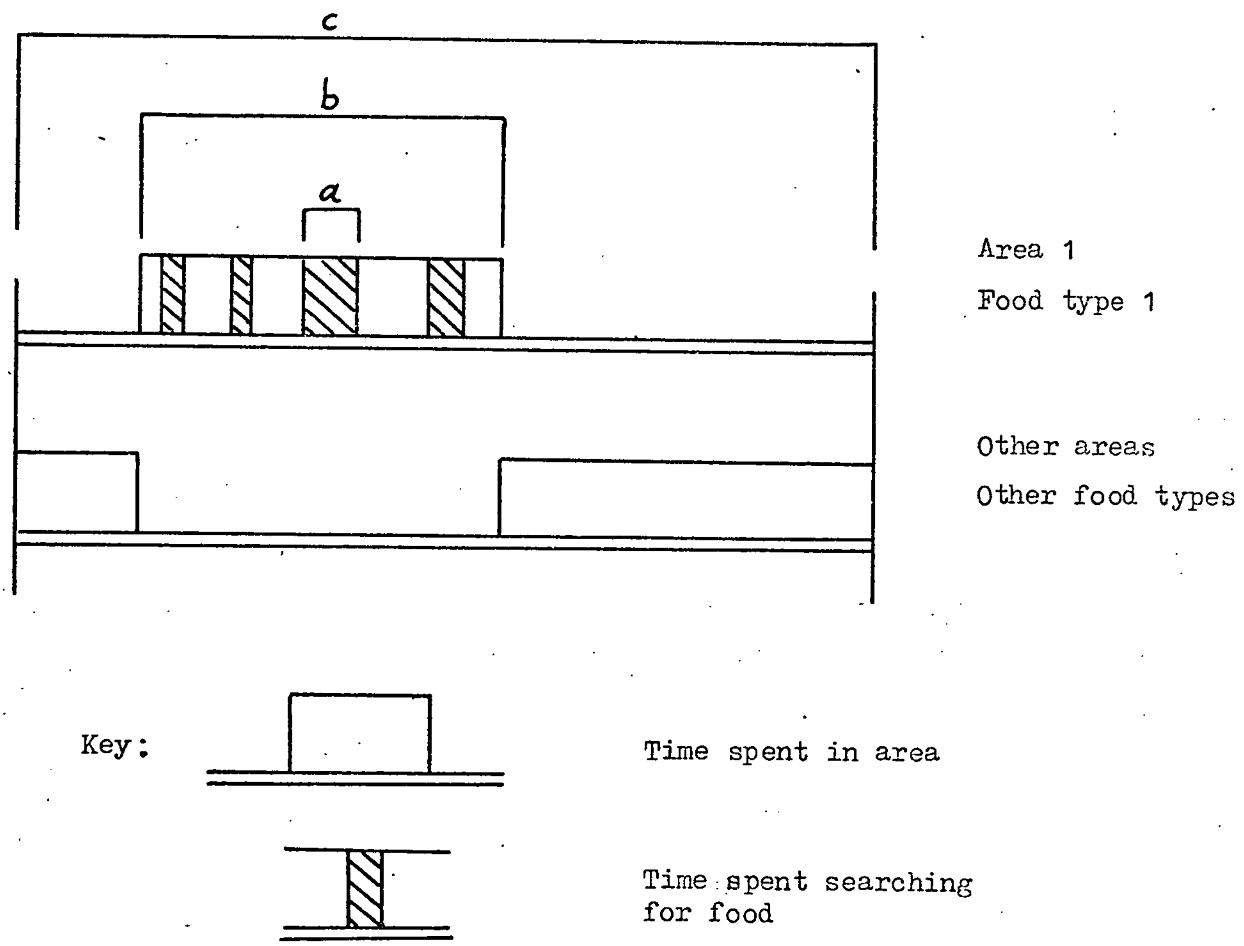
However, it is still necessary to retain the terms "functional response" and "numerical response" to describe on the one hand those situations where one is measuring the rate of attack or eating (number per unit time), and on the other hand the density of the predator/parasite (number per unit area), as a function of food density. In view of this, but taking into account the points raised by Hassell, the following scheme is proposed.

The functional response - rate of eating prey.

a) the functional response during searching periods (see Fig. 2.3-1). This is the rate of eating prey while the animal is actually engaged in searching and handling prey items, that is, when the animal is in a feeding mood and in the feeding area.
b) the functional response during the time spent in a particular food area. Here the rate of eating prey is determined from the number found and the total time spent in the appropriate area.
c) the functional response during very long periods of time. In this case, which involves at least two foods in corresponding areas, the functional response for one of the foods is found from the number of the specific type eaten and the total time spent in all areas.

Fig. 2.3-1

Levels at which the term "functional response" may be used.



The numerical response - predator density.

a) numerical response to spatial variations in food density. This corresponds with the aggregative response.

b) numerical response to temporal variations in food density. This corresponds with the "intergeneration relationships".

The interpretation of spatial variations, in terms of implications for regulation of prey populations, depends on the knowledge relating to specific situations, as to whether the observed spatial variations result from reproduction and mortality, or from movements of individuals. In the latter case, this effect represents at the population level the type of effect indicated in (c) above, where the individual can move between separate areas, except that in the numerical response the different areas contain the same food type, though at different densities.

In the present study, all the determinations of the response are in terms of functional response (c), the most generalised of the three types, and type (b). In both cases, the basic unit of time is the day, so that the functional response is thus expressed in terms of the number of groat grains eaten per day.

The functional response is defined in terms of rate of eating of food items. This represents the end result of many factors which change in relation to food density, and these may be taken as indices of the functional response. For example, in the present study the distance travelled by the animal per day was taken as such an index, and proved to be very useful in indicating the basis for the functional response proper, and in showing how the animal responds at very low densities of groats when too few would be eaten to give an accurate value for the functional response.

2.4 Previous work on the functional response

The close similarity between predation and parasitism, in terms of the similarity of the mechanisms involved, has been pointed out by several authors (Holling, 1959b; Hassell, 1966; Rogers, 1972). For example, in both situations, searching for the prey or host is involved, and in both cases the predator or parasite needs to devote a certain amount of time to handling the prey or host. Despite certain differences between the two processes (a parasite may re-handle a host item, and encounter with a host does not affect the parasites hunger level), consideration will be given here to studies of both processes.

In the feeding context, it is unfortunate that there are not more general terms to apply to generalised feeders, as predator and prey are used in relation to carnivores. When analysing the functional response, it is recognised that there is a continuous range of situations from a predator feeding on mobile prey, to one feeding on immobile prey (Holling, 1959a, 1965), to seed-eating herbivores, to grass-feeding herbivores. Although the analysis of feeding in the literature has been largely confined to the predator-prey situation, the conclusions are equally applicable to a herbivore, assuming that the food distribution fits the assumptions of the analysis; it is only when these assumptions do not hold, as in the case of abundance of all food types (Westoby, 1974), that the analysis must be extended.

Table 2.4-1 summarises much of the work that has been done on the functional response. This table does not claim to be complete, but is intended to show the main areas in which work has concentrated. The table is divided into field studies and laboratory studies; each of these is subdivided into studies on single-food and multi-food situations, and within these the studies are presented in an order based on feeder or parasite taxonomic group; invertebrate, fish, bird and mammal.

The studies have fallen into two main groups. First, field studies have concentrated on birds and mammals using complex food resources. These studies have generally been rather coarse, in that only broad features of the functional response have been determined; exceptions are the studies of Holling (1959a) and Murton (1970), in which accurate determinations of the response over its whole range could be made. In Holling's case, the predator population size could be adequately determined, as could the number of prey attacked and not attacked over a known period. Murton was able to watch individual pigeons feeding under conditions of accurately known food density; his results thus differ from those of Holling in corresponding with my functional response type (a). In most of these studies, the basis of the approach is an interest in the feeding animal and the way that it obtains its food; few of these studies have been motivated by a

Table 2.4-1

Previous work on the functional response

		Single or multi food	Field or lab.
INVERTEBRATES			
Bernays and Chapman (1970)		multi	lab
Burnett (1951)	(paras)	single	lab
Burnett (1958)	(paras)	single	field
Cheke (1974)	(paras)	single	lab
Davies and Reynoldson (1971)		multi	field
Dixon (1970)		single	lab
Hassell (1966)	(paras)	single	field
Holling (1966)		single	lab
Lawton et al (1974)		multi	lab
Morgan (1972)		multi	field
Nelmes (1974)		single	lab
Wratten (1973)		single	lab
FISH			
Beukema (1968)		single	lab
Ivler (1961)		multi	lab
BIRDS			
Buckner and Turnock (1965)		single	field
Gibb (1962)		multi	field
Goss-Custard (1970)		single	field
Heppleston (1971)		multi	field
Manly et al (1972)		multi	lab
Mook et al (1960)		multi	field
Murton et al (1963)		single	field
Murton (1971)		multi	field
Royama (1970)		multi	field
Smith and Dawkins (1972)		single	lab
Tinbergen (1960)		multi	field
MAMMALS			
Arnold (1964)		multi	field
Holling (1959a)		single?	field
Holling (1965)		multi	lab
Hunter (1954)		multi	field
Southern (1970) (indirect reference)		multi	field

(paras) : parasite-host system

desire to elucidate the factors affecting the population dynamics of the food species.

In comparison, the other main line of research, involving laboratory studies of the functional response of invertebrates under single-food conditions, are mainly concerned with the implications of the functional response for the regulation of the population of the prey species. It is perhaps for this reason that Hassell (1966) has advocated that the response to density should be expressed in relative terms: sub-proportional and super-proportional responses, in which the number of prey eaten or hosts found increases slower or faster than increasing density, correspond with the terms "inverse density dependence" and "direct density dependence" used in relation to population regulation. The predominance of invertebrates in laboratory studies arises partly from the large number of studies on parasites, and partly from the difficulty of creating in the laboratory a suitable range of food density conditions for larger, warm-blooded animals.

In all cases, the functional response is limited by behavioural or physiological constraints of the animal. This means that all animals will have a sub-proportional effect on their prey, at least above a certain prey density. In this case, the predator will not be able to regulate prey density through the operation of the functional response alone if prey density rises high enough (Holling, 1965). Davies and Reynoldson (1971) found that predation of triclads was not large enough to regulate the triclad population, and in a similar way Wratten (1973) has shown that the coccinelid beetle, Adalia bipunctata, is ineffective in regulating the lime aphid. In addition, many studies have shown that at least a portion of the rising part of the functional response curve shows a negatively-accelerated rise to the plateau; this will also produce a sub-proportional effect. When the whole functional response curve follows this pattern, it is usually invertebrate species that are involved, though it has also been demonstrated for fish (Ivlev, 1961), and birds (Murton et al, 1963).

Two of the invertebrate responses quoted in the Table, and all of the remaining vertebrate responses, show a portion of the response at low density in which the number of food items taken increases faster than the increase in food density; that is, they show a super-proportional effect. The presence of this positively-accelerated portion of the response curve is found either by determining the complete curve (Holling, 1965), by comparing the response at a small number of density levels (Tinbergen, 1960; Gibb, 1962; Royama, 1970; Smith and Dawkins, 1972), by deductions from experiments indicating that an animal is less willing to take food when the food is scarce (see Krebs, 1974, for review), or by deducing that the individual predator spends more time in areas of higher food density from observations that there are relatively more predators in these areas, (Goss-Custard, 1970). The results from the two invertebrate species are of particular interest, since it has been assumed that the positively-accelerated response can only be generated by a sophisticated learning mechanism (Holling, 1965). Hassell (1966) reports that the percentage parasitism of winter moth larvae by Cyzenis albicans increased with winter moth larval density, which is equivalent to a positively-accelerated response, and Lawton et al (1974) found that the heteropteran Notonecta glauca showed a positively-accelerated response to the density of mayfly larvae (with Asellus present as an alternative food) only when the predator had obtained several days experience of the experimental situation.

There is one report of a predator, the tawny owl, (Southern, 1970), which actually eats fewer voles and mice as the density of these increases. The reason for this is that in early spring, when the prey density is low, ground vegetation is also scarce, so that the owl is able to hunt with high efficiency; as the population increases, the concurrent increase in ground cover greatly increases the difficulty for the owl of detecting and catching the small mammals. This emphasises an important point which must be borne in mind when considering the functional response for a particular food; the observed response represents the net effect of a genuine response to the food itself together with the effect of responses to independent factors. In particular, when the feeder partitions its time between separate areas, it must not be assumed that the observed partitioning of time is solely determined by some feeding strategy. Simple animals show basic taxic responses to environmental factors which will tend to bring them into regions of higher densities of their food, andhigher animals show complex and subtle habitat selection (Wecker, 1964) which may not be related to the immediate food conditions.

In some more complex multi-food situations, the functional response for specific foods cannot be determined owing to the concurrent changes in the densities of other foods. One such example is given in Hunter (1954), which shows changes in the comparative grazing index (an index representing sheep selectivity) over two years for several pasture species. What is required is a method which would permit the information needed to construct the functional response curve for one food, assuming constant density of alternative foods, to be extracted from such sets of data. No such general method exists, though Lawton et al (1974) have developed a restricted method based on Holling's (1959b) disc equation and applied to a two-food situation. Royama (1970) also recognises the role played by alternative foods in affecting a specific functional response, and used such information in a qualitative manner to assist in the interpretation of some of his results. Work on sheep grazing also indicates that one food species may represent more than one food type: the quality of grasses, for example, may change seasonally (Eadie, 1970), invalidating any attempt to find the functional response for the species as a whole.

A further complicating factor is the fact that functional responses determined in the field or in the laboratory are assumed to represent equilibrium conditions (the animal would continue to eat the food at the same level indefinitely if the food density was held constant), when in fact there is rarely any certainty that this is so. Beukema (1968) found two ways in which a stickleback's response to Drosophila larvae or pieces of Enchytraeus worms changes over time. First, the new prey was initially avoided altogether. Second, after this period the distance at which the prey were detected gradually increased over a period of several weeks. Similar delay effects are likely to operate in nature, especially for short-lived plant food species or invertebrate prey species, and especially when prey populations increase and decrease in several areas, but these effects are rarely recognised.

The literature on the functional response of animals thus ranges from the description of broad qualitative effects to precise descriptions of the response. In many cases, the response as observed could include external effects: the density changes of alternative foods, the accidental association of habitat factors with food density, and temporal effects. Multi-food situations present special difficulties, since only rarely is it possible to observe the response for one food when all other foods are abundant; any other situation requires that the functional response for a specific food be expressed by an equation incorporating the density of all foods. The role of the functional response in regulating prey or host population is unlikely to be large, since super-proportional effects are only found for low prey or host densities.

2.5 The modelling approach to the functional response

Goodall (1972) states that: "A model of a system is a representation of it in other terms, often symbolic, and almost always simplified".

A model can be developed to meet some, or ideally all, of a number of objectives (Holling, 1966). It can be realistic, to represent a specific system as closely as possible; holistic, to include all relevant components of the system; general, so that it can readily represent similar systems in a variety of circumstances, by being formulated in terms of common principles; and precise, yielding quantitative answers which can be accepted with a high degree of confidence. Levins (1966) has argued in favour of robustness, or the ability of a model to generate similar qualitative conclusions using different simplifying assumptions. This approach can remove the caveat which applies to the results of most modelling exercises.

Three main approaches have been used in modelling the functional response.

a) Analytical models are general and precise, but lacking in realism. They are formulated in terms of equations which are capable of analytical solution, though the equations readily become intractable if they are expanded beyond the trivial. Examples of this approach can be found in Holling (1959b), Watt (1959), Hassell (1966) and Rogers (1972).

b) Qualitative models may be realistic and general, but lack precision. They may only be capable of predicting the presence or absence of a particular effect, and are usually tested by comparison of results with those expected from a simple analytical model (Tinbergen, 1960; see section 6.2).

c) Systems models may be realistic and precise, but are usually based on specific systems, and may therefore lack generality. By analysing a system at a variety of levels, it is possible to construct a model as a hierarchy of sub-models (Goodall, 1972).

Experimental component analysis (Holling, 1963) describes the process of identifying the key components in a system and defining their interrelationships through experiment. This approach has been used to analyse the functional response of the praying mantid (Holling, 1966), the deer mouse (Holling, 1965), which provided the inspiration for the present study, the wolf spider (Hardman and Turnbull, 1974), and the three-spined stickleback (Beukema, 1968). The approach is discussed in section 5.1.

Section 3. Description of the Response

3.1 Introduction

Holling (1965, 1966) recognised the need to actually describe an animal's functional response to food density, even though the basis of the research may be to analyse the components of feeding behaviour which determine the response. There are three reasons for this, of varying importance to other workers, which are all relevant to this work.

First, a description of the functional response for a particular species can be taken as a basic parameter defining the population processes of the species, in much the same way that one could define, for example, the relation between growth rate of an individual and amount of food eaten. Holling (1965) has commented at length on the role played by the shape of the functional response curve in determining stability between predator and prey populations.

Second, a study of the shape of the functional response curve can be used to make deductions about the underlying mechanisms. Thus, Tinbergen (1960) derived the concept of searching image from the apparent sigmoid shape of the functional response curves obtained from great tits: he explained the fact that fewer prey were eaten at lower density than would be expected by assuming that at these densities the birds were not able to develop the searching image for the specific type.

Finally, knowledge of a functional response can be used for validating a model of the feeding animal, whether the model be based on component analysis or on a theory of the factors governing feeding behaviour. Holling (1966) was able to obtain a good quantitative fit between the functional response curve for the praying mantid, and the curve produced by a mathematical model of the feeding mantid which was entirely based on independently-determined relationships and parameter values. On a cruder, qualitative level, Royama (1970) points out that the sigmoid-shape functional response curve commonly found in birds and mammals is predicted by his hypothetical model for an optimum feeding strategy in a heterogeneous environment. Clearly, however, a purely qualitative agreement between observation and model is less convincing, and in Section 6 I will show that the sigmoid shape is a common prediction of several models of the feeding animal.

Once convinced of the need to describe the functional response, the question then arose as to the best way to measure it. The choice lies between field or laboratory studies, both of which have been used by other workers (Section 2.4). In the case of the small mammal herbivore such as the bank vole, the choice is not difficult to make, since the field situation presents several problems.

First, although the main food of the vole tends to be seeds, berries, nuts and green plants (Watts, 1968; Drozdz, 1966, 1967, 1968), it would be difficult to rule out the possibility that other food items, less easy to measure, were not also being consumed. Changes in the abundance of these other food supplies could distort the results.

Second, it is very difficult to be sure that all items of a particular food source are equally available to the feeding animal, or to provide a measure of availability if they are not. For example, seeds suspended above the ground would differ in availability depending on their height above the ground, while even those on the ground would be more or less accessible depending on the thickness of the surrounding vegetation.

Third, the difficulties in operating such an experimental system would be considerable, both in terms of manipulating the food densities over the required range, and in terms of accurately measuring, on a day-to-day or short-term basis, the actual quantity of the different foods eaten.

Fourth, even if these experimental difficulties could be overcome, the complexity of the system would make interpretation of the results difficult. This complexity would be apparent both in the food supply itself, with several foods whose densities are constantly changing, and in the number of external environmental factors. The amount of data that needs to be collected is exponentially related to the number of different food types and the number of external environmental factors, if a given level of accuracy is required, so that the effort involved in a field approach would need to be much greater.

In addition, if the aim of describing the animal's functional response is to relate it to components of feeding behaviour determined experimentally, it would be desirable if the functional response could be determined under approximately the same conditions as used to investigate the components. Although this is not a general argument against the field approach for describing the response, it is highly relevant when, of necessity, the mechanisms underlying the response are to be elucidated in the laboratory.

Having moved into the laboratory, it is very easy to forget that the ultimate aim is to describe and explain the behaviour of the animal in its natural setting. Indeed, when the response is required purely as input for a practical management study, such as an investigation into the impact of sheep on pasture, it would be necessary to determine the response under natural conditions and to accept the difficulties involved.

But when the aim in determining the response is not to provide input for a higher-level system, but to provide a check on the operation of a lower-level model, then the measurement of the response under artificial conditions is quite justified. The underlying assumption is that the mechanisms governing the functional response are the same in the field as in the laboratory. This assumption is supported by two points. The first is that the voles appear to adjust well to laboratory conditions, as witnessed by the length of time that they live in captivity, their maintenance of body weight and their behaviour. The second is that the problems faced by the animal are the same in the two sets of conditions - when to start eating, when to switch from one food to another, and so on, and so it is reasonable to assume that the same physiological apparatus will be used to solve them. Thus, although the value of a 'start-eating' threshold may change with different conditions, we still assume that such a threshold operates under the new conditions.

Contrary to what one might think, the move to the laboratory can in fact make it easier to solve practical problems. The reason for this is that it is in principle a straight forward matter to determine in what way these more fundamental components behave as a function of those factors which differ between the natural and the artificial situation. The benefit of such a process will then be that it yields a model of general applicability, easily adapted to other situations by adjusting the fundamental components, whereas the description of the natural response under natural conditions, even as a function of these factors, would not permit its extrapolation to a slightly different habitat. The experimental component analysis approach was discussed in section 2.5; it is only used here in support of the decision to adopt a laboratory approach to describing the functional response.

The requirements of an artificial system for measuring the response will be described in the next part. Following that, the results obtained from the 'brushes' system will be presented, as this method was the most successful of several methods tested in meeting the various requirements and in providing a reasonable picture of the vole's functional response.

3.2 The requirements of an artificial system for measuring the functional response of the vole

The requirements of an artificial system can be considered under two headings, those which would need to be met no matter which species of feeding animal was being used, and those which are specific to the bank vole. I shall consider the general requirements first.

The animal should not find more than a small fraction of the food available in the course of the time unit used in the study. In the present case, the time unit was always one day, which means that the experimental set-up must be arranged so that there is a certain amount of difficulty in finding the food, preventing more than say 10% being found in one day.

There are two reasons for this requirement. The first is that, if the vole could find most of the food put down in the course of the twenty-four hours, then the results obtained for the functional response would be meaningless, merely reflecting the current density level, up to the point where satiation would limit intake.

The second reason is that, if more than say 10% of available food is found during a day, then the effective food density may be changed, and a significant exploitation component (Holling, 1966; Rogers, 1972; Hassell and Rogers, 1972) introduced into the situation. The change in food density over the day would make the results difficult to interpret without some a priori knowledge of the functional response itself, which is the thing being investigated in the first place.

There is however one very important qualification to this requirement. There are, in the above paragraph, implicit assumptions that the animal is searching randomly for its food, that all parts are equally accessible and that the animal has a constant probability of covering a particular part, whether or not it has been previously covered. These assumptions are commonly adopted but are not inevitably true (Rogers, 1972). Exceptions would occur if, for example, the feeding animal had a memory of the area already visited and avoided those places in future, if it left some sign in those places when first feeding there (Holling, 1959a; Gibb, 1962), or could decrease the difficulty of covering the area as a result of its first visit. The main method that I used for measuring the functional response, the brushes system (3.4), provided examples in which the last two of these exceptions appeared to be realised. The vole, when searching for food, pushed aside the fine peat scattered on the floor, and forced an opening in the bristles which covered the whole area of food availability. Both these operations could indicate to the vole on a later visit that it has been there previously, while the latter could make it easier to cover the area already searched. This is supposition, but was confirmed by the set-up used for determining the speed of movement of the vole in the same 'brushes' system (section 5.5). Fig. 3.2-1 shows the way the vole used the area during one feeding session: it is clearly non-random, with each run mainly covering a fresh area. Simple observation of the vole showed that when it did travel along the same track twice in one session, it required much less effort the second time. Since it is implicit in the idea of the 'functional response' that effort needs to be expended in order to find food, it follows that, if the vole has already opened up an area and removed the food from it, then the area itself ceases to be part of the test area. Consequently, the density of the food in the remaining test area is unchanged. This means that we can tolerate much higher proportions of the food being found in the course of the time unit. Thus, while the basic requirement

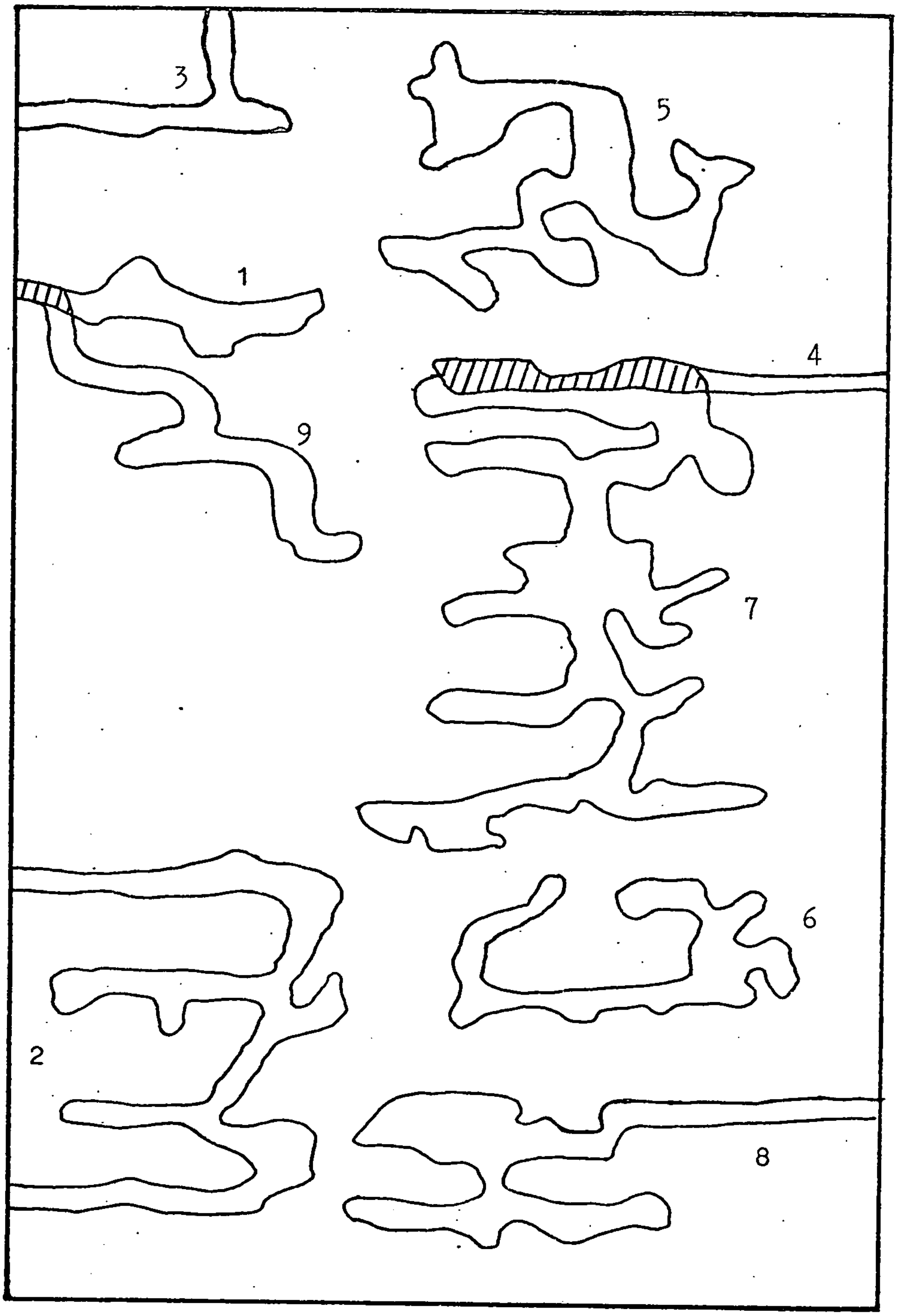


Fig. 3.2-1

Vole's use of brush area during nine consecutive runs.

remains, that the feeding animal should not greatly affect the density of the food supply, this can be qualified in particular cases where the animal searches non-randomly.

There are three basic ways in which this requirement, limiting the proportion of food found per unit time, can be satisfied. The first is to set up the experimental area so that the feeding animal can move around at its normal unimpeded speed and perception of the prey is not interfered with: in this case, the factor limiting the rate at which the animal finds the food is the large size of the area relative to the food density. This approach is practical for slow moving animals, such as a snail, where the size of area calculated to satisfy the above requirements could easily fit into a laboratory system. This was the approach used by Holling (1966) in his study of the invertebrate functional response when the experimental animal was the praying mantid. In this case, the rate at which the mantid could search the area depended entirely on the rate at which its prey, the housefly, entered its field of vision, and at low densities of the prey this rate was lower than the requirements of the predator. However, in the case of small mammals, for example, such a system would call for an impossibly large surface area over which the animal could search. Thus, a vole travelling at 0.5 m/sec. and with a reactive distance of 0.05 m could cover 90 m^2 in every hour of activity, assuming no overlapping of tracks. If this was to represent 10% of the total area, then the experimental area would have to measure 30 m x 30 m. To overcome this problem, the experimental area can either be arranged so that the animal perceives the food item at a smaller distance, i.e. we deliberately reduce its reactive distance and thus reduce the rate at which food is encountered, or we can reduce the speed at which the animal covers the area by impeding its rate of travel. Holling (1965) needed to use one of these methods when studying the functional response of the deer mouse, Peromyscus leucopus, to sawfly cocoon density. Since, when the cocoons were removed, "digging was random, rather than confined to the points where the cocoons were buried", this implies that the deer mouse could normally detect the cocoons from the surface. Since the feeding area measured less than 4 m^2, and since the deer mouse could move freely over the surface, the animal's responsiveness must have been reduced by either the effective area of sawfly cocoon odour being very small at the surface of the peat, or else the recognition success (Holling, 1966) must be less than 1.0. In either case, the effective reactive distance of the animal is reduced.

In the present study, the methods tested concentrated on reducing the vole's speed of movement, rather than decreasing its reactive distance. In fact, the medium used for reducing the speed could have either decreased or increased the vole's reactive distance, depending on the specific combination for rate of diffusion of the aromatic molecules and the vole's smell threshold.

The second requirement is that the experimental set-up should be as similar to the neutral situation as possible. This is more a question of the responses which one is expecting to elicit from the animal, rather than the types of materials used. In the case of the vole, which can burrow, travel across the ground or climb, the choice of situations is potentially quite large, whereas for a grazing sheep, which "moves in a horizontal plane and selects in a vertical plane", (Arnold, 1964) it may be much more difficult to meet this requirement. Smith (Smith and Dawkins, 1972) noted abnormal stereotyped behaviour patterns in blue tits searching for food in his artificial arrangement. Whereas these birds normally search for insects and grubs on the bark of trees and under leaves, they were now faced with row upon row of aluminium foil lids on little cups, and their reaction was to go rapidly along a row flicking the lids off in quick succession. The actual behaviour pattern was similar to turning over a leaf, but the artificially regular arrangement of the potential food source elicited an abnormal response.

Third, it is important to ensure that the unit of time and the unit of food used in the study are satisfactory. For most higher animals, the presence of a twenty-four hour cycle in their behaviour must be allowed for, and this means that the minimum time unit must be one day. In other words, the animal's response to a particular density level is assessed at the end of every twenty-four hours. On the other hand, most higher animals which are suitable for a laboratory work have a life-span measured in months or at most a couple of years, and this means that the duration of the experiment should be kept as short as possible in order to minimise the effect of long-term changes in the animal's behaviour. Therefore the period of one day should also be the maximum time unit as well. The unit of food used, assuming that discrete food items are involved, needs to be chosen so that a reasonably large number are eaten per day at the highest food densities. If not, the resolution of the response at lower densities will be impaired by the relatively large effect of a difference of one item, and by the larger sampling error associated with a smaller number of items taken in the course of the day. In the case of the bank vole the food item chosen as the principal food was the groat (naked oat grain), of which between 50 and 120 would normally be eaten per day when in abundant supply.

The above requirements call for large numbers of food items, distributed in a medium which is difficult for the animal to penetrate, to be handled every day. In order to minimise disturbance to the experimental animal, and to enable several animals to be run simultaneously, the experimental design must be such that the daily procedure is not time consuming. This need for ease of handling played a major role in the designing of the methods I tested for measuring the functional response. In no case did the period in the experimental room itself last longer than one hour in the day, nor did the procedure involve the trauma of chasing the vole into its nest box, since the cover in the area was arranged in blocks, and the vole simply ran from one to the next as each was raised and the food under it recovered and replaced.

Further general requirements can be specified more briefly. The food units should be uniform in size, since although the response is measured in terms of the number of units taken, it is likely that the vole operates on the amount eaten, rather than the number eaten. Conditions should be kept as constant as possible during the experiment, and a period of adjustment to the experimental conditions should be given with no change in the experimental variables. It is advisable that during this time the same recordings should be made as during the experiment proper, both because the disturbance caused by the experimental procedure could affect the animal's behaviour and therefore needs to be kept as constant as possible, and because in this way it can be demonstrated that the behaviour of the animal has settled down to a constant pattern, rather than just assuming that it has.

Consideration also needs to be given to the sequence of food densities provided for the animal on consecutive days. The case in favour of using a cyclical density change is set out in section 3.3.2. In short, the advantage of this pattern is that it approximates more closely to the natural system, and that the change from one day to the next is kept fairly small. If a random sequence of food densities is used, then each density should be maintained for several days, so that the data can be inspected for evidence of any trend following the step change in density. Even in the case of a cyclical change in the food densities, more valuable information can be obtained by having half the number of density levels, and doing two days at each level, rather than having a larger number of levels with no two consecutive days at the same level, again so that any carry-over effect can be detected.

For many small mammals which hoard food, including the bank vole, a more specific requirement needs to be met. That is to ensure that the artificial habitat is not so complicated that hoarded food can not be readily recovered each day. Presumably this did not trouble Holling, since the deer mouse is a carnivore, although its actual feeding behaviour, feeding on cocooned sawfly prepupae, more closely resembles a herbivore. Most voles in his type of experimental set-up would have hoarded grain in the thick peat layer, as indeed tended to happen in the vole's maintenance cage, which had a layer of peat on the bottom. Such a method would thus be impractical for a vole, and the only way to obtain meaningful results from it would be to sieve the whole 0.2 m^3 of peat every day in order to recover the hoarded food. This consideration means that the cover used should be able to be lifted off the floor each day, to expose hoarded food, and that grains hoarded inside it will readily fall through to the floor.

3.3 The brushes system for determining the functional response

3.3.1 Introduction

Several experimental methods for determining the functional response of the bank vole under laboratory conditions were tried. Descriptions of all except one of these methods are relegated to an Appendix (A1), since these earlier methods were either rejected after initial trials, or, in one case, was found to be unsatisfactory after one functional response experiment. In this last case, the vole could find a high proportion of the available groats each day, making the results difficult to interpret since it was not known whether the vole was searching randomly or not. The functional response curve was negatively-accelerated to a plateau, but insufficient levels were used at low densities to detect a possible positively-accelerated section in this region.

The brushes system was devised to satisfy the requirements specified in the previous section and to overcome the difficulties of the earlier methods. In this method, the vole was to search for its food through an area covered by broom heads, with the bristles pointing down. This satisfied the requirement of ease of operating the experiment, since the broom heads could be fixed in blocks and lifted up together. In addition, little debris, apart from some loose or chewed bristles, was left behind on the floor with the grain at the end of each day, so that it was a simple matter to recover the grain left behind. This ease of handling contrasts with the wood-chippings system, described in Appendix A1, in which wood-chippings left behind each day had to be separated by flotation from the grain. Initial trials with the brushes system suggested that it was considerably more difficult for the vole to find food in this situation compared with earlier systems. I therefore divided the available floor area into four sections, so that four voles could be run at the same time. It is not easy to decide whether the vole finds less of the available food in this situation because it could not find more even if it wanted to, or whether it simply decides that it is not worth the effort. But this question is probably not crucial since in any situation we can only measure the animal's response, not the motivation behind the response.

The brushes system turned out to have two unexpected advantages. The first was that, if some fine peat was scattered on the floor, the vole left a permanent record of its movements since the previous day: as it forced itsway through the bristles, it left tracks in the peat which could be seen very clearly when the brushes were later lifted up (Fig. 3.3.1-1). From records of these tracks I could find out how far the vole had travelled the previous day. This gives an alternative measure of the vole's response to food density; this measure may be more precise, in the sense that it is not subject to random sampling effects at low food densities, even though it may not be very accurate, if not all movements are related to food searching. I also could use the track records to get an estimate of the reactive distance of the vole, since this can be calculated from the distance travelled and from estimates of the fraction of the total area covered based on a knowledge of the fraction of food found. This will be described in a later section.

Another advantage of the brushes method was that the same system could be used for measuring the speed of movement of the vole (section 5.5). This was done by placing the brushes on a plate of glass, and observing it from below; in this situation, the whole belly of the vole showed up very clearly against the black bristles, and it only remained to record the vole's movement. This feature is of some importance, since the vole's speed is likely to be influenced by the medium that it has to travel through. It is therefore desirable to use the same material for measuring its speed as for the functional response experiments themselves.

One disadvantage of the brushes system was that it was not uniformly difficult to travel through. First, it was apparently easier for the vole to travel through the bristles along the middle

Fig. 3.3.1-1

View of vole tracks left in the peat, in an area covered by four blocks of brushes.

The close-up view shows how the peat is pushed aside, exposing the light-grey floor.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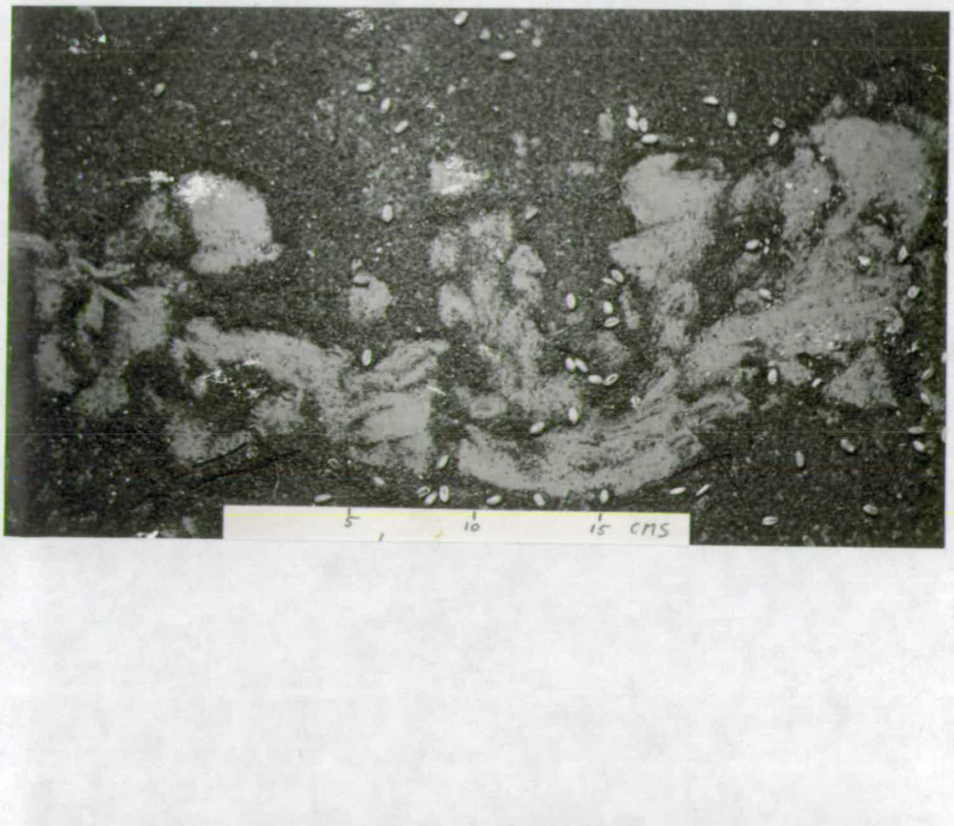
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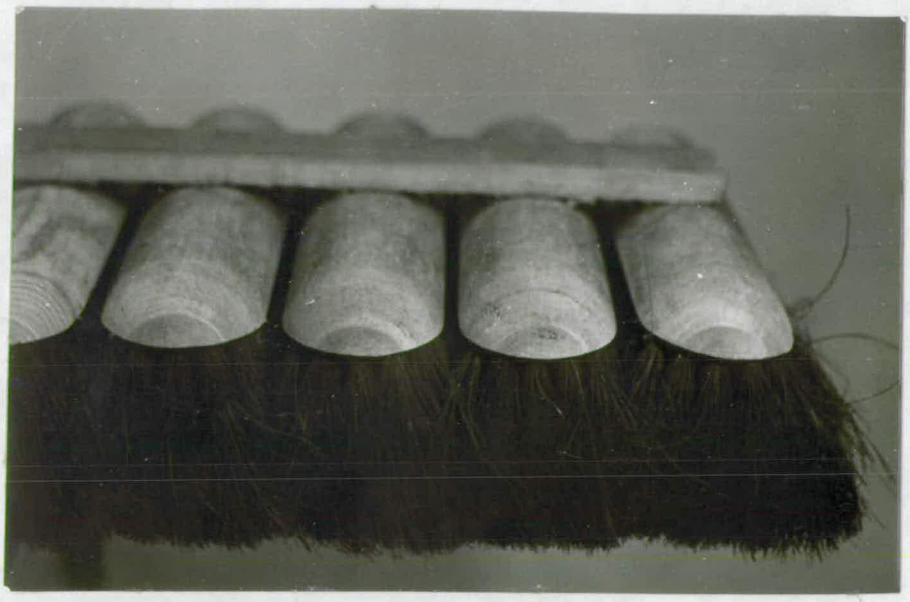
of the brush rather than at the edge, where they were pressed by the neighbouring brush. Second, each vole appeared to have its preferred set of tracks, and after several days it was clear, by looking at the brushes from underneath, that the bristles were parted slightly in these positions. However, in any system, different parts of the area will be accessible to different extents. Even if the food was scattered on a very large flat surface, the animal would need to put in more effort to find food items furthest from its current position. Thus, in no situation of this type can we assume that the fraction of the total food found is directly proportional to the effort put in to searching by the animal; rather, it is only an index of the animal's effort, and the exact nature of the relationship between the index and the actual effort will depend on the type of situation in which the animal is searching.

3.3.2 Method

The brushes used were ordinary 11½" (29cm) household broom-heads, with a wooden base and black Mexican fibre bristles. The brushes were fixed in blocks of twelve by nailing the bases onto a board at 7.5 centimetre centres (Fig. 3.3.2-1). A gap of approximately 0.5 cms was left between the brush bases, to avoid compressing the edge bristles too much. Each block measured 30 cms by 90 cms, allowing for the spread of bristles around its periphery. The bristles, which were 7 cms long, were in direct contact with the floor, as there was no other support for the block.

Fig. 3.3.2-1

General view and a close-up of a block of 12 brushes used in the functional response experiments.



Each experimental area consisted of eight blocks, arranged in two groups of four, with each group measuring 120 cm by 90 cm. Viewed from underneath, each group would appear as a continuous bed of bristles, with no gaps between the blocks. One block in each group touched an end wall of the experimental area, and there was a gap of 30 cm between the two groups in the middle of the room. Fig. 3.3.2-2 illustrates the lay-out.

The experimental room measured 484 cm by 272 cm, giving four experimental areas of 121 cm by 272 cm. The areas were partitioned using $\frac{1}{2}$-inch chipboard 40 cm high, and capped by a continuous band of inverted Manilla files, fixed by adhesive tape to the chipboard, giving a total height of 60 cm. The partitions were made higher at those points in the room were they intercepted electric wall heaters, which stood 30 cm off the ground, as it was possible for a vole to jump on to these from the top of a block of brushes. The floor was covered with plastic sheeting, so that the vole would travel over a surface similar as regards friction to the glass used in the speed-of-movement experiments.

The room was lit by two 60 W lights, switched on for eight hours from 0900 to 1700. Temperature was controlled at 16°C; the temperature was recorded for four weeks on a chart recorder, and during this time stayed within the limits of ± 1°C. No attempt was made to control or record humidity.

Each area had a nest-box, measuring 6 cm by 10 cm, and 5 cm high. Initially ample bedding was supplied with the nest-box, though it was not replaced if moved out at a later date by the vole. Water was supplied in a large plastic water bottle,

Fig. 3.3.2-2

Arrangement of brush blocks in the experimental area. This shows the arrangement for these sessions using a double area (s3, s4). In the other sessions, a partition was placed from left to right.

which rested between two brushes on top of a block near the middle of the room, near the nest-box.

Grain was prepared by visually selecting uniform grains from stock. For both wheat and groats, grains were rejected if they were broken, considerably smaller than average, or still had a husk. The average weight of the groat grains used in the functional response experiments was 28 mg, and that of the wheat 54 mg.

For the purposes of data recording, each group of four blocks was treated separately; in addition, the grain in each hoard was kept separate, as was the grain left behind in the nest-box.

The first part of the daily procedure involved separating the grain recovered the previous day from any fibres and peat collected with it. First, each lot was sieved in a 2 mm wire sieve, to remove most of the peat and some of the fibre. Then, the remainder was put into a flat-bottomed tray, and the lighter peat and fibre separated slightly angling the tray, and blowing up the slope as the grains rolled down. Finally, the grain was sieved in a 3 mm wire sieve which let most of the groats fall through; the remaining groats were picked out by hand, as were any chewed wheat grains. The number of groat, wheat and chewed wheat grains were then counted and weighed to the nearest mg.. This degree of accuracy was used since an accuracy of tens of mg is too coarse if only one or two seeds are being weighed. The grains were counted as well as being weighed since the basic response of the vole was being measured in terms of the number of grains eaten, and it would only increase the variability if this was estimated from the weight eaten and the mean weight of the grain. Moreover, when a large amount of food was put down, even small changes in the mean weight per grain, due to humidity changes, would cause a large error in an estimate of weight eaten based on the difference between weight put down and weight recovered.

The grain required for the current day was taken from a stock consisting of grain previously recovered plus freshly-prepared grain. Again, the grain for the two halves was counted and weighed separately. This meant that the grain was allocated equally to the two halves of the area, and that more information could be obtained about the way that the vole exploits the total area.

Each area was dealt with in turn. First, the grain from the nest-box was collected and replaced by the new lot; this avoided disturbing the vole later on if it went there after being flushed from the brushes. Then the blocks from one side were lifted to the other, and a record made of the tracks on a plan of the area. All the material on the floor was placed in a 2 mm metal gauze sieve, and the peat sieved back over the area; the contents of the sieve being transferred to the appropriate container. If the number of grains to be put down was small (less than about 15) the grains were allocated to positions on the floor using random numbers; these indicated under which block, and which brush in that block, the grain should be placed, subject to the constraint that a grain could not be placed under the two end brushes of each block. If the number of grains was larger, the grain was scattered by hand as randomly as possible, again leaving a band free of grain around the periphery of the area; this was to prevent the vole picking up grains without really entering the area. The method of distributing the grain is open to criticism, but the alternative, of using random numbers, was ruled out by the large numbers involved: on some days over 2,000 groats were put down. It also appears, from statistical tests done on scattered grains (Appendix A2) that the distribution was in fact reasonably random, and it is likely that any bias will be similar at different food densities. There was, however, evidence for lower groat density in a peripheral 10 cm strip.

The process was repeated for the remaining areas, finally checking on the water bottles.

Table 3.3.2-1 lists the experiments that were done with the brushes system. Each experiment is denoted by a code which indicates during which session the experiment occurred (S1-S6), and in which area the experiment was conducted (I-IV). Note that in sessions S3 and S4, areas I and II were combined, with one vole in the joint area, as were areas III and IV.

The groat distribution was always pseudo-random, and in most cases the density was uniform over the area. The standard situation was for the density to be changed in a cyclic manner, either starting at a high density, gradually changing to a low density and rising to a high density again (high-low-high), or the other way around (low-high-low). The density was changed in a step manner, with the vole being kept at each level for two days. There were between six and eight density levels, including zero density, and each level represented an approximately two-fold increase or decrease on the previous level. This procedure, which

Table 3.3.2-1

Summary of functional response experiments

Experiment	Date	Vole	Groat Distribution	Wheat Distribution
S1(I)	17/10/72 -23/11/72	4D	low-high-low	nest-box
S2(II)	"	4P	"	"
S1(III)	"	4Z	"	"
S1(IV)	"	4AD	"	"
S2(I)	24/11/72 -19/12/72	4D	low-high-low	"
S2(II)	"	4P	different dens. over area	"
S2(III)	"	4Z	random sequence	"
S2(IV)	"	4AD	low-high-low	under brushes
S3(I+II)	1/2/73 -6/2/73	5U	high-low	nest-box
S3(III+IV)	22/1/72 -16/2/73	4Z	low-high-low	"
S4(I+II)	28/2/73 -6/4/73	5U	low-high-low	"
S4(III+IV)	28/2/73 -6/4/73	5J	high-low-high	"
S5(I)	6/6/73 -10/7/73	6		"
S5(II)	6/6/73 -10/7/73	60	high-low-high	"
S5(III)	6/6/73 -11/7/73	6N	low-high-low	under brushes
S5(IV)	6/6/73 -13/7/73	6V	high-low-high	"
S6(I)	11/7/73 -8/8/73		mainly one groat density, with changes in groat size and wheat distribution	
S6(II)	11/7/73 -8/8/73	6W	"	"
S6(III)	12/7/73 -8/8/73	6N	"	"
S6(IV)	14/7/73 -8/8/73	6V	"	"

gave a maximum density thirty-two to one hundred and twenty-eight times greater than the lowest non-zero density, was designed to include both those densities where the vole would be most sensitive to change and densities so high that any further increase would not be expected to cause more to be eaten. Assuming that a vole could eat one hundred grains per day, and that it could potentially exploit 50% of the area, this meant that the highest density should be around 400 grains; and, if the vole was to eat say 10%of its maxumum intake at the lowest non-zero density, then there should be about 20 grains at this density.

A cyclic change in density levels was chosen as the basic pattern for two reasons. First, this was meant to be more realistic as a representation of the natural situation than a random sequence of density levels; however, I did use a random sequence in S2 (III) for comparison with Holling's investigation of the functional response of small mammals (1965). Second, this pattern means that the change in densities will be more gradual, thus reducing the possibility that a vole's observed response to a new density is due to the change itself rather than to the actual density. This view turned out to be justified by some cases where larger step changes in density were used. Finally, I had to allow for the possibility that there might be gradual changes in the vole's motivation over the course of the experiment, so that a better idea of the vole's response would be obtained if similar densities were close in time.

In one experiment, S2(II), the density was not the same in different sections of the area; this was to test Royama's concept

(1970) that response to density is related to the profitability of searching in different areas. S6 was devoted to two other aspects of the vole's response: the effect of changing the mean weight per seed of groats, and the effect of changing the distribution of wheat, the alternative food.

The wheat was either placed in one pile, usually in the nest-box, or else scattered at high density (1600 grains per area) under the brushes; this was to simulate the two ways in which an alternative source of food may be available either mixed with the preferred food or spatially separate. In an attempt to reduce variability, all voles chosen for these experiments were adult males, which had shown a high preference for groats (greater than 80%) when given an ad lib supply of wheat and groats in the maintenance cages.

3.3.3 Treatment of data

It will be evident from the fore-going section on methods that these experiments were not very efficient at generating data, because of the requirements of space and effort; only four voles could be used at any one time, with the daily procedure taking at least three hours. In addition, as each session typically lasted a month, this meant that only a limited number of vole-sessions could be fitted into the ten months available for this series of experiments. In fact, twenty vole-sessions were conducted. Consequently, a decision had to be made as to whether to go for replicability of one experiment, or to investigate a wider range of conditions and sacrifice replication.

I decided on the latter course, since I was basically interested in discovering what voles could do under various conditions, not what the average vole did do under a particular set of conditions. This meant that the possibility of a quantitative verification of an eventual model was being sacrificed to a broader basis of qualitative verification; the model should be potentially capable of producing the observed types of response, even if the model's response for the average vole could not be compared with the actual response of the average vole.

The decision to put each vole through a complete session, rather than to keep each vole at just one density and average the results, was also based on the limited number of voles that could be used, together with the known variability of voles under experimental conditions. This meant that each vole was to be its own control and its own replicate, a procedure followed by all known investigators of vertebrate functional response, whether those looking at natural situations (Tinbergen, 1960; Royama, 1970), or those using laboratory experimental methods (Holling, 1965; Smith and Dawkins, 1972).

This approach has the following implications for data handling. First, the statistics used will be basically descriptive; this especially applies to comparison of data obtained from the individual vole, due to the lack of independence. Second, when data for several voles is lumped, this will need to take the form of lumping the response of the voles to a given change in conditions (for example, expressing the response to a step change as a fraction of the value before the step), rather than averaging the values obtained before and after the step change, and looking to see if there was a significant effect. In this latter case, the variability in the before-and-after data may mask any real effect, even though each vole may be affected to the same degree. Thus, in comparing the results obtained from different voles for the same set of conditions, the data will be reduced to some arbitrary standard.

In the following sections, three methods will be used for doing this. The first involves expressing the data as a percentage of the maximum obtained by each vole for the period being considered; this artificially depresses the data for those voles which happened to have an unusually high value on one occasion. In the second method, the data is expressed as a percentage of an arbitrarily-defined plateau value, for those cases where the vole is kept under the same conditions for several days before or after a step change; this method can magnify values above the plateau value. The term "plateau value" is explained in section 3.4.4.1. Finally, the data, (for example, amount eaten or distance travelled), can be summed over the period under consideration, and the value for any one day expressed as a percentage of the summed data.

3.3.4 Results

3.3.4.1 Initial adjustment to brushes

This section uses various indices of the vole's behaviour to estimate how long it takes the vole to adjust to the new environment. This meant keeping the vole under the same conditions from one day to the next during its initial acclimatisation. Since it can be expected that the vole would adjust fairly rapidly, this period was short - five to seven days. This does not preclude the existence of longer-term changes, due to changes in the vole's internal motivational state or changes in for example the difficulty of penetrating the brushes, but these will be considered in a later section.

In view of the inherent variability of data of this type, plus the fact that there would not be many values at the plateau level, it was necessary to establish an arbitrary criterion for the plateau. This was formulated as follows: the plateau starts with that value which has a lower value following it, not necessarily straight after. This implies a rise to the final level, and this would be expected for all the indices chosen; there was no evidence against this. This criterion is illustrated in Fig.3.3.4.1-1, which shows the day on which the plateau is deemed to start, for hypothetical series of data.

Table 3.3.4.1-1a summarises the data, showing the number of days before the plateau for the various indices. In Table 3.3.4.1-1b, I have summarised the number of instances in which 0, 1, 2 or 3 days elapsed before the start of the plateau region, together with the number that would be expected if there was no

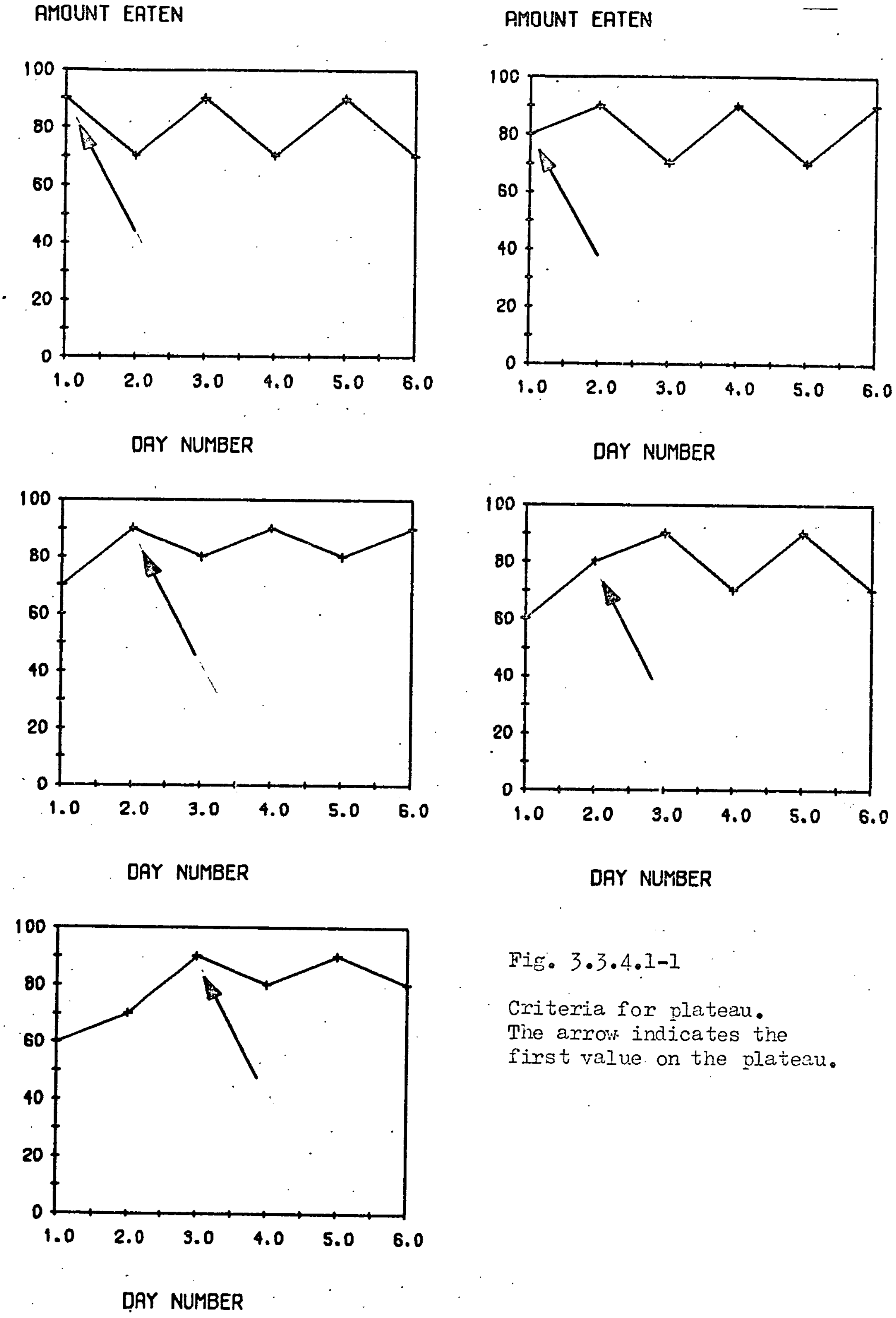


Fig. 3.3.4.1-1

Criteria for plateau.
The arrow indicates the first value on the plateau.

Table 3.3.4.1-1a

Number of days before the plateau level is reached for new voles

Session	Vole	Total weight eaten	Total distance	Groats per unit distance	Period of constant conditions
S1(I)	4D	2	2	0	7
S1(II)	4P	1	3	1	7
S1(III)	4Z	3	3	3	7
S1(IV)	4AD	1	1	2	7
S3(I+II)	5U	2	2	1	5
S3(III+IV)	4Z	0	1	-	6
S4(III+IV)	5J	1	0	1	7
S5(I)	6H	2	2	-	7
S5(II)	6O	2	1	0	7
S5(III)	6N	1	1	-	7
S5(IV)	6V	1	0	0	7
S6(II)	6W	1	0	1	5
Mean		1.42	1.33	1.00	

Table 3.3.4.1-1b

Observed and expected number of voles showing stated number of days before the plateau

Days to equilibrium	Total weight eaten		Total distance		Groats per unit distance	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0	1	10.2	3	10.2	3	7.7
1	6	1.5	4	1.5	4	1.0
2	4	.2	3	.2	1	.2
3	1	.06	2	.06	1	.06

trend towards a plateau, and if the period of constant conditions was characterised by only random variation in the indices. For example, if the period of constant conditions lasted for 5 days, then the probability that the first day will have a lower value than any of the rest (i.e. that there is one day before the plateau is reached), is 1 in 5, or 0.2; and the probability that there are two days before the plateau is reached is reached is 1/5 x 1/4 or 0.05.

The figures given take into account the fact that the number of days under constant conditions ranged from five to seven.

a-Total weight eaten

All but one vole reached the plateau level by the third day, and the average was 1.4 days before equilibrium. This effect is shown in Table 3.3.4.1-1b to be significantly different from that expected according to the null hypothesis of no true plateau and random variability of data points: eleven of the twelve voles took one or more days to equilibrium, whereas only 1.8 would be expected according to the null hypothesis.

It seems likely that this delay in adjusting is not due to the time it takes for the voles to learn about their new situation. Rather, it seems to be an example of a common phenomenon with laboratory animals, a general shock reaction at being transferred from a familiar to an unfamiliar set of conditions.

In Fig. 3.3.4.1-2, I have plotted the value for one day against the value obtained for the subsequent day; days prior to the

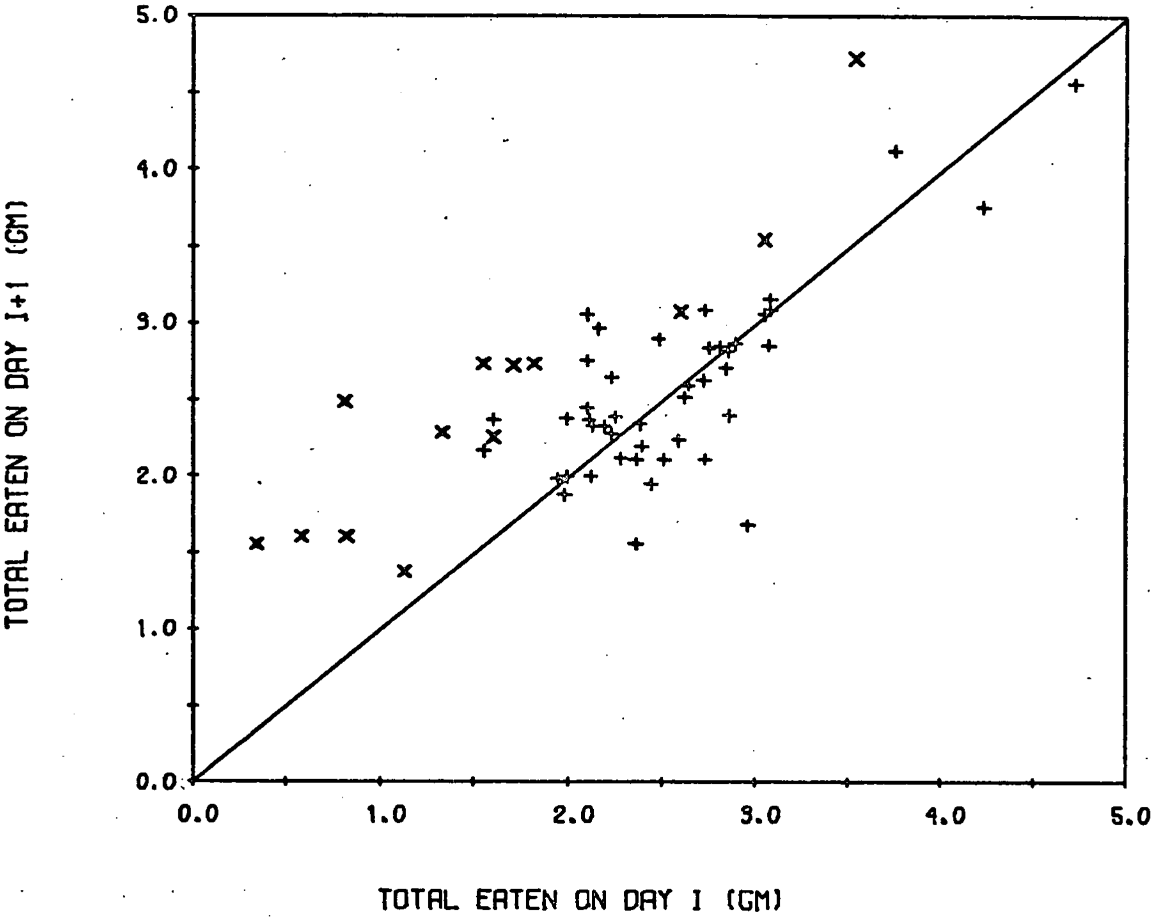


Fig. 3.3.4.1-2

Relationship between total amount of food eaten on consecutive days

× : Pre-plateau days
\+ : Plateau days

plateau are distinguished by a cross. It is apparent that, apart from supporting the criterion used for separating pre-plateau days, the graph shows that the idea of plateau is a valid one: the associated data points are evenly distributed around the 45° line.

b- Total distance travelled

Again, most of the voles failed to reach the plateau on the first day, nine of the twelve instead of the 1.8 expected. Similarly, Table 3.3.4.1-1b shows the same type of pattern as for total eaten, and therefore does not agree with the idea that each vole has a constant probability of reaching the plateau on each day. However, the mode is not so pronounced as in the previous case.

The reason for this can be deduced by comparing the first four cases in part (a) of the Table, when the brushes had not been used extensively, with those of the remaining sessions. The first group averaged 2.25 days before reaching the plateau, while the latter group averaged 0.88 days. This can be put down to changes in the difficulty of penetrating the brushes, with latter voles being able to move more readily through those parts of the brushes used more frequently by previous voles.

Fig. 3.3.4.1-3 shows that the relationship between preceeding and succeeding days is similar to that obtained for total weight eaten. However, it is clear that the variability in the data is larger. This variability appears to be basically due to a difference between voles, as the

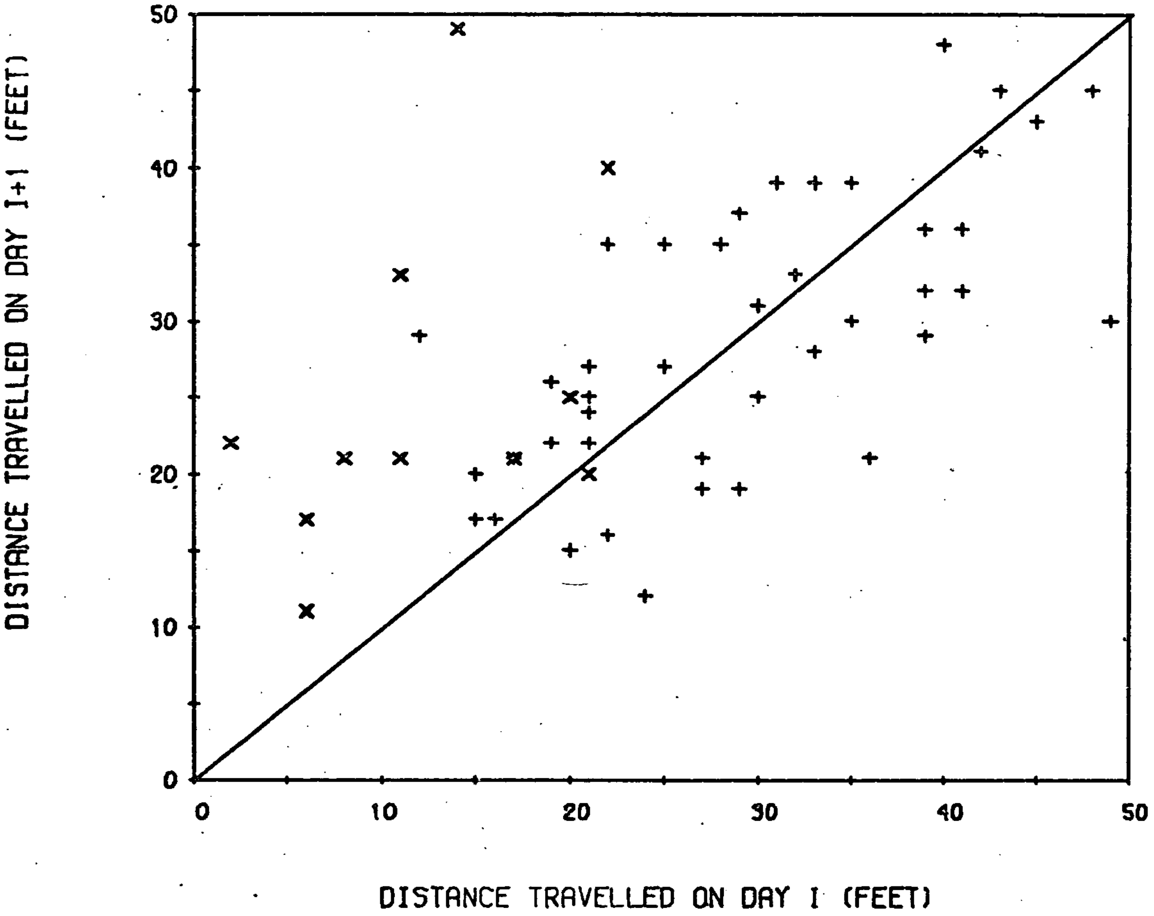


Fig. 3.3.4.1-3

Relationship between distance travelled on consecutive days.

× : Pre-plateau days
\+ : Plateau days

limits of the data for the plateau values (16 to 42 units) is relatively larger than for weight eaten (1.9 to 3.0 gms). Some idea of the variability within voles can be obtained by considering that fraction of the plateau values which lie outside the two dashed lines; these lines include those points where the succeeding value differs by less than 25% of the preceeding value. In the case of total weight eaten, 7 of the 46 points lie outside this range, while for the distance data the figures are 13 of the 43 points: this difference is not significant ($Chi^2 = 1.8$). Again, this graph indicates that the plateau values fall evenly around the 45° line, confirming the absence of trend after the initial adjusting period.

c- Groats per unit distance

The previous two indices of the vole's adjustment deal with aspects of its activity. The present index deals with a measure of the vole's perception; specifically, its ability to detect food as it moves through the brushes. This assumes that all movement is related to searching for food, and, if this is so, then we would expect to find that the vole finds more groats per unit distance as it becomes used to searching for food in this situation, if there is any trend with respect to time. While there is no direct evidence to support this assumption, its conclusion is supported by the observations described above, showing that the distance travelled tends to increase with time; if there is any movement not directed to searching for food, it would be expected to occur in the later days, but this in turn should decrease the vole's searching efficiency, not increase it.

Table 3.3.4.1-1a,b show that the mean number of days to the plateau is 1.0, lower than the two previous cases; it can also be seen that more voles take one or more days to reach the plateau than would be expected by chance, but that this again is not so marked. Note that only nine voles are considered, since, in three cases, the voles adjusted to the area with no groats under the brushes.

Fig. 3.3.4.1-4 supports the contention that this index was not influenced to the same degree by the initial adjustment period. The points representing the pre-plateau period are much closer to the origin than in the previous two cases.

The decile limits for the plateau values (1.5 to 6.0) are relatively larger than in the two other cases. Again, this probably reflects a difference between voles, since the number of points outside the range of 25% variability (11 out of 38) is not significantly different from the previous cases.

d- Conclusion

The above results have shown that there is an initial adjustment to the brushes situation, and that this adjustment is paralleled in three separate indices. However, it is clear that the period of initial adjustment was completed before the end of the acclimatisation period; according to the criterion of the plateau level used above, no vole had an adjustment period greater than three days, and no index had a mean adjustment

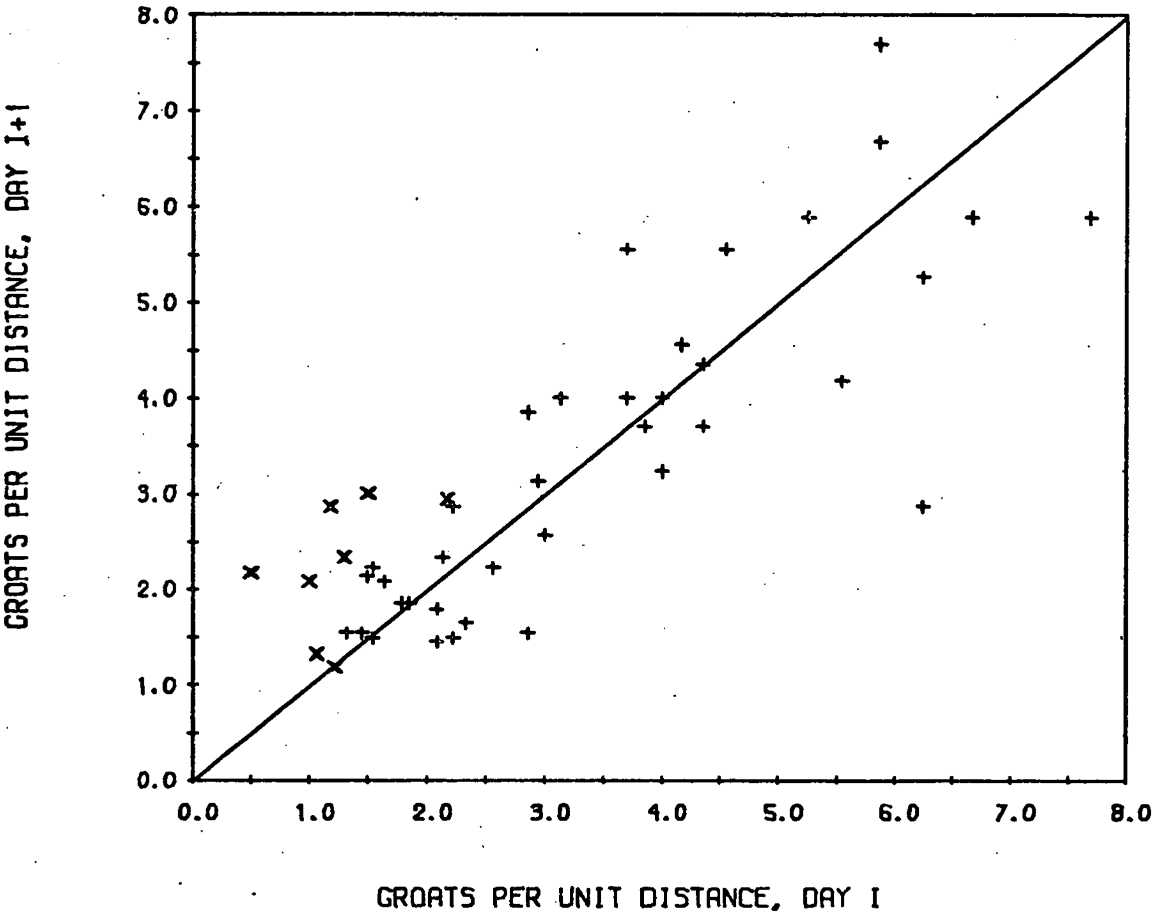


Fig. 3.3.4.1-4

Relationship between efficiency of searching on consecutive days

× : Pre-plateau days
\+ : Plateau days

period greater than two days.

It seems likely that the reason for the initial adjustment varies according to the index being considered. The adjustment in total weight eaten is probably due to the shock of being transferred from familiar to an unfamiliar environment. However, the adjustment period according to the other two indices is probably related to the need for the vole to learn about its environment, modified by the extent to which the brushes have been used before.

It appears that the index involving the perception of groats (or, more precisely, the response of the vole to a perceived groat) is less sensitive to adjustment than the two indices involving the activity of the vole.

It is not surprising that, once the plateau has been reached, the measure of total weight eaten is the least variable between voles of the indices. We would expect the various voles to differ to a greater extent in their behavioural rather than their physiological responses. We would also expect this to apply to the individual animal at different times but the indications are that there is little difference in the day-to-day variability according to the different indices.

3.3.4.2 Long-term Changes

The previous section has dealt with equilibrium in the short term. Each session in this course of experiments has, however, lasted about a month, which forms a considerable part of the life of a vole. It is therefore to be expected that long-term changes could take place in the response of the vole, as indeed has been shown in the case of voles kept under constant conditions (Section 4.4, 4.5). Although the basic schedule for the experiments on functional response was designed to minimise the effect of such long-term changes, it is nevertheless desirable to check for their presence, and, if they do exist, the direction of the change, especially as part of the analysis of the response involves comparison of the two sides of the density function, the part of rising density with the part of falling density.

There is a certain problem here, in that subsequent measurements under the initial conditions lasted for only two days, so that these measurements could still be responding to the immediately preceeding conditions. It is unlikely that this artefact completely accounts for the apparent long-term changes, since there is little evidence that the second of the two measurements is closer to the initial plateau level.

In addition to the previous three indices, I have included an additional index, the weight of groats eaten as a percentage of total weight eaten. The first part of the analysis looks at the lumped data for all voles, and attempts to find if more of the data points are outside the range of the values for the plateau period than would be expected by chance. If there are five days in the initial equilibrium period for a particular vole, then the probability that any one subsequent value is greater or less than the plateau range, assuming complete randomness, is (2 x 1/(5+1)), or 0.4; then, if there are four subsequent days under the same conditions, we would expect

(0.4 x 4), or 1.6 days on average outside the initial range. The days expected to lie outside and inside the plateau range is then summed for all voles, and compared using Chi^2 with the observed numbers.

Table 3.3.4.2-1a summarises the results of this analysis. In all four cases, more days fell outside the range of the plateau period than would be expected by chance, and for two indices - total eaten and percentage groats eaten - the difference is highly significant. These results indicate that in at least two of the four indices, all the days under the same conditions do not form a homogenous collection. It now remains to see if this is due to an increase in variability of the data, which seems unlikely or whether it indicates the presence of long-term changes. Table 3.3.4.2-1b analyses the percentage change from one day to the next for the initial plateau period and the subsequent period under the same conditions. The data is expressed as the number of transitions lying inside or outside a given limit for percentage change for the two periods. Chi^2 analysis shows that there is no evidence for more transitions in the subsequent period to lie outside the specified limits, and so we can conclude that variability does not increase as the experiment progresses.

It therefore follows that the data for the subsequent period tend to fall outside the range for the initial equilibrium period because of long-term changes. Table 3.3.4.2-2 analyses some aspects of these changes. The data is based on the percentage change in each index from the initial plateau period to the subsequent period. For each index, the Table shows the median value for both the actual data, and the data expressed in absolute

Table 3.3.4.2-1a

Number of subsequent days within and outside the range of the plateau period

	No. of values inside range		No. of values outside range		Chi^2
	Obs.	Exp.	Obs.	Exp.	
Total eaten	17	26.86	28	18.14	8.98
Distance	22	27.61	23	17.39	2.94
% Groats eaten	19	28.51	25	15.49	8.88
Groats/unit dist.	21	25.4	21	16.6	1.93

Table 3.3.4.2-1b

Number of transitions for plateau period and for subsequent period lying inside and outside specified percentage change limits.

		Plateau period	Subsequent period	Chi^2
Total eaten	Inside 10%	18	19	
	Outside 10%	18	10	1.59
Distance	Inside 16%	13	13	
	Outside 16%	23	19	.21
% Groats eaten	Inside 10%	28	19	
	Outside 10%	13	9	.10
Groats/ unit dist.	Inside 16%	16	16	
	Outside 16%	12	16	.27

Table 3.3.4.2-2

Long-term changes in the functional response experiments.

	Percentage change over course of session for:			
	Total weight eaten	Distance travelled	Groats per unit distance	% Groats
Values for individual voles, ranked separately for each index by increasing absolute value	-6	-4	+5	-1
	-11	-4	-8	-2
	+12	+9	+11	-3
	+13	+11	-11	+8
	-13	+13	+12	-9
	-19	+14	-16	-15
	+22	+40	+29	-23
	+33	+42	+32	+25
	-39	+58		+43
	+43			
Actual median	+3	+13	+7	-2
Absolute median	16	13	11	9

form, that is, without taking account of the direction of change.

Two things are apparent from this Table. First, in only one index - distance travelled - do voles show a consistent trend, tending to travel further per day towards the end of a session. This is reasonable, since it is known that each vole develops a preferred set of tracks. The other indices show changes equally in both directions, implying that the changes are due either to random changes in the index, or changes in the animal unrelated to the experimental situation, rather than being caused by some long-term effect of the brushes system. Second, it is clear that the reason for the significance of the test for long-term changes is that a few voles showed very large changes, rather than all of them showing medium changes.

3.3.4.3 Response to step decrease in groat density

The introduction of a step change in the density schedule can give a new insight into the mechanism of the vole's overall functional response. This is because it deals with the dynamic properties of the response, rather than with the response under constant conditions. To the best of my knowledge, Holling is the only investigator to have included a dynamic property into a functional response model, when he considers the role of learning, particularly with reference to the decay of the learnt response when the preferred food is removed (1965). This aspect of his work is considered in detail elsewhere, but can be summarised briefly as follows: in relation to a preferred food, contact with that food increases the vole's response to it, and absence of contact causes a decrease in the operational measures of the response. This decrease is modelled as an exponential decay of the learnt function.

Before the decrease in density, each vole was kept for several days at a fairly high density. The mean distance travelled during this period was taken as a reference value of 100%, and the subsequent values expressed on the same scale. In Table 3.3.4.3-1 the response of the vole is recorded as a change in percentage points from the initial equilibrium value of 100% for the step change itself, and on subsequent days as a change from the previous day. In this way, all voles are reduced to the same initial reference point, and subsequent changes should be comparable.

It is apparent from the Table that on the first day of the reduced density, the distance travelled increases by an average of 35 percentage points over the equilibrium value. On the next day there is an average drop of 43 percentage points from the previous day's high point. A simple sign test indicates the significance of these trends. The mean percentage points changes on the next two days are +5 and -2 respectively, and no trend is discernible.

It therefore seems that the reduction of groat density to zero results in increased activity on the first day, followed by a steady low level of activity on subsequent days. These results are contrary to the findings of Holling's apparently analagous experiment, in which he recorded the number of holes

Table 3.3.4.3-1

Response to step decrease in groat density, measured in terms of distance travelled.

Experiment	Change in Density	Percentage Points Change Equilm. - Day 1	- Day 2	- Day 3	- Day 4	Max.
S1(I)	400 - 0	+16	-56	-8	-9	164
S1(II)	400 - 0	+62	-58	+4	-7	218
S1(III)	400 - 0	+74	-99	+12	-23	213
S1(IV)	400 - 0	+38	-47	-17	+33	185
S2(III)	200 - 25	+36	-18			140
S2(III)	400 - 50	+54	+8			190
S2(III)	100 - 0	+5	-23			124
S2(III)	400 - 100	+56	-5			190
S4(I+II)	512 - 0	+51	-72	+9	-5	175
S6(II)	200 - 0	+5	-39	-13		105
S6(IV)	200 - 0	+8	-25	+51		128

dug by a shrew searching for sawfly cocoons after the food had been removed, and found that the rate of hole digging decayed exponentially with time. However, this is probably a poor index of actual searching effort, since the shrew normally only digs when it has detected a cocoon, and the discrepancy should not concern us. In fact, the parameters for Holling's model can be adjusted to produce the effects described above.

Turning now to the factors affecting the magnitude of the step change and the subsequent level of activity, I need to define an index for the maximum distance travelled by a vole during the course of the experiment and this is taken as the average of the three largest values for distance travelled obtained in one series, expressed on the same scale as before, i.e. with the pre-step equilibrium taken as 100%. It is assumed that during the course of the experiment the vole does in fact show the maximum activity that he could show.

The magnitude of the step increase on the first day is likely to be determined by the size of the pre-step activity, (relative to the maximum that the vole could show), which itself will be a function of the groat density during this period and the nature of the vole's functional response. There is a strong correlation between the size of the step increase and the maximum possible increase (Fig.3.3.4.3-1), with the former averaging 0.55 of the latter. Thus, when the groat density is high, and the vole is not searching near the maximum, the step increase is quite large, but when the groat density is intermediate, the the vole is already travelling near the maximum distance per day, the size of the step increase is smaller.

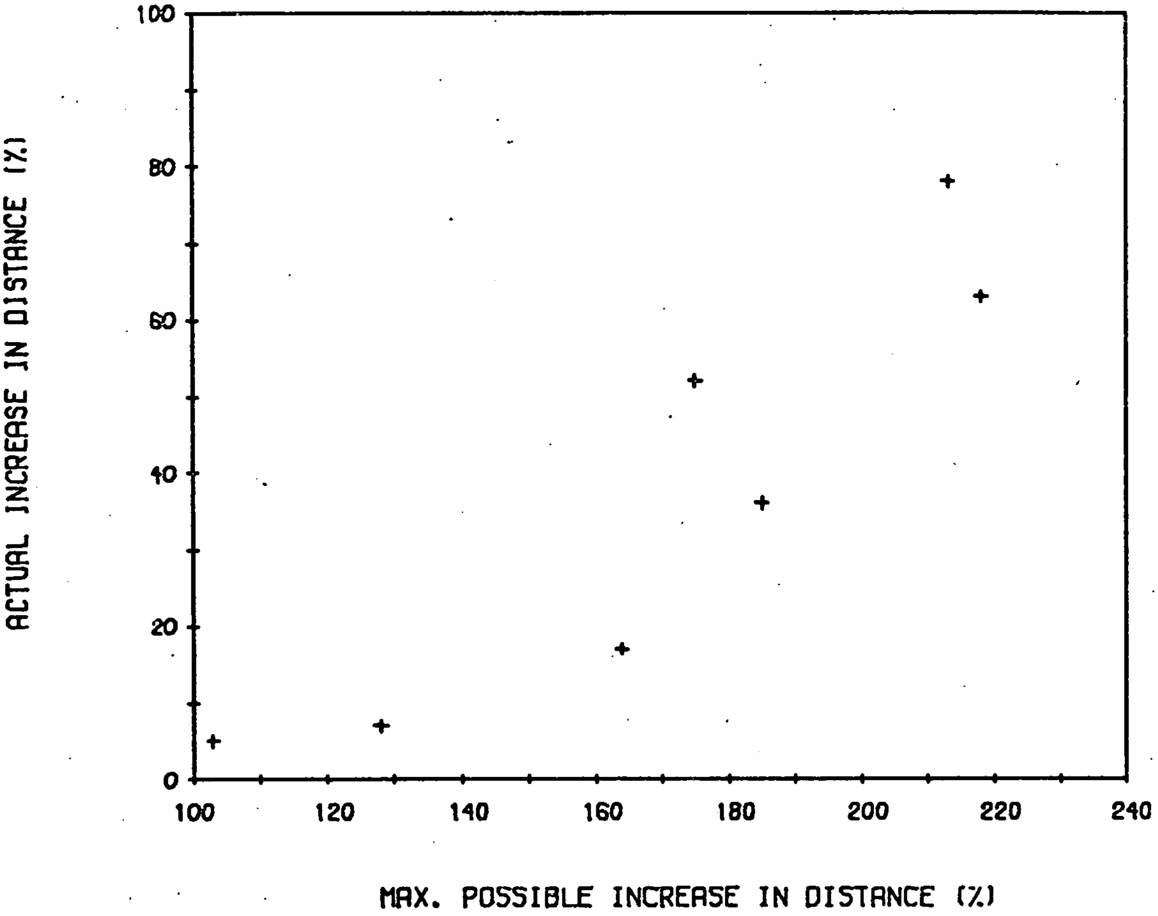


Fig. 3.3.4.3-1

Relationship between actual and maximum possible increase in the index of distance travelled following change to zero groat density

This is not an artefact of the method used for establishing the maximum for a particular vole, since this index did not use values for the step increase.

It could be that the step-wise reduction of density to a low value causes a constant level of activity for the first day at 0.55 of the maximum. However, this is unlikely in view of the much lower value for subsequent days, and a more reasonable interpretation of these results is that, straight after the reduction in groat density the vole is searching at a rate equal to or greater than the "maximum", but that this rapidly drops off during the first 24 hours. This interpretation would enable the results to be consistent with a model based on an continuous decay of the searching rate.

The size of the subsequent decrease to the post-step equilibrium appears to depend on at least two factors. The first factor is the value of the post-step density. It would be expected that, provided this density is not too high, the increased activity of the first day would tend to be maintained on subsequent days more than when the step is to zero density, and therefore the decrease in activity on the second day should be less. There are only three cases of a step-change to a non-zero density, and these with the same vole, but in each case the decrease, on the percentage points scale, is smaller than for any change to zero density. If these three cases were independent, the probability of getting this result in the predicted direction would be $1/(9^3)$, 1/729, but the lack of independence precludes an estimate of significance. Nevertheless, this result tends to confirm the original idea, especially when, as shall be seen, these intermediate densities tend to be associated with high levels of activity.

The decrease is also related to the size of the Day 1 increase: the larger the increase, the larger the subsequent decrease. See Fig.3.3.4.3-2. If we denote the changes on Day 1 and Day 2 by Ch1 and Ch2 respectively, both being measured in percentage points, then

$$Ch2 = -(25 + 0.8 \times Ch1)$$

assuming a linear relationship. As we shall see in the next section, this relationship results from the fact that searching at zero density tends to be a constant fraction of the maximum searching effort that a vole can show.

In conclusion, the introduction of a step decrease in groat density causes an increase in searching, as measured by the index of distance travelled. This is probably due to the vole having an expectation of finding groats which persists up to one day even if it is not reinforced. If groat density is zero, then the expectation decays and searching on subsequent days decreases; if food density is at a low density, then the high level of searching is maintained. The size of the initial increase is determined by the extent to which the vole is already near its maximum search rate before the step change is increased; the nearer it is, the smaller the increase. The size of the decrease in searching on the second day is superficially related to the size of the previous increase. In fact, as will now be considered, the equilibrium searching of the vole at zero density appears to be related to maximum searching effort, and this accounts for the size of the decrease.

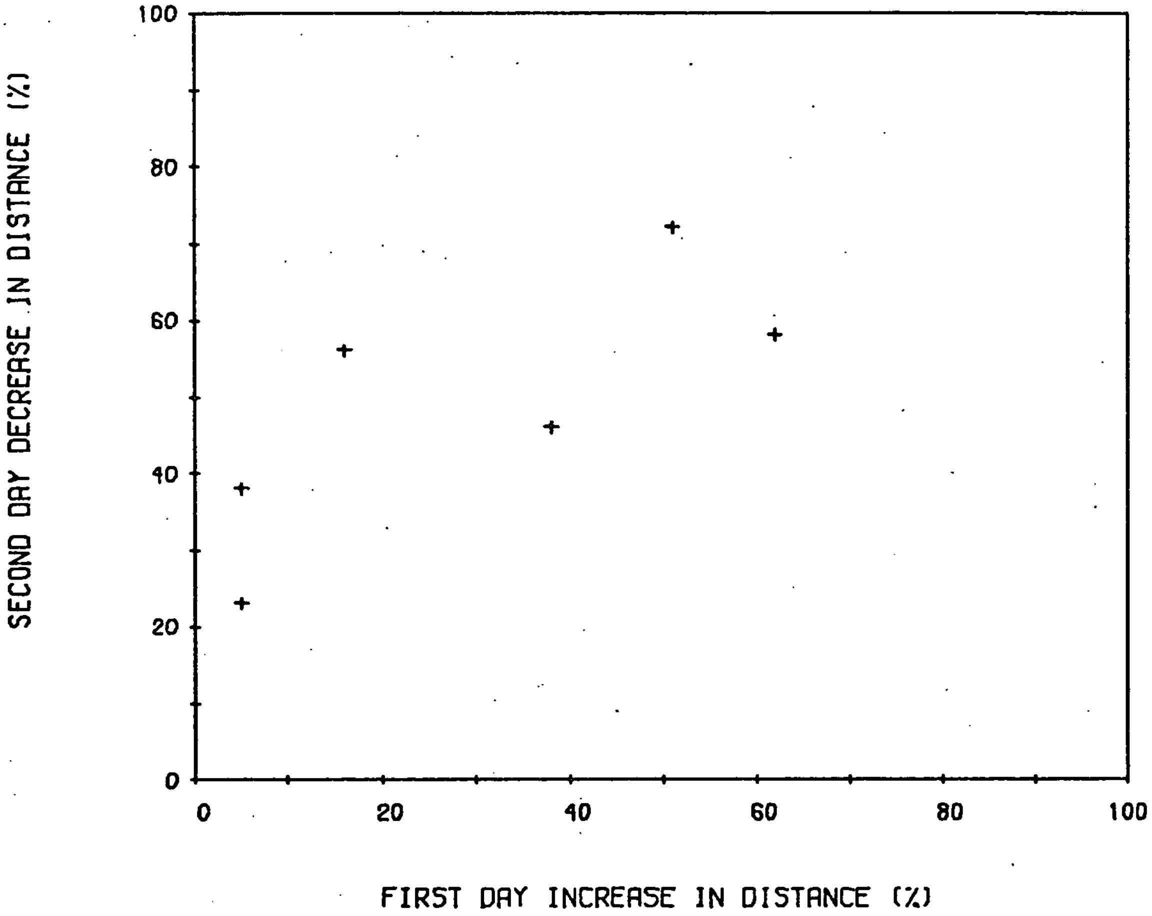


Fig. 3.3.4.3-2

The second day decrease in distance index related to first day increase, following change to zero groat density.

3.3.4.4 Distance travelled at zero groat density

In the previous section, it was found that distance travelled at zero density tended to an equilibrium value. We shall now consider this in more detail, including all cases of zero groat density, not just those preceded by a step change.

Fig 3.3.4.4-1 shows the relationship between the mean distance travelled at equilibrium for zero groat density for each relevant session and the maximum distance travelled in that session, where the maximum distance is again defined as the average for the three highest days. Note that even if there were two periods of zero density in one Session, they were lumped for the purpose of calculating the average value, even if the data for one period appeared to differ significantly from that for the other period. This procedure had to be adopted in the absence of any better method for associating the maximum with either period. Similarly, if one vole was used in two consecutive sessions, and a period of zero density linked the two, then this data was related to both maxima. It was thought that these steps would tend to correct for any long-term changes in the level of the vole's zero-density searching.

It can be seen from the graph that there is a weak but definite correlation between zero-density distance travelled and the maximum. This correlation is insensitive to the following changes:

a- Defining the maximum by the single highest value,

b- Considering the data by vole rather than by session, thus removing some data points.

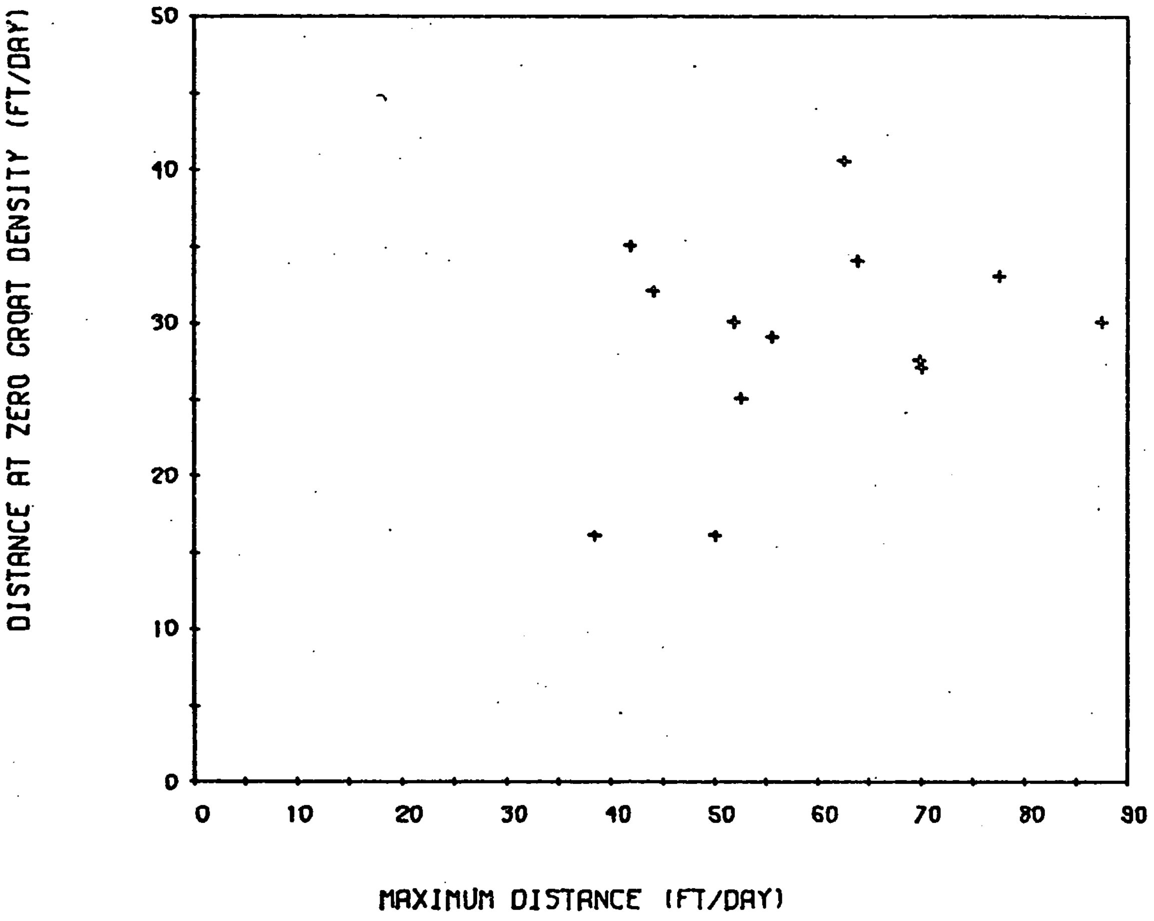


Fig. 3.3.4.4-1

Relationship between distance travelled at zero groat density, and maximum distance travelled.

The median ratio between the two variables is 0.42, with a range from 0.30 to 0.64.

This correlation suggests that voles are characterised by different levels of activity, which are revealed both in the distance a vole travels when the motivation for searching is greatest, and in basal level of searching when food density is zero. This conclusion is supported by the case of one vole, used in sessions S1(I) and S2(I), which was put through two complete cycles of groat density consecutively, giving three periods of zero density and permitting two "maxima" to be defined. There is a significant correlation between distance travelled at zero density and time since the start of the experiment, and this is paralleled by an increase in the maximum from 39 units per day to 64 units per day (both values being the average of the three highest points).

It is difficult to account for the remaining variation in the correlation between maximum searching and searching at zero density. To some extent, it may be that the period at zero density was not long enough to eliminate carry-over effects from the previous period of low density, especially when the density had not been low enough to cause a reduction in searching. However, the main reason would seem to be that the two measures of searching measure different aspects of the vole's activity, and that, while the two are correlated to some extent, each factor is in fact a response to the given conditions of the environment, rather than the one being simply a constant fraction of the other.

3.3.4.5 Response to method of wheat distribution

In nature, the alternative foods available for an animal can either form a more or less homogenous mixture with the preferred foods, as may occur in many sheep grazing situations (e.g.Arnold,1964), or may be spatially separated from them, as Royama (1970) postulates for the food species of great tits. For any one animal, either condition may occur; thus preferred pasture species of grass may be intermingled with old leaves of the same species, and also spatially separate from less preferred species. Then, if the sheep is in a region of a preferred grass species whose palatable parts are at low density, it has two types of decisions to make:

a- whether to eat the old leaves or to move on a step in the hope of finding younger leaves;

b- whether to stay in the area of preferred food at low density or to move to the area of less preferred food at high density.

Clearly, the shape of the animal's functional response curve to changes in the density of the preferred food could depend on the type of decision it had to make.

If we now imagine one type of preferred food and one type of abundant alternative food, which can either be mixed or separate from the preferred food, then it would be expected that the functional response curve would rise more steeply when the alternative food was spatially separate. The reason would be that, under these conditions, the decision to switch to the alternative food would require more energy than if this food was readily at hand, and therefore the decision would be made less readily.

The brushes situation enabled this conclusion to be tested, as the wheat could either be presented under the brushes with the groats, or all the wheat could be left in a pile outside the brushes. In the latter case, the pile was usually left inside the nest-box, so that from the start the vole was familiar with its presence. Although the wheat density under the brushes was very high (usually 1,600 grains/area, or c.64/sq.foot), the certainty of finding the grain in a particular place was clearly greater in the case of the wheat in a pile, and if anything this would tend to produce a bias against the idea proposed above.

One vole provided suitable data for testing the above idea. It was run in two consecutive sessions, the first with the wheat in the nest-box, the second with the wheat scattered under the brushes at the density of 1,600 grains/area. Apart from that, and the skipping of the highest groat density in the second session, the two sessions had identical schedules, consisting of a rise from zero density to the maximum, and then returning using the same intermediate densities. In addition, the density of 25 groats/area was repeated with wheat in the nest-box at the end of the second session. On several of the last days of the first session, the vole had escaped from the area to a boarded-off section of the room; since there was food and water in this section, the days of escape could be detected by a fall in the total amount eaten in the experimental area, even when the vole had been found there when the brushes were lifted. In practice, only those distance results were discarded for those days on which total eaten was less than 50% of normal. Any bias introduced by this criterion will work against the hypothesis.

The results are shown in Table 3.3.4.5-1 where the figures represent distance travelled with the wheat under the brushes as a percentage of distance travelled for the corresponding conditions with the wheat in the nest-box. The data for each case is the mean for two consecutive days at the same density, except for those figures marked by an asterisk, where only one value was used for the condition of wheat in the nest-box.

Table 3.3.4.5-1

Distance travelled with wheat under the brushes as a percentage of distance travelled with wheat in nest-box

	Groat Density (Grains/total area)					
	0	25	50	100	200	400
Density Increasing	108	50	66	69	80	63
Density Decreasing	92	71+	54+	-	52	54
Re-test	.	43	.	.	.	.

These results indicate that the presence of wheat under the brushes reduces the distance travelled per day compared with equivalent conditions with the wheat in the nest-box. This is not an artefact due to long-term changes in the vole, since the re-test at a groat density of 25 grains/area with wheat in the nest-box showed the expected increase in searching. Changes in the number of groats found at each density are very similar, enabling us to conclude that the presence of the wheat with the groats actually result in wheat being eaten in place ofgroats, rather than simply reducing travelling not related to searching for food. This confirms that the vole travels through the brushes primarily in search of food. The distance travelled at zero groat density appears to be unaffected by the presence of wheat under the brushes. This supports the idea that effect of the distribution of the wheat basically results from its interference with the (eat groat/eat wheat) decision-making mechanism, rather than the having a direct action on the tendency to travel.

Both the distance travelled and the number of groats eaten at the highest groat density are correspondingly less when the wheat is under the brushes, even though in all cases the maximum value for these two parameters had been reached at the next lowest density (200 groats/area). Thus, it is not only the slope of the functional response curve that is altered by the nature of the wheat distribution, but also the plateau value. This is a similar effect to that found by Holling (1965) when he compared the shape of the functional response curve for deer mice when the alternative food was moderately unpalatable (sunflower seeds), or very unpalatable (dog biscuits): in the former case, the functional response curve flattened out at only 60% of mean daily intake, as compared to almost 100% in the second case.

In addition to the above experiment, the form of wheat distribution was also changed in three sessions of the last series, namely S6(II), S6(III) and S6(IV). In the first of these, the wheat was normally in the nest-box, and was put under the brushes for five days. The conditions were the reverse in the other two, except that for S6(III) the wheat was put in the nest-box for two periods of two days, separated by two days with the wheat under the brushes as normal. Apart from these differences in the wheat distribution, the three voles were under identical conditions, with a groat density of 200 grains/area.

The results are summarised in Table 3.3.4.5-2.

Table 3.3.4.5-2

Summary of results from series S6 for changes in wheat distribution.

		S6(II)	S6(III)	S6(IV)
Normal distribution		W.i.n	W.u.b	W.u.b
Number of days:	W.i.n.	10	4	5
	W.u.b.	5	7	7
Mean dis./day:	W.i.n	50.8	36.7	56.4
	W.u.b	52.0	31.4	26.8
(W.u.b/w.i.n) x 100		102	86	48

Note: W.i.n = Wheat in nest-box
W.u.b = Wheat under brushes

In only one case is there agreement with the results obtained before, this being in the case of S6(IV). Here, the effect is undoubtedly significant, as the highest value for distance travelled with wheat under the brushes is only 66% of the lowest value with wheat in the nest-box. The ratio of the two mean values is also similar to that previously obtained. In the other two cases, there is little evidence for any <u>stable</u> difference in response to the two distributions: this is obvious from the summary table for S6(II), while in the case of S6(III) three of the four values for wheat in the nest-box are well within the range of values for wheat under the brushes. However, there is some evidence of a transient response, since in both cases a transition from wheat under the brushes to in the nest-box is followed by a marked but temporary increase in searching.

The data for number of groats eaten for the conditions described above shows the same pattern in the cases of S6(II) and S6(IV). In S6(III), however, there is a marked difference between the mean number of groats eaten with the wheat under the brushes, and the mean number eaten with the wheat in the nest-box, the figures being 53 groats/day in the first case and 72 in the second. This difference is found to be significant using the Mann-Whitney U-test. In view of the lack of significance with the distance data for this vole, it would be expected that efficiency at finding food, as reflected in the figures for mean distance travelled per groat, reflected in the figures for number of groats found per unit distance travelled, should also be greater with the wheat in the nest-box, and this is found to be correct: 1.64 groats are found on average per unit distance with the wheat under the brushes, while 1.96 are found with the wheat in the nest-box. This could either result from the odour of the wheat masking that of the oat grain, or else this could be another example of a trade-off between distance to travel and reward. The latter explanation seems less likely, since,if a groat has actually been detected, the slight extra effort involved in getting it is unlikely to deter the vole, as it is demonstrated elsewhere (section 3.3.4.6) that the distance of perception appears to be of the order of only several centimetres in the brushes set-up.

In conclusion, it is clear that the nature of the wheat distribution can have a marked effect on the distance that a vole is prepared to travel in search for groats, and also on the efficiency of the vole at detecting the presence of a groat grain. Although not every vole shows either of these characteristics, their effect when either does occur is to alter the amount of the preferred food eaten. Thus, the functional response of the voles is very dependent on the way in which the alternative food is made available to the animal.

3.3.4.6 Estimation of reactive distance

The distance at which an animal perceives and reacts to a food item is a basic component of its functional response, (Holling, 1966), since it determines the number of items detectable by the animal for a given distance travelled. This component will be treated experimentally in section 5.7, but it would clearly be useful to be able to estimate typical values that this component can take under the conditions of the functional response experiments.

The track records enable us to estimate the distance travelled by the vole during a day. The percentage of groats found can be calculated knowing the number of grains put down and subsequently found. These two parameters can then be used to estimate the vole's reactive distance, under the following assumptions and limitations:

a) the reactive distance is defined operationally as the distance normal to the recorded tracks within which groat grains are not only detected but also taken;

b) the reactive distance does not change during the course of a session (typically twenty to thirty days);

c) the vole only travels over the area in search for food - that is, the vole always takes a groat whenever it comes within the reactive distance;

d) the distance travelled in the groatless border around the area is negligible - examination of the track records support this assumption, since virtually all of the activity in this region is just for access to the area where the groats are scattered;

e) criss-crossing of tracks does not introduce a significant error through including the same region twice - this assumption will hold if the actual reactive distance is small enough, in particular if it is less than half the distance between the brush centres, or about four centimetres.

Finally, consideration should be given to one element of the vole's behaviour under the brushes, namely its tendency when searching for food to move its head at intervals off the centre line to a distance of one to two centimetres. Since the track records could not resolve these small excursions off the main line, this must be taken as a part of the reactive distance. However, as this is a behavioural rather than a sensory feature, it is likely to be much more plastic; in particular, to be more pronounced at low groat density.

We can comment on the bias that assumptions (c), (d) and (e) will introduce if they are invalid. Assumption (c) will be less likely to apply at high food densities, when groats are easier to find, and will tend to produce an apparently smaller reactive distance at these higher densities. Assumptions (d) and (e) will also tend to produce smaller reactive distances than actually apply, since in both cases the vole through the groat area is overestimated. Assumption (e) is more likely to introduce bias the greater the distance travelled by the vole, since under these conditions there will be a larger amount of track covering the same area twice.

The reactive distance is calculated as follows:

$$A = 17{,}000 \times \frac{P}{100} \qquad \ldots \quad 1a$$

or: $$A = 34{,}000 \times \frac{P}{100} \qquad \ldots \quad 1b$$

$$R = \frac{A}{2 \times 30 \times D} \qquad \ldots \quad 2$$

where: A = area assumed covered by vole, (sq.cm)

P = percentage of available groats found,

D = distance travelled (arbitrary units, 1 unit = 30 cm).

"A" is calculated as a fraction of the total area of scattered groats, and equation 1a or 1b is used, depending on whether two or four blocks of brushes were used in the experiment.

The data was analysed graphically by plotting the reactive distance calculated for each day against the groat density for that day. A typical graph is shown in Fig.3.3.4.6-1. It can be seen that at low densities the median value for estimated reactive distance remains fairly constant, but drops off at higher densities. As the value will never reach zero provided that some groats are taken, we may assume that this part of the graph is best explained

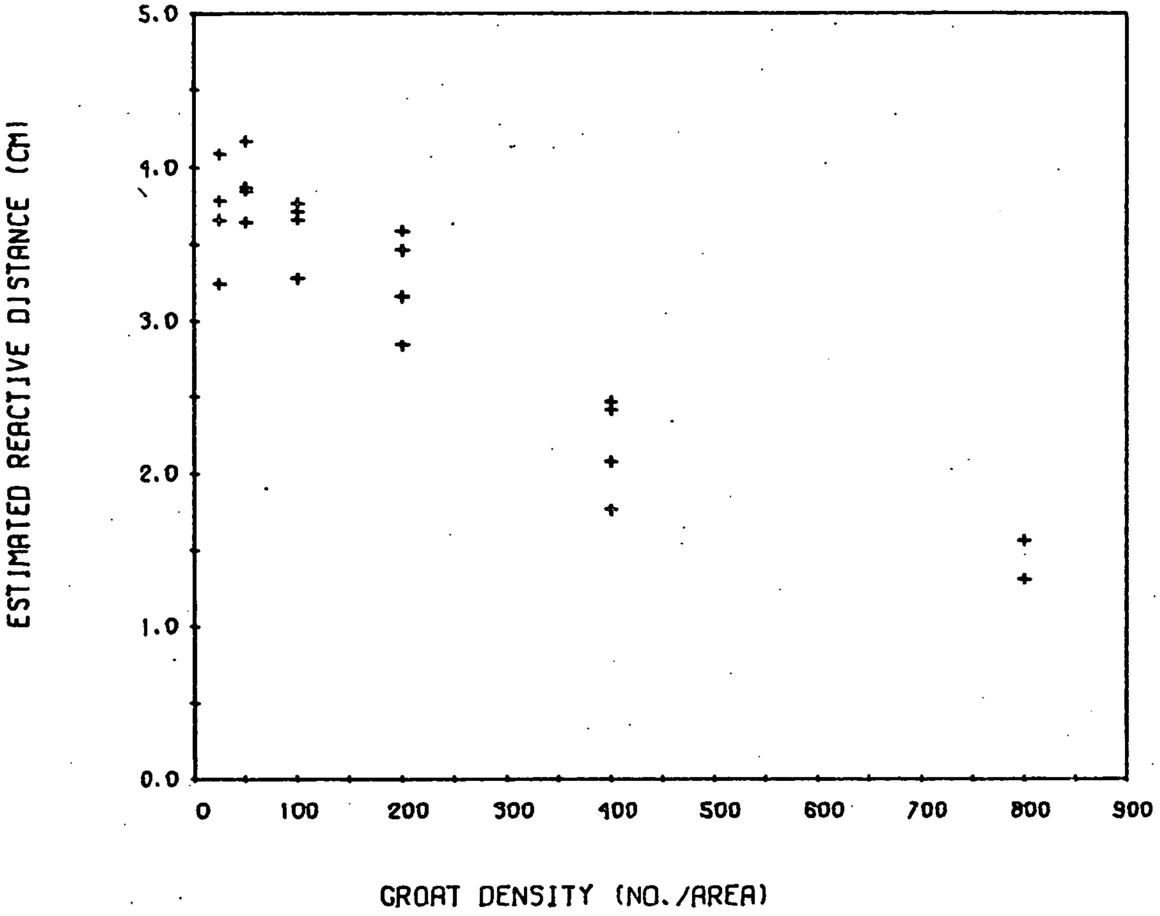


Fig. 3.3.4.6-1

Change in estimated reactive distance with groat density.

by some type of asymptotically decaying function. If a constant number of groats were taken and a constant distant travelled at these higher densities, then we would expect a reciprocal relationship between apparent reactive distance and density. In fact, as will be seen in later sections, distance travelled does drop off at higher densities, but to a lesser extent than would be expected if searching was kept to the minimum necessary. However, for present purposes the data does not merit fitting theoretical curves to the drop off of distance travelled with increasing groat density, and applying this to the decrease in apparent reactive distance. Instead, the graph for each vole was characterised by three features, which are summarised in Table 3.3.4.6-1. These features are:

a) The estimated reactive distance in the "constant" region of low groat densities;

b) The groat density at which the apparent reactive distance drops off;

c) The rate of change of reactive distance with respect to groat density. An empirical relationship was adopted, which assumed that an increase in groat density of 100 grains per area produces a constant percentage drop in reactive distance. That is, for any one vole,

$$\frac{dR}{dD} = c.R$$

where: R = reactive distance,

D = groat density (above threshold density),

c = a constant, expressed as a percentage in Table 3.3.4.6-1

Table 3.3.4.6-1

Key parameters from graphs of estimated reactive distance against groat density

Session	Median maximum value (cms.) (a)+	Threshold density (b)+	Rate-of-change coefficient (c)+
S1(I)	3.1	200	10%
S1(II)	2.8	100	25%
S1(III)	3.5	50-100	15%
S1(IV)	3.5	100	16%
S2(I)	3.7	100	14%
S2(III)	3.5	50	11%
S2(IV)	3.5	50	28%
S3(I+II)	4.4	60-150	?
S3(III+IV)	4.8	No change in reactive distance	
S4(I+II)	5.0	32	22%
S4(III+IV)	4.8	32	20%
S5(II)	3.4	200	8%
S5(III)	3.1	100-200	14%
S5(IV)	3.8	100	15%

+ The meaning of the column headings is explained in the text. The letters a, b and c refer to the corresponding paragraphs in the introduction to this Table.

In the case where there is no apparent drop in reactive distance, the last two items are omitted.

Note that the quantity referred to in (c) above need not be interpreted as a change in reactive distance. If the vole simply spent more and more time in travelling through the brushes without searching for food as groat density increased, then the effect would be just the same, and the two possibilities are indistinguishable. If this interpretation is correct, then the values in (c) of the Table can be interpreted as the rate of decrease of pure searching for the stated change in groat density. Another alternative is that the apparent decrease in reactive distance represents a change in the behavioural, rather than the sensory, component of the "reactive distance", but this is less likely in view of:

(i) the large decreases obtained in some cases, and

(ii) the lack of evidence for a stable value of the reactive distance at higher densities, as would be expected if the sensory component remained constant.

The results indicate that the maximum value for the reactive distance fall into two distinct groups, depending on whether two blocks (S1, S2 and S5) or four blocks (S3 and S4) were used for each vole. The range in the first case is 2.8 cm to 3.8 cm, while in the second case it is 4.4 cm to 5.0 cm. The reason for this result is not known; it is not due to an artefact of the method of calculating the reactive distance, since the differences in the areas had been allowed for. It is possibly a reflection of the fact that, at low groat densities, the voles in the second group did not travel twice as far as those in the first group and since their distance travelled was spread out over a larger area, the error introduced by criss-crossing and overlapping of tracks would be reduced. The direction of the error is consistent with this idea.

3.3.4.7 The functional response to groat density

In this section, I will deal with three questions:

a) What is the shape of the functional response curve?

b) How is the response affected by the temporal patterning of the groat density schedule?

c) How is the response affected by other factors, in particular the type of wheat distribution?

The density of the groats will be expressed in terms of numbers of groats, rather than weight of groats, per unit area. The reason for this is that the grain is the unit of selection, so this is basically describing the functional response from the vole's point-of-view. From a plant or prey's point-of-view, the response of a consumer might be more meaningfully expressed in weight units.

The response of the vole to the groat density will be described using two indices. The first will be the number of grains found per day, while the second will be the distance travelled by the vole per day.

The first index is in line with that commonly used elsewhere, and is the measure normally used in the actual definition of "the functional response" (2.3) since it measures both the effect on a prey species and the gain to the feeding individual. It does however suffer from the normal limitations applying to small samples of discrete units, namely that each value will have an error term due to the random sampling of the groats by the vole, and this error will be proportionally larger the smaller the number of groats found, as described by the confidence internal for the binomial distribution (Snedecor, 1967). The index based on distance travelled is free of the stochastic element inherent in the measurement of number of grains eaten, and provides a direct insight into the possible mechanisms underlying the functional response. In particular, it can help to elucidate the reasons for the proportionally smaller intake at low food densities shown by other species of small mammal and bird, once it has been demonstrated that the vole also exhibits a sigmoid response curve. This index does suffer from the fact that we can never be certain that all travelling is related to searching for food; this point is discussed more fully in section 3.3.4.6, but it appears that it is only at the higher food densities that significant amounts of travelling occur which are not food-related.

The description and classification of response curves presents something of a problem. Presenting the data graphically is useful for illustrating what is happening, but in itself does not provide a concise description of the results, or a basis for classification. Holling's classification (1965), in which only three shapes of the functional response curve are recognised, described in section 2.4, is a widely quoted system, but has two basic flaws. The first is that, for the types 1 and 2 response, he applied to the whole curve a property which may be reasonably expected to apply to part only of the response. Thus, in the type 1 response, amount eaten is supposed to be a linear function of food density from zero to a threshold value, whereas a more flexible approach would be to say that a linear relationship may hold over a certain range of food densities. Second, the negatively-accelerated part of the types 2 and 3 curves are based on a theoretical foundation which is itself very shaky, namely that the reason for the flattening of the curve is primarily due to the effect of handling time reducing the amount of time the predator has available, according to the equation:

$$N = a.D.T\ (1 + a.D.H) \quad \ldots \quad \text{see section 5.1 for symbols.}$$

This may be true in some cases, but hardly seems likely to apply to an animal like the vole, which may only spend at the most two hours in every twenty-four feeding. The equation is not very flexible, and there is therefore no basis in retaining it as an empirical basis for describing a functional response curve. Thus, while Holling's system can be retained for a very broad classification of response types, it can not be used for the empirical, algebraic description of response curves.

A more profitable approach is to recognise that the curve may be described by one or all of the three elements identified by Holling: a linear, negatively-accelerated or positively-accelerated relationship. Initially, a particular curve would then be described in terms of these three elements, and then if required it could be expressed algebraically in terms of simple expressions generating the appropriate section of the response curve. By this means, the data is not forced to fit an over-simplified relationship, and further insight into the animal's feeding process can be obtained by analysing the different curve segments.

Using this system, seven different types of response can be broadly identified. If we define the abbreviations

LIN ... linear relationship,
POS ... positively-accelerated relationship,
NEG ... negatively-accelerated relationship,

then we can assume that they can only occur in the sequence POS-LIN-NEG. This yields the following seven types:

One segment: POS
LIN ... Holling's type 1 response.
NEG ... Holling's type 2 response.
Two segments: POS-LIN
POS-NEG ... Holling's type 3 response.
LIN-NEG
Three segments: POS-LIN-NEG.

In the following pages, I shall concentrate on describing particular characteristics shown by representative response curves, rather than on describing the response curves in their entirety. There are two reasons for doing this: the first is that this approach gives a greater insight into the mechanisms which govern the shape of the curve, as argued above. The second reason is that, at least initially, I am not interested in how "the average"vole behaves, but rather in the range of responses that voles can show. This removes the need to present graphically all the results obtained, with an associated commentary, though it does make it more difficult to compare results obtained for different species. But if this takes us away from the idea implicit in Holling's grouping of species by the shape of their functional response curve, i.e. that each species has a characteristic response, then this may be a useful change in approach.

The characteristics shown by the curves can be conveniently sub-divided into the qualitative and the quantitative. The former include those features which can either be present or not, and each feature will be illustrated by a representative curve. I will consider the following points:

a) Do the responses tend to a plateau?
b) Do responses contain a linear section?
c) Do responses contain a negatively-accelerated section?
d) Do responses show a positively-accelerated section?
e) Are there differences between the period of falling and of rising groat density?
f) Are there differences between the two days at each density level?

Although these questions are framed in terms of the index of number of groats eaten, the index of distance travelled will be considered in parallel when dealing with each feature.

Any functional response model proposed for a particular species must be capable of reproducing the range of qualitative effects demonstrated by that species. In addition, given that there are qualitative differences between the individuals of the species, it follows that quantitative verification of a model based on experimental component analysis can not be made by finding the average value for the parameters of each component, and simulating the model obtained in this way to produce the "typical" functional response for the species. Such verification could only be obtained by simulating the model with the range of values found in the individual components, to see if this agreed with the range of responses found, or by comparing the functional response of each individual with the predictions based on parameter values obtained for the same individual. This latter approach is likely to be impractical in terms of the time needed to analyse all the components and the response for the same animal.

However, there are other reasons, apart from the verification of a functional response model, for describing the response curve quantitatively. It can provide a better basis for comparisons within and between species than one based on the presence or absence of certain qualitative features. Furthermore, if we remember that the reason for studying the functional response lies in its importance in determining the nutrition of the feeding animal and in its impact on the food species, then it is clear that it is useful to express this numerically. I shall consider the following quantitative features of the response curve:

a) At what groat density does the response curve reach the plateau?

b) What is the groat density at 50% of the plateau value?

c) What is the groat consumption and the percentage preference of groats at the plateau?

d) What is the maximum search rate of the vole, using both the measure of distance travelled and the measure of percentage of available groats actually found?

Qualitative Features

a) Plateau

No animal, in the presence of ad lib.food, can eat an unlimited amount, so it follows that there must be a limit to the rise of the functional response curve for any species. In the case of predators, which tend to be opportunist feeders, this limit may be flexible, and the amount eaten per unit time may drop off at high densities of the preferred food as the predator becomes satiated. The vole, however, in common with most herbivores, shows well-regulated consumption even under ad lib. conditions in cages, rapidly adjusting its intake to a constant level. It is axiomatic, therefore, that all voles show a response curve which tends to a constant level of intake of the preferred food, and of total consumption. Whether or not the response curve actually shows a plateau depends on whether the animal was tested sufficiently at groat densities above that corresponding with the start of the plateau. Fig. 3.3.4.7-1 shows one case where the plateau is clearly apparent.

b) Linear rise

If the vole covers the same fraction of the food area per day at different groat densities, and if its reactive distance does not change, then there should be a linear relationship, passing through the origin, between groat density and the number of groats found. Fig. 3.3.4.7-2a,b shows two cases where a linear

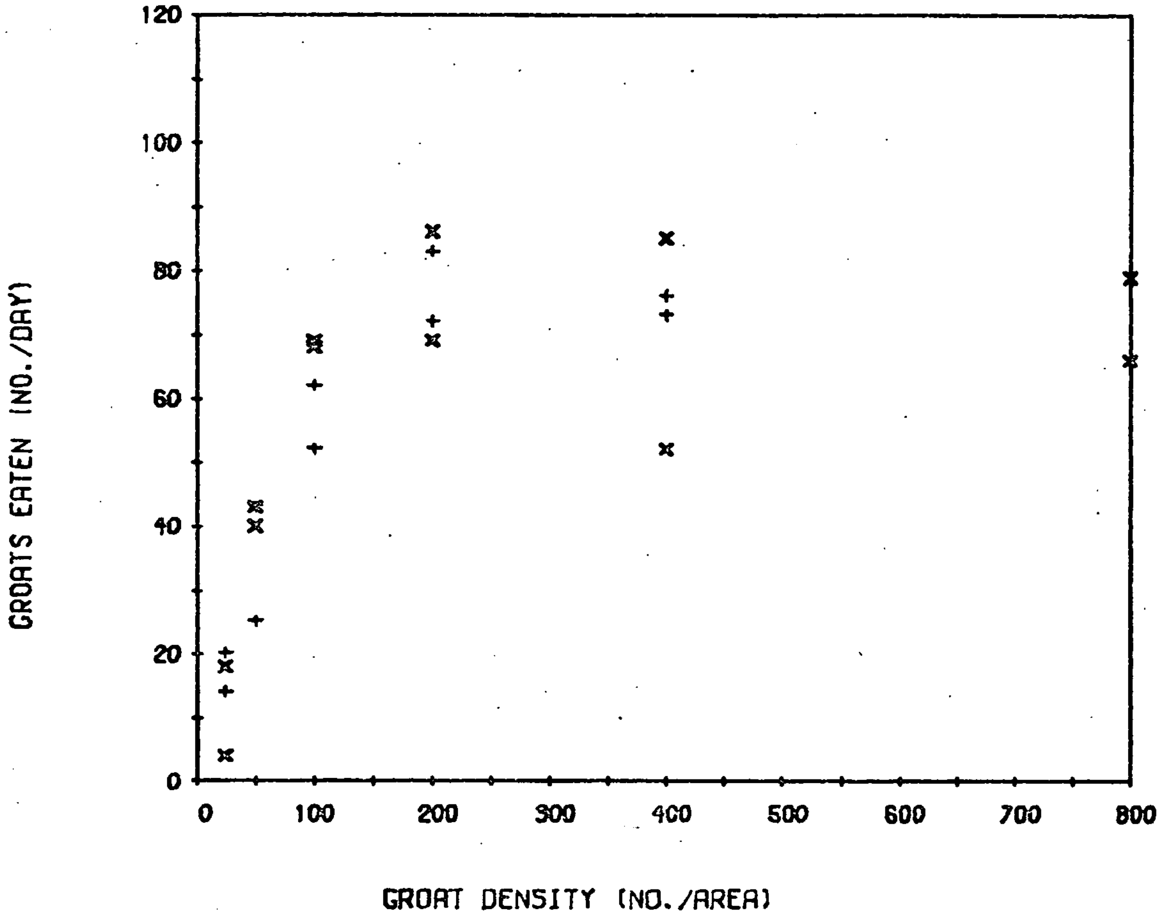


Fig. 3.3.4.7-1

Functional response to groat density for session S2 (I) illustrating presence of plateau region.

x : Groat density increasing
\+ : Groat density decreasing

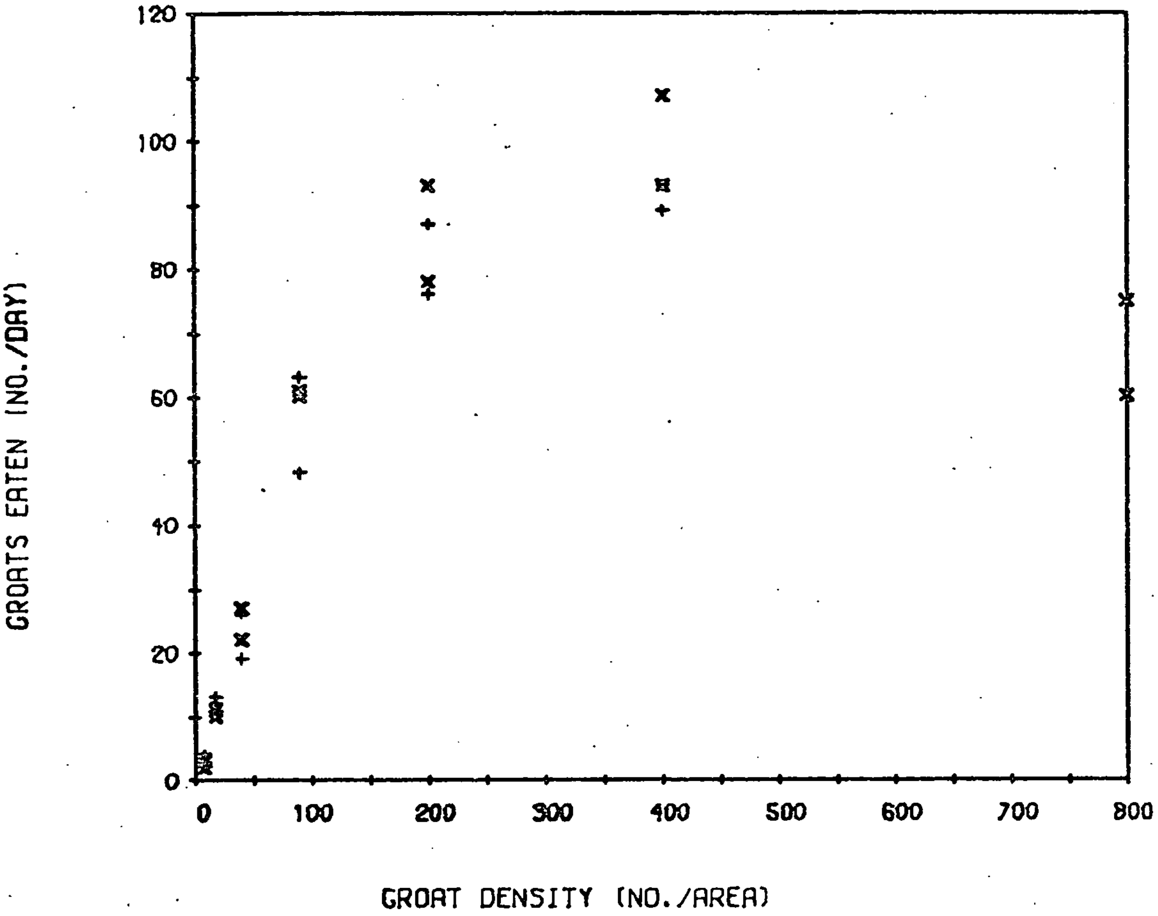


Fig. 3.3.4.7-2a

Functional response to groat density for session S5 (III), illustrating linear rise.

× : Groat density increasing
+ : Groat density decreasing

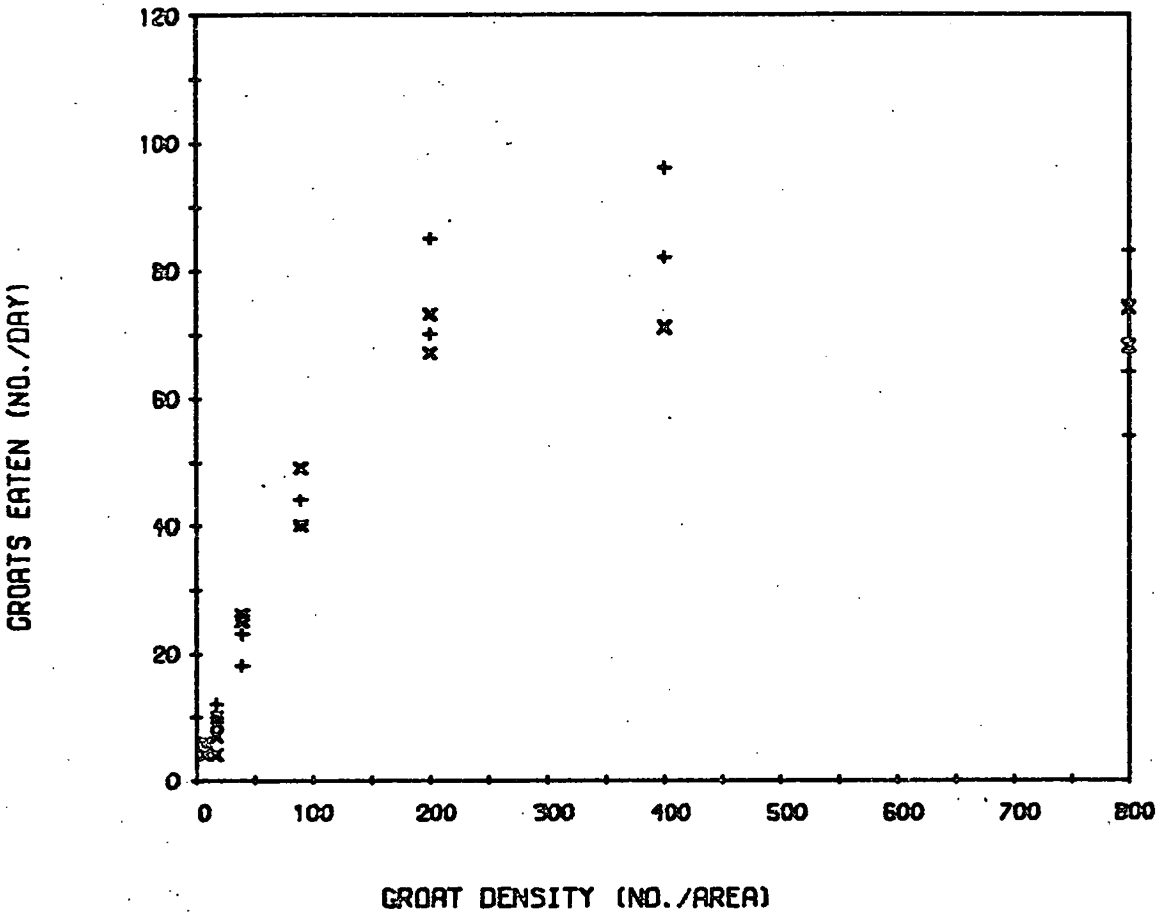


Fig. 3.3.4.7-2b

Functional response to groat density for session S5 (IV), illustrating linear rise.

× : Groat density increasing
\+ : Groat density decreasing

relationship appears to hold at the lower groat densities; the variation around the line being explainable by sampling effects by the searching vole.

If the assumption behind the index of distance travelled is correct, that the distance travelled by the vole is proportional to the percentage of the area covered, then over this range of groat densities the vole should travel a constant distance per day. In Fig.3.3.4.7-3a,b the distance data for the same two voles is plotted, also as a function of groat density. In one case, (Fig.3.3.4.7-3b), there is indeed no significant trend over the lower density range, but in the second case, it is apparent that the distance travelled at the very low densities (0 to 25 grains per area) is considerably less than at the intermediate densities of 50 and 100 grains per area. Why was this not apparent from the functional response graph? There are two reasons for this. The first is that, because only a small number of groats are available at these lowest densities, even proportionally quite large effects will make only a small change in absolute terms, so that the data points still appear close to the fitted straight line. The other reason also has to do with the small total number of groats available at these densities: sampling theory tells us that the confidence limits associated with a sample taken from a small population are relatively larger than for one taken from a larger population. Thus, a 20% sample from a population of 25 groats has confidence limits from 0 to 40% of the population size, while for a population of 100 groats, the limits are 11 to 29%. Clearly, there is a greater chance of the limits

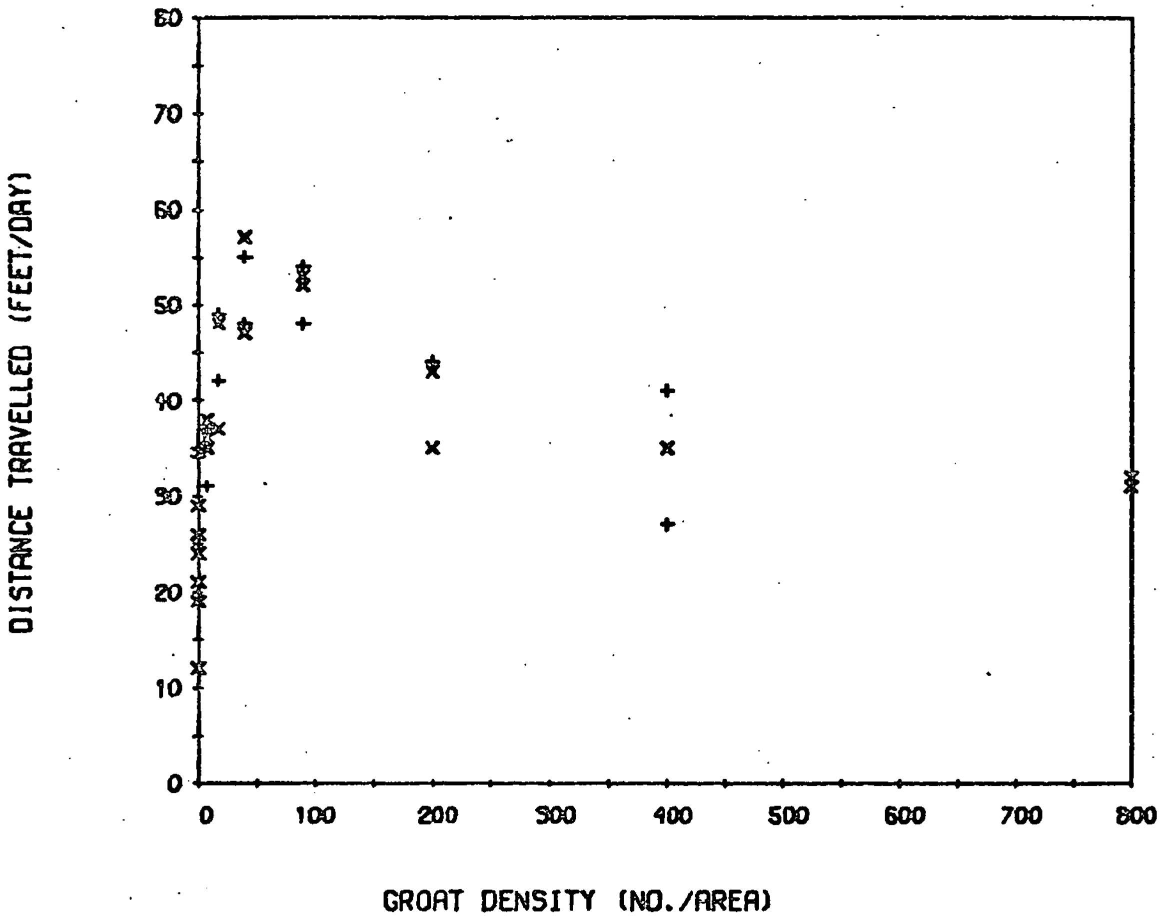


Fig.3.3.4.7-3a

Distance index related to groat density for session S5 (III), corresponding to functional response shown in Fig. 3.3.4.7-2a.

× : Groat density increasing
+ : Groat density decreasing

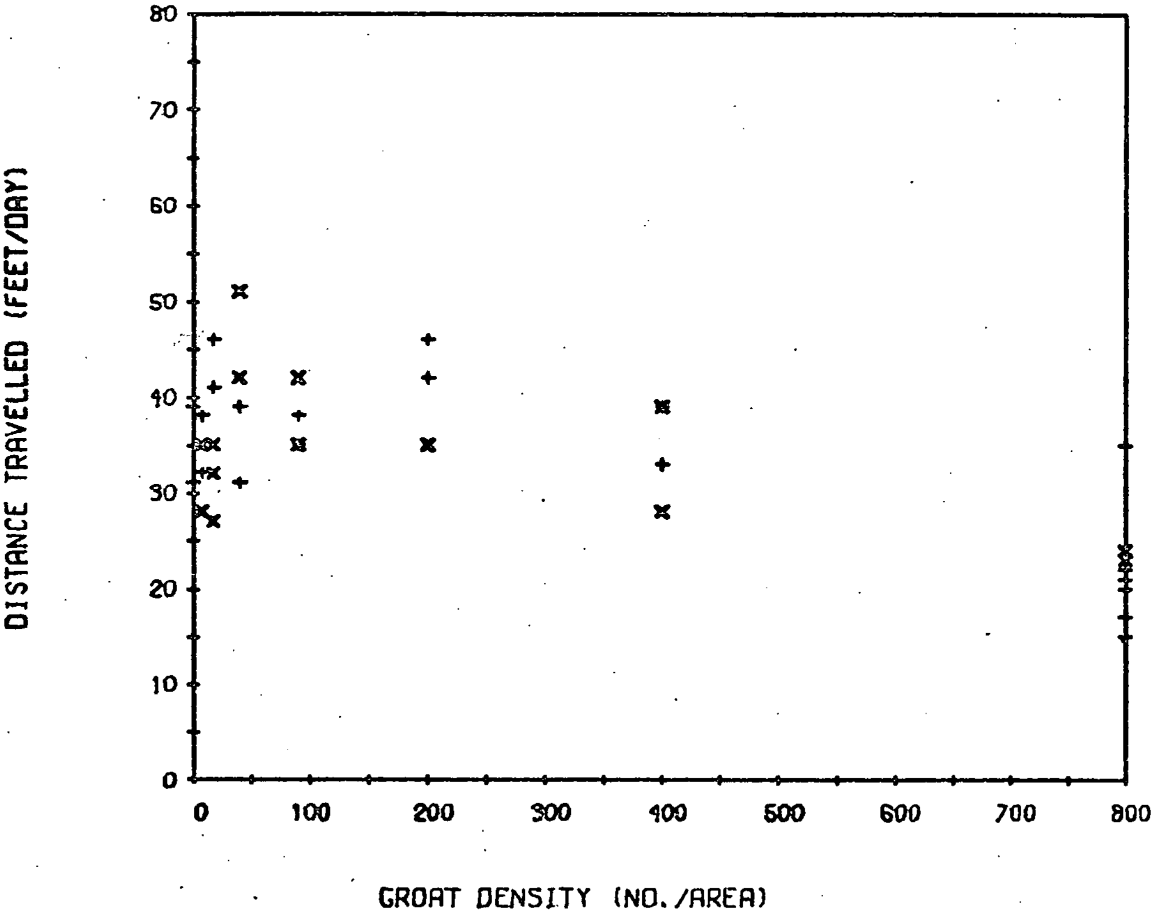


Fig. 3.3.4.7-3b

Distance index related to groat density for session S5 (IV), corresponding to functional response shown in Fig. 3.3.4.7-2b.

× : Groat density increasing
\+ : Groat density decreasing

crossing a given straight line at the lower densities.

This indicates that, while some voles may indeed show a linear functional response over a certain range, the use of the distance-travelled index to complement the groats-found index is useful in demonstrating that the response may not be truly linear. This refinement may not be very significant from the point of view of the feeding animal's nutrition, or the impact on the food species, but it is important when we are considering the mechanisms underlying the functional response, and may be crucial to the persistence of rare food species.

c) Negatively-accelerated rise

If the search rate of the feeding animal drops off as preferred food density increases, then the relationship between density and amount eaten ceases to be linear, but can be represented by a curve which bends towards an upper asymptote, showing a negatively-accelerated rise.

As we shall see, although this feature appears to be a common feature of functional response curves for various species (Ivlev, 1961; Murton et al, 1963; Holling, 1959b, 1966) there is no general explanation, in terms of behavioural or physiological mechanisms, which can account for all cases. While the role of handling time proposed by Holling (1959b) has gained a large degree of acceptance (Murton et al, 1963; Royama, 1970), it is clear that it cannot apply in the case of the vole, since this is a two-food situation, and since eating only groats takes up only say 5% of the day - it is hard to believe that this is the only time available for eating. So it is important to see if voles do in fact show this feature.

In view of the fact that the number of groats eaten at any one density typically shows a range of 20% of the mean value, it is not immediately obvious from the data whether the functional response is best described by two straight lines - a linear rise followed by a horizontal plateau - or whether the region of intersection of these two lines is better represented by a curve. The data did not permit of a test which could treat individual voles separately, so it was necessary to lump all the data together. Then, if evidence for a curved relationship was found, it could be assumed that this was true at least for some individuals.

The null hypothesis was based on the idea of a linear increase up to a threshold density, above which a constant amount of groats was eaten. If the true relationship tends to be curvilinear near the threshold density, then we would expect that the number of groats eaten in this region would be lower than predicted by the two straight lines. The threshold density could normally be placed unequivocally between two experimental densities.

The following description of the method used may be easier to follow with reference to Fig. 3.3.4.7-4 which shows the functional response for a typical vole, with construction lines showing the assumed density threshold density, the assumed plateau value, (based on the mean of the values above the threshold), and the assumed linear increase to the plateau (based on the data values for the density arrowed).

The analysis was in two parts:

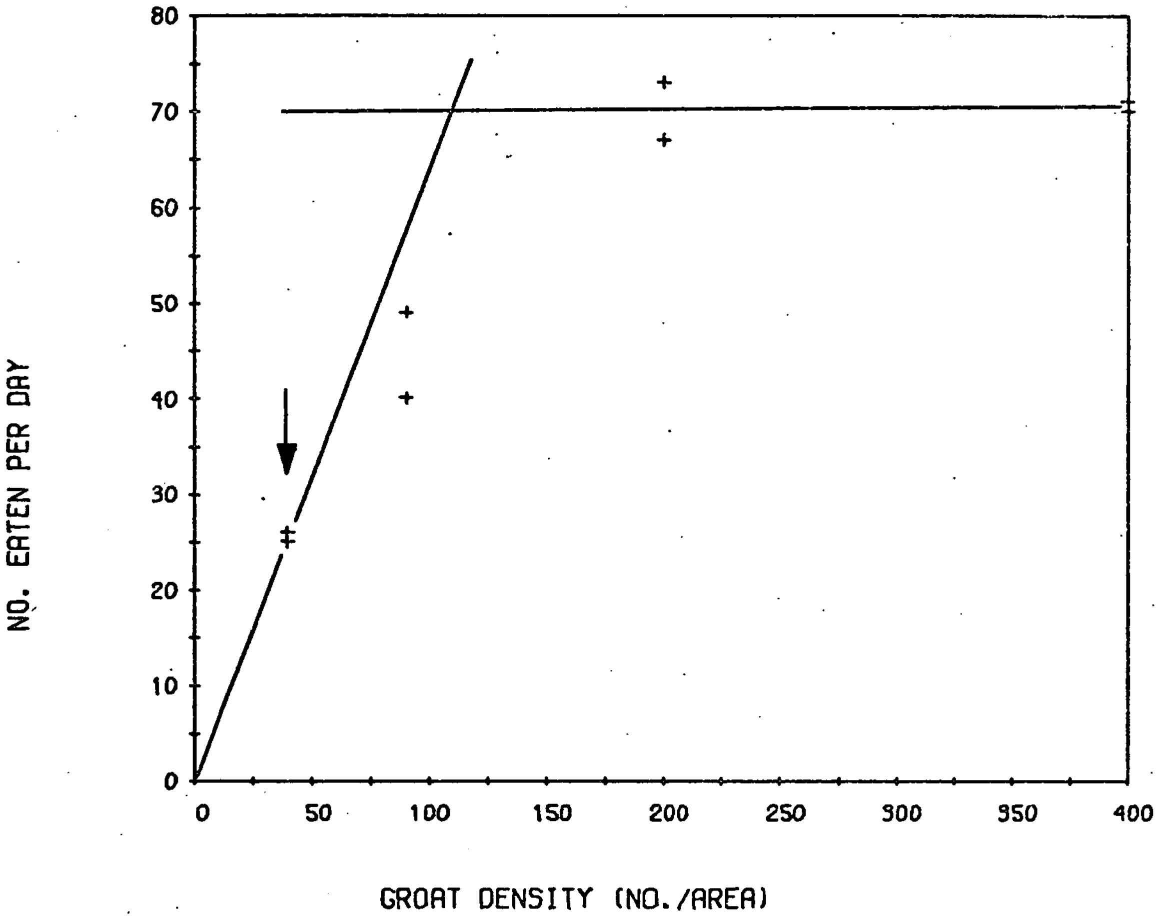


Fig. 3.3.4.7-4

Construction lines used for testing for a negatively-accelerated segment of the functional response.

a) above the threshold density, the reference value was found by averaging the numbers of groats eaten. The two values for the density level above the threshold were then compared with this reference value, both individually and meaned. The numbers falling below and above the expected value were then totalled for conditions of increasing and decreasing groat density.

b) Below the threshold density, the assumption of linear rise should mean that a constant proportion of the available groats are found. However, as we shall see later on, it is clear from the data that at very low densities this proportion drops off, so that it was unreasonable to compare the percentage of groats eaten at the density below the threshold density with a reference value consisting of the average of the percentage of groats found over the range. Instead, the reference value was taken as the mean of the two values for the density two below the threshold, and the two values just below the threshold were compared with this reference, as above.

In both cases, the null hypothesis is that an equal number of points lies above and below the expected value. The results are presented in Table 3.3.4.7-1, which lumps the data for above and below the threshold density, but separates it for increasing and decreasing groat density, and for the individual and meaned data.

Table 3.3.4.7-1

	Individual data			Meaned data		
	Above expected	Below expected	Chi^2	Above expected	Below expected	Chi^2
Density increasing	15	26	2.95	6	15	3.86^+
Density decreasing	17	27	2.27	8	14	1.60
All data	32	53	5.19^+	14	29	5.23^+

It is clear that, overall, there is a significant drop in the values found in the region of the threshold density, compared with those expected on the basis of a linear increase to a plateau with constant intake thereafter. I therefore conclude that voles do show a negatively-accelerated portion in their functional response, but it is not possible to say whether this is a characteristic which is present in some voles and absent in others, or whether all voles tend to show this response to some extent.

d) Positively-accelerated rise

It appears to be a common feature of the functional response of higher vertebrates that, at low food densities, an increase in the food density results in a more than proportional increase in the amount eaten (Holling, 1959a, 1965; Royama, 1970; Tinbergen, 1960; Mook,et al (1960). In the case of Holling's work has this response hasbeen demonstrated under controlled conditions; the other cases involve field studies which include the element of the temporal patterning of the food density, which could produce the same effect through a learning process. The question arises whether the same characteristic can be demonstrated in the present study, and whether the use of the index of distanced travelled can reveal something of the mechanism operating.

Inspection of the functional response curves themselves do not reveal an obvious upward-sloping curve. But this could mean that such an effect is limited to the lowest densities, and is masked by the over-all variability of the data. In order to reveal any effect, the data for each vole was converted to a standard basis, in which the amount eaten was expressed as a percentage of the individual's plateau value, and the groat density was expressed as a percentage of the threshold density, calculated from the intercept of the plateau groat consumption value and a linear rise up to the plateau. The results of this standardization are shown in Fig.3.3.4.7-5a,b, in which the results are presented separately for conditions of increasing and decreasing groat density. From this, it is apparent that for increasing density there is a reduction of intake at low densities, below about 20% of the threshold density. For decreasing density, the only apparent effect is a small one below 10% of the threshold density. So, on the general level, it appears that there is a small reduction at low densities combined with a temporal patterning effect.

This visual impression was confirmed by counting the number of times that the percentage of available food eaten at the lowest density was lower than the mean percentage for the next highest

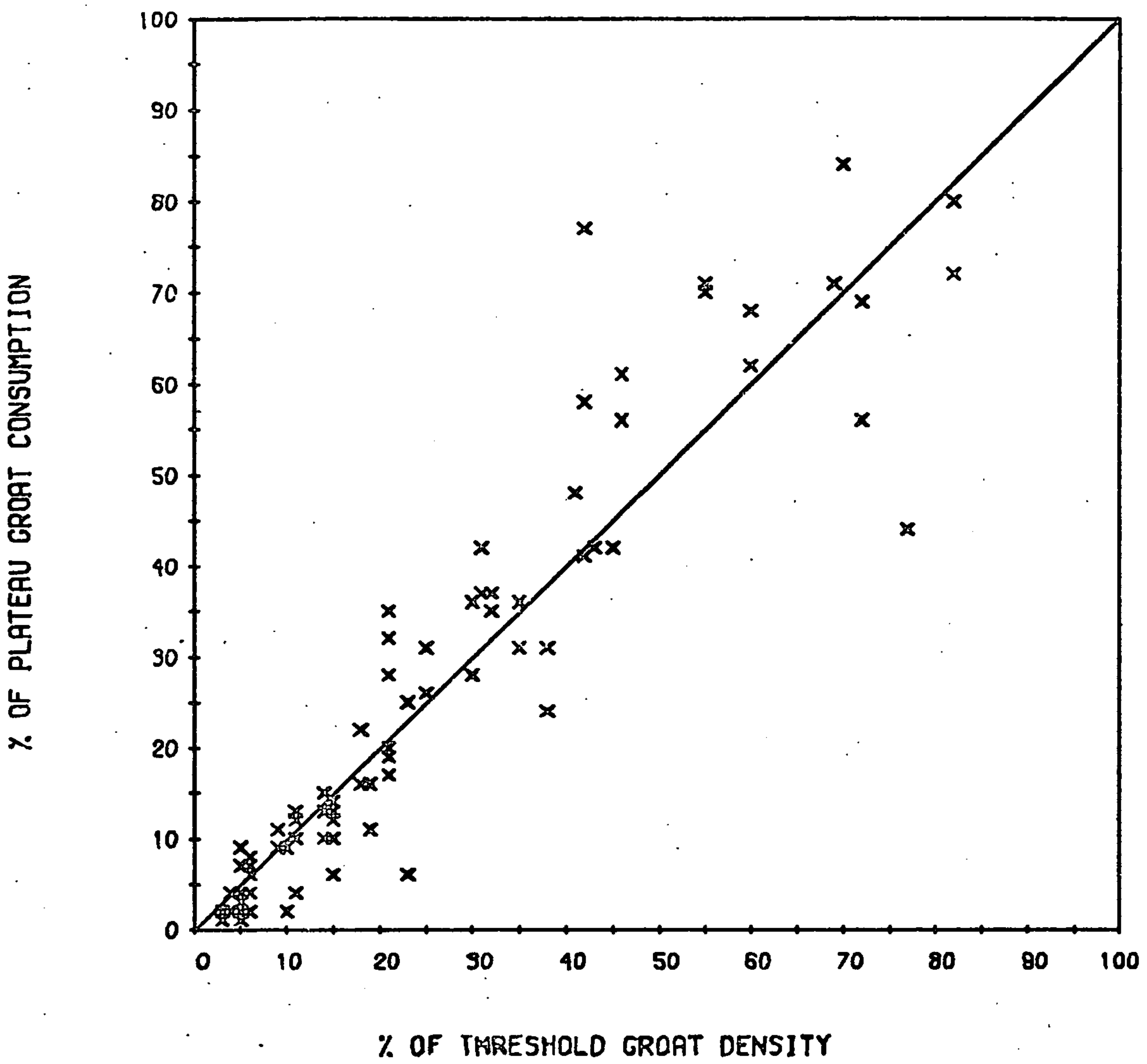


Fig. 3.3.4.7-5a

Standardised functional response for all voles, for increasing groat density.

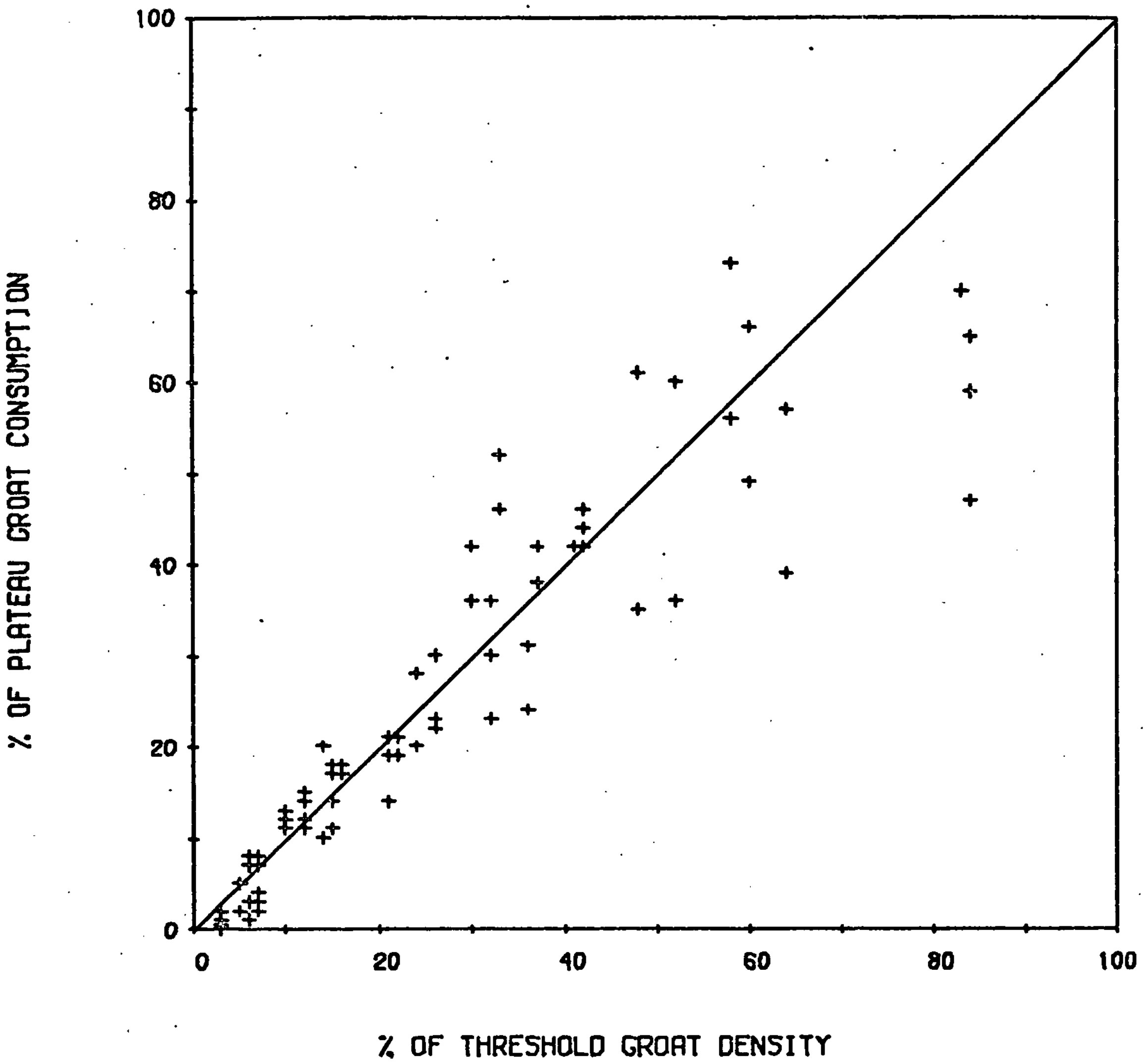


Fig. 3.3.4.7-5b

Standardised functional response for all voles, for decreasing groat density.

density, for increasing and decreasing densities respectively. The results are given in Table 3.3.4.7-2.

Table 3.3.4.7-2

	Less than	Greater than	Chi^2	
Density increasing	19	4	9.8	$p < .005$
Density decreasing	22	9	5.5	$p < .025$
All data	41	13	14.5	$p < .001$

The values for each vole at the lowest density are not truly independent, but the same result is obtained if the mean value at the lowest density is used instead, though the values of Chi^2 are lower at 5.3, 2.3 and 7.3 respectively, due to the smaller numbers involved.

Once again, it is not possible to state with certainty that a specific individual demonstrates this effect, using the index of number of groats eaten, since the numbers are very small and therefore have a relatively large margin of error. It happens, however, that the index of distance travelled is well suited to resolve this aspect of the response, since we would expect a smaller distance to be travelled at the low densities, and the index does not suffer from the drawbacks of one based on a small sample of discrete objects. In addition, it can tell about the vole's response at zero density, which is otherwise impossible to measure. There is no reason to believe that the response at zero density will be qualitatively different from very low densities.

Using this index, it is possible to determine a significant reduction in the index at low densities for individual voles. Fig. 3.3.4.7-6a,b shows the results for two voles, selected to show the reduction at low densities. They may be compared with the results obtained for one vole whose distance index remains constant at low densities (Fig. 3.3.4.7-3b).

The first of these shows the clearest of these results, in which both for conditions of increasing and for decreasing groat density, there is a smooth increase in the distance travelled from about 20 feet per day at zero density to a maximum of over 50 feet per day at density levels of 50 and 100 groats per area. The second graph shows a similar effect for a vole that was only tested on a decreasing density schedule. In the third case, the reduction in the index is only apparent at zero density; so although there is a definite effect which would probably manifest itself at groat densities lower than those used, the mechanism which produced this effect would have little impact on the functional response itself, due to its restriction to such a small density range.

I therefore conclude that some voles do show a reduction in searching at low groat densities, resulting in a positively-accelerated segment for the functional response curve. This effect is limited to a small fraction of the active range of groat densities, however, and is therefore of more interest for the light that it sheds on the mechanism of the vole's response, rather than for its consequences for either the food population or the feeding animal. The fact that this effect is reflected in the index of distance travelled is of great importance when we come to consider the components of the response: moreover, despite its

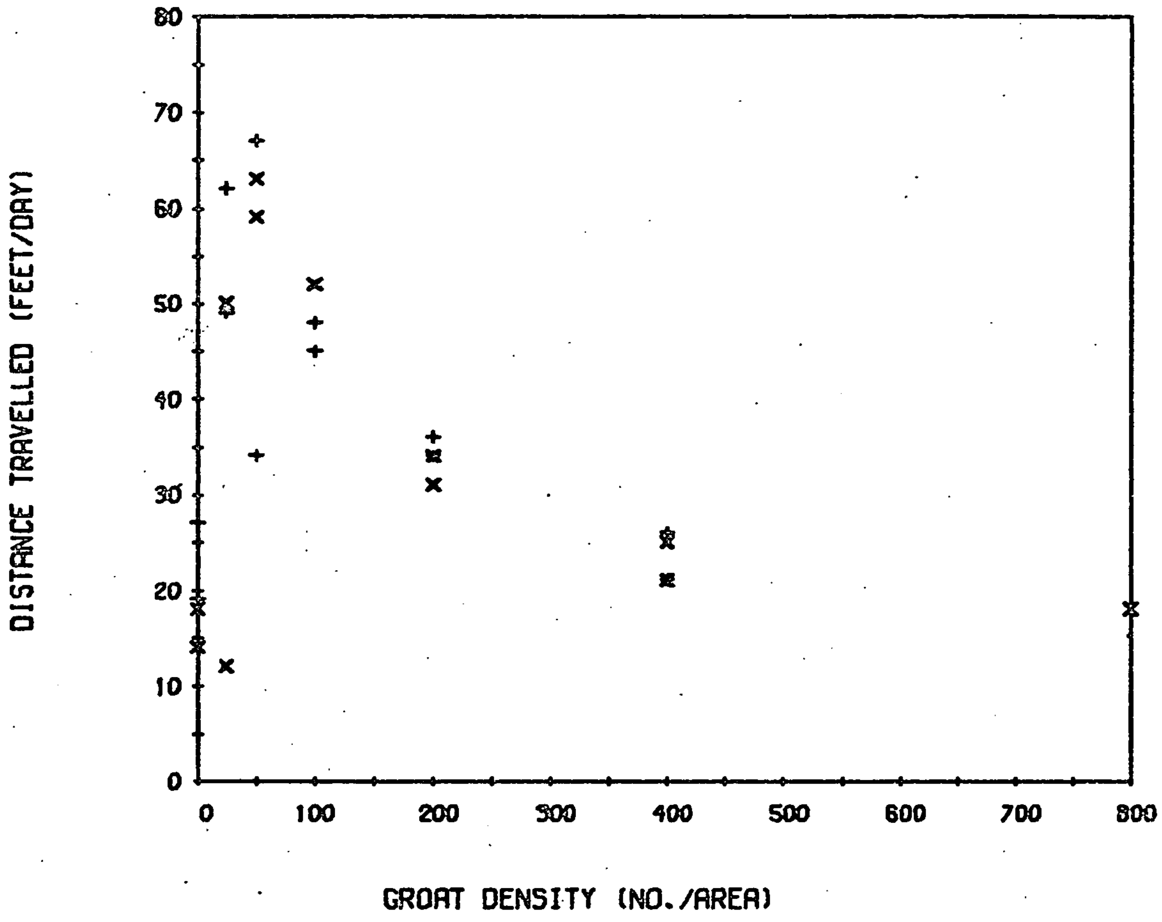


Fig. 3.3.4.7-6a

Distance index related to groat density for session S2 (I) illustrating depression of the index at low groat density

× :Groat density increasing
+ :Groat density decreasing

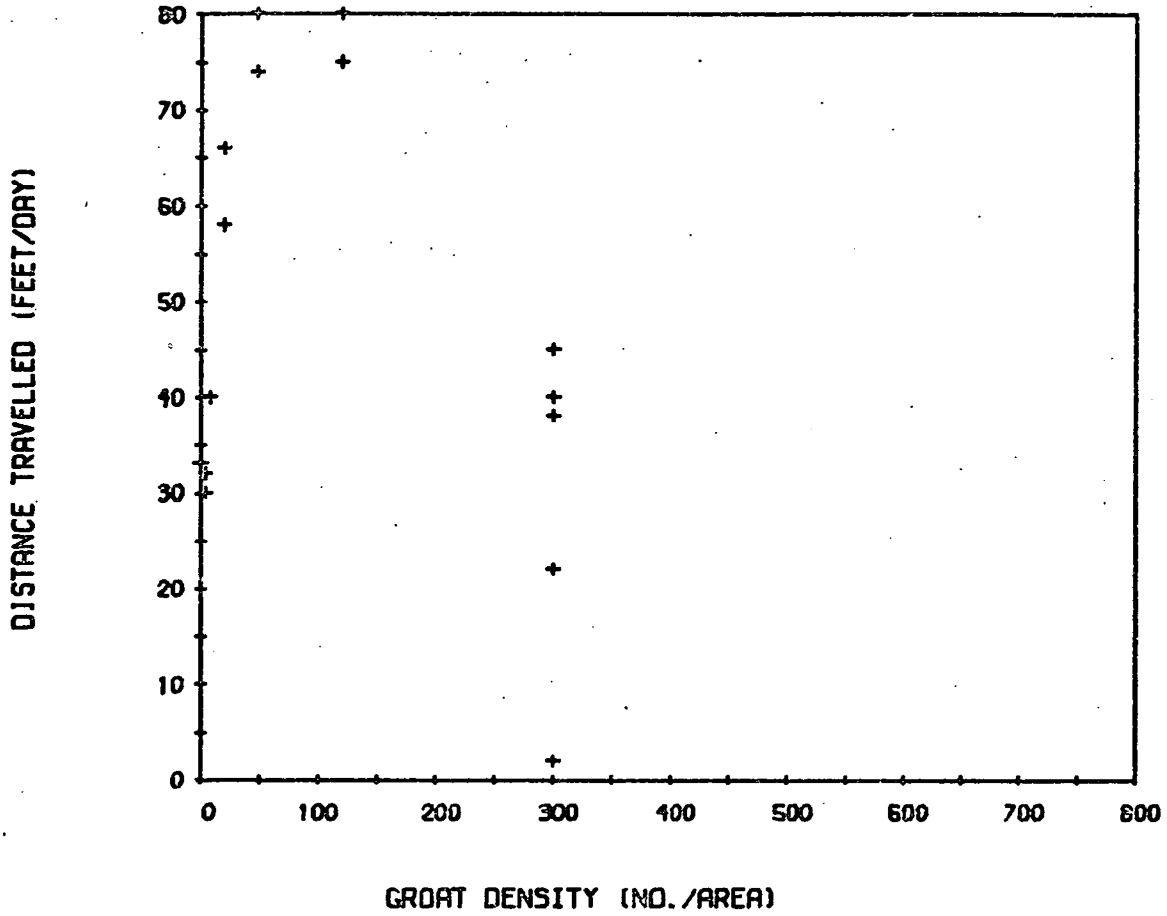


Fig. 3.3.4.7-6b

Distance index related to groat density for session S3 (I + II), for decreasing groat density only.

common-sense appeal, it is not predicted by the classical concept of "searching image", and can therefore be useful in re-formulating this concept (see section 6.2.4).

e) Effect of density schedule

It has sometimes been necessary above to distinguish between the results obtained when the groat density was decreasing, and those obtained when it was increasing. Since the density schedule was chosen so as to represent that found in nature, with a smooth pattern of increase and decrease rather than the random sequence used by Holling (1965), it is worthy of closer examination.

The simplest way of visualising this effect is shown in Fig. 3.3.4.7-7a,b. In these figures, the density schedule is shown plotted as the histogram at one-eighth scale, with the series of points indicating the number of groats eaten. In the first case, there is no obvious difference between the conditions of increasing and decreasing density, while in the second case it is clear that the vole finds a much higher proportion of the available food when the density is decreasing than when it is increasing. In Fig. 3.3.4.7-8a,b a similar effect is shown for voles subject to the reverse density schedule, i.e. a decrease followed by an increase in density. Thus, although the results for some voles may be affected by a long-term trend in their feeding or preference, it is clear that the results obtained here can not be ascribed entirely to such an effect.

An alternative way of treating the data is to consider how the magnitude of this effect varies as a function of groat density. To do this, the mean distance travelled at each density for

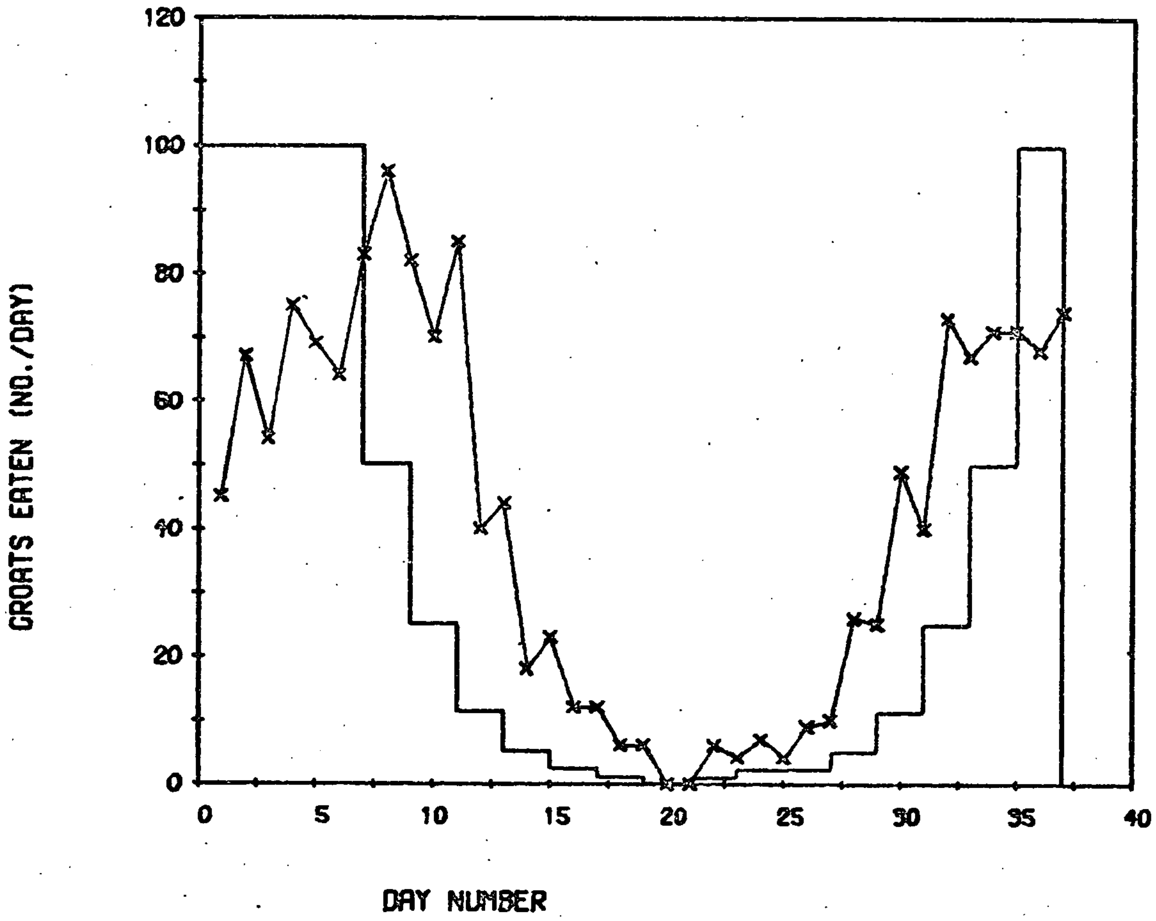


Fig. 3.3.4.7-7a

Groat consumption in relation to periods of decreasing and increasing groat density, showing no apparent difference.
The density schedule is scaled down by a factor of eight in this and the next three Figures.

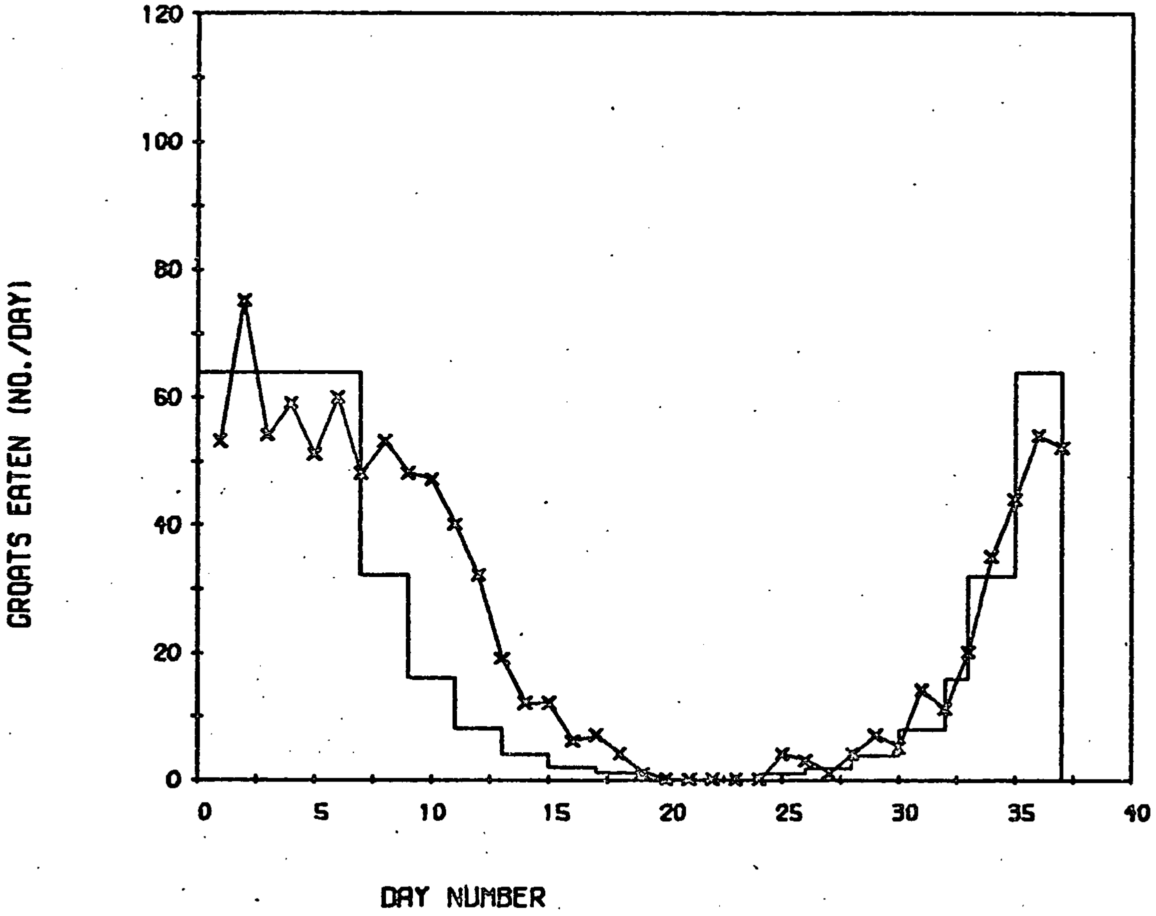


Fig. 3.3.4.7-7b

Groat consumption in relation to periods of increasing and decreasing groat density, showing a difference between periods.

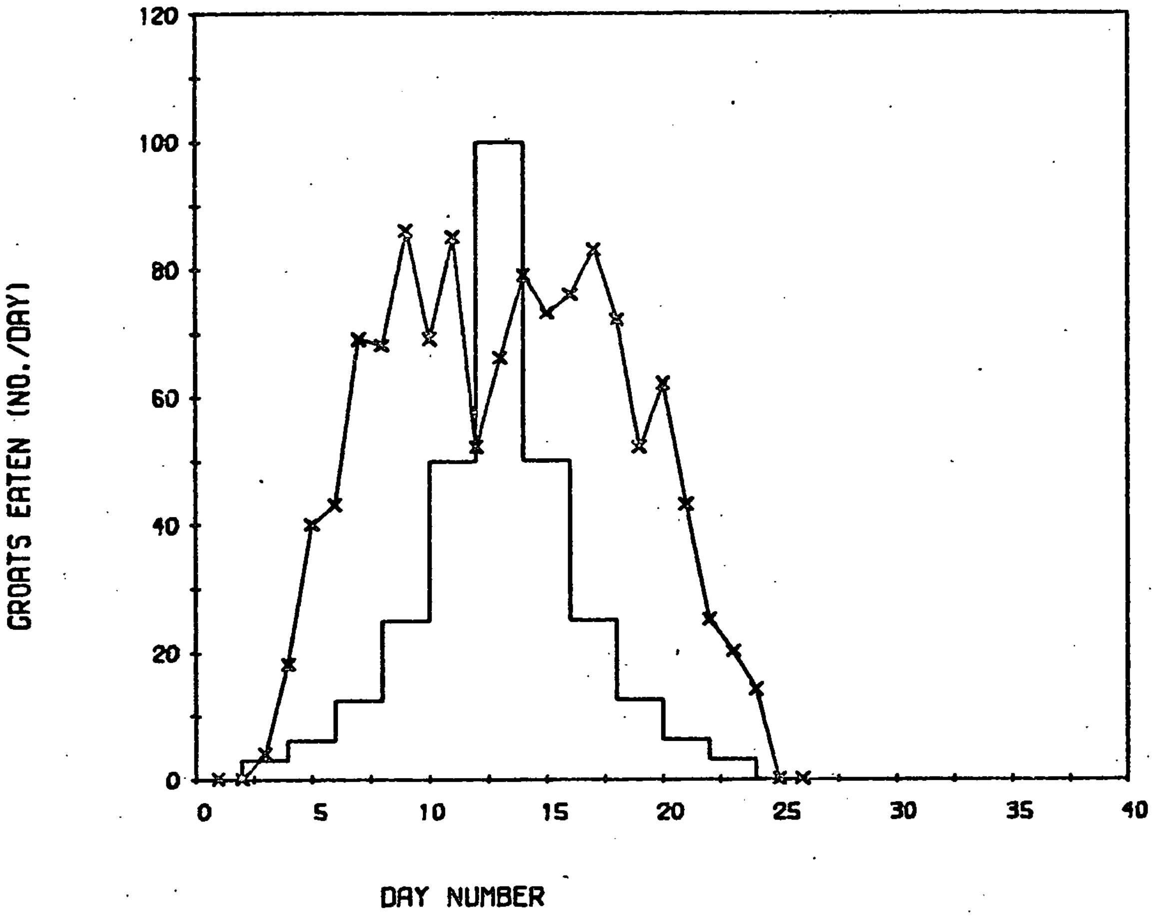


Fig. 3.3.4.7-8a

Groat consumption in relation to periods of increasing and decreasing groat density, showing no apparent differences.

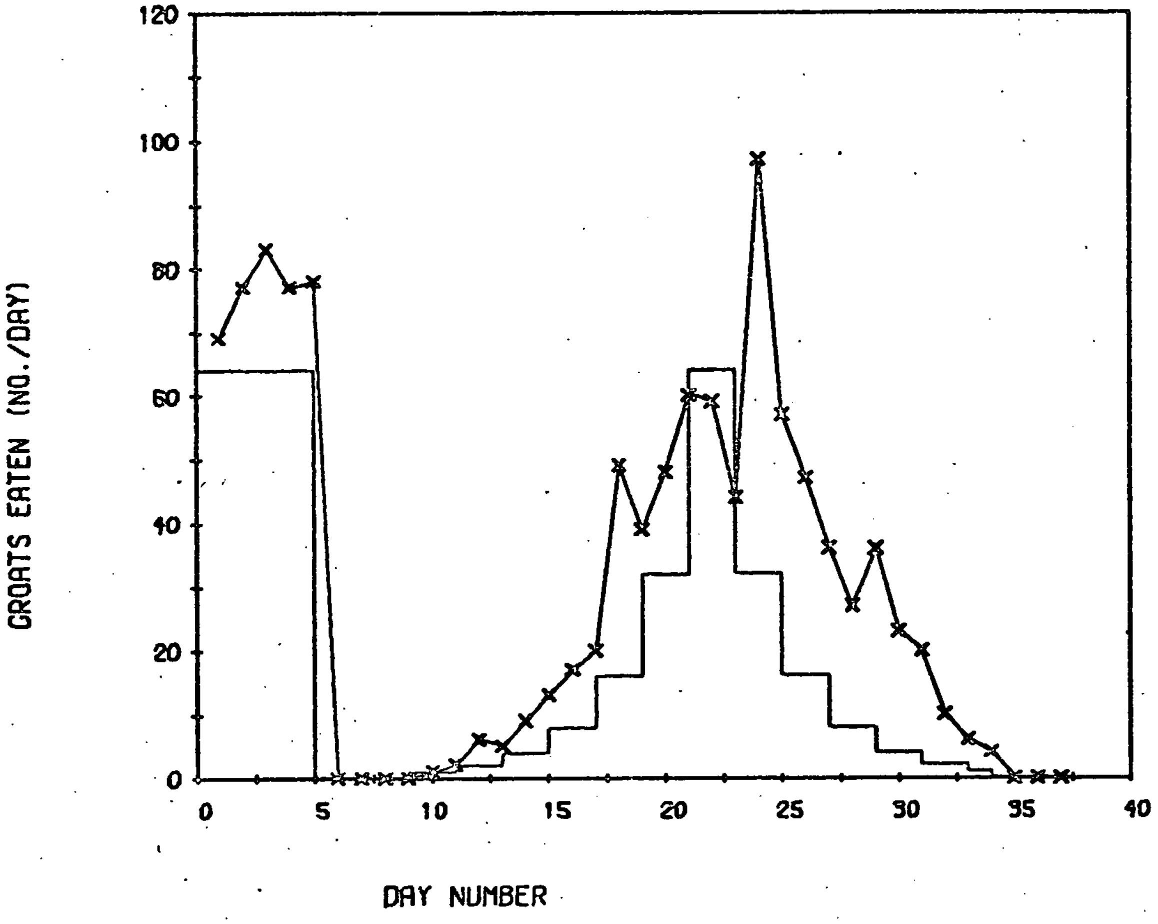


Fig. 3.3.4.7-8b

Groat consumption in relation to periods of increasing and decreasing groat density, showing a difference between periods.

increasing groat density is expressed as a percentage of the mean distance travelled for decreasing density. The results for the two voles illustrated above which did show a density schedule effect are presented in Fig.3.3.4.7-9 a,b.

It is apparent that the curve is approximately U-shaped, with the values at both very high and very low densities being similar for the increasing and decreasing density conditions. This is interesting though not surprising: at the higher densities the vole will be mainly limited by satiation, while at the very low densities the change in the reward rate in absolute terms over the last few days would have been quite small. Since the greatest effect is found over the major part of the rising section of the functional response curve, these findings are of particular importance when we come to consider the effects of the functional response on the food population and for the feeding animal, since this effect will result in quite large differences in the relative importance of different food species in the animal's diet between the two density conditions.

f) Adjustment to density level

It was pointed out in section 3.3.4.3 that the vole may take a day to adjust to zero density after a period at a higher density; the first day at zero density tends to result in an increase in distance travelled, followed by a decrease on subsequent days. In the functional response experiments themselves, the vole could only be tested for two days at each density level. The question then arises as to whether the first day is affected by the change

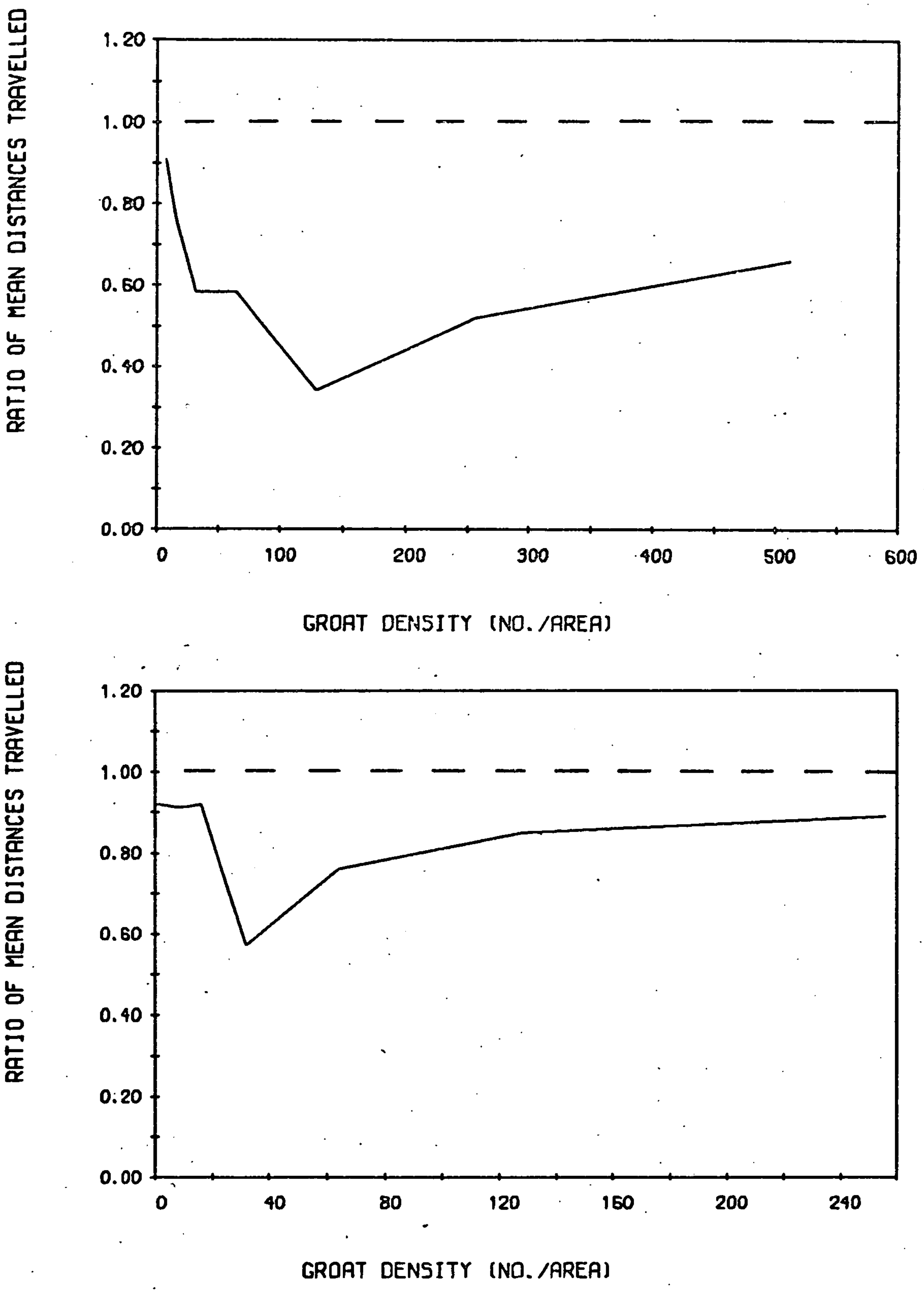


Fig. 3.3.4.7-9a, b

Ratio of mean difference travelled at each groat density, for increasing over decreasing density schedules.

from the previous day, or whether it represents the stable value for that density. If the latter is the case, then there should not be a significant difference between the two readings for the same density level.

The results presented above showing a difference between the rising and the falling part of the density schedule suggest strongly that there should be a difference between the two days at each density. This seems reasonable since the most likely explanation for the density schedule effect is a carry-over response from the previous density, perhaps a slowness to forget the previous density. We would not expect that this could affect the vole's true stable response for a particular density. Rather, the vole should tend to this stable value independently of the previous schedule, so that there should either be a rise between the two values during a period of rising density, or a fall during the period of falling density, or both.

The data for all voles was divided into the periods of increasing and of decreasing groat density. For each period, the data was scored depending on whether or not the second value at each density was less than or greater than the first, using the index of distance travelled, since this is the more direct measure of the vole's response and is less variable. The results are shown in Table 3.3.4.7-3.

Table 3.3.4.7-3

	Second value in relation to first, at each density		
	Smaller	Greater	Chi^2
Density decreasing	37	27	1.6 n.s
Density increasing	27	33	0.6 n.s

Although the trend was in the anticipated direction in both cases, there was clearly no significant effect.

Part of the reason for this, however, could be that within a period of increasing or decreasing density, the vole can be behaving differently at different densities. At the higher densities, the vole can find all the groats it requires without much trouble; one would not therefore expect any carry-over effects within this range, and the second value should have the same chance of being greater or smaller than the first. It is only below this range that the significant trends should show up. Another complication is that it is difficult to estimate the vole's subjective assessment of a particular density change; especially at lower densities, it could be that the change in density has a relatively small carry-over effect.

One way to resolve this problem is to consider the magnitude of the changes at any one density: this should be larger if the effect is genuine rather than if it is due to the inherent variability in the data. Consequently, a table similar to the one above was drawn up, but including those changes at each density which were larger than an (arbitrary) eight feet per day. (Table 3.3.4.7-4).

Table 3.3.4.7-4

	Second value in relation to first at each density			
	Smaller	Greater	Chi^2	
Density decreasing	19	6	6.8	p = 0.01
Density increasing	8	10	0.2	n.s

Now, while there is still no significant trend in the case of the increasing density, there is a strong effect in the case of the decreasing density.

In addition to this analysis, the data for number of groats eaten was analysed according to the same simple scoring system used initially. This showed results similar to those obtained here, with no significant effect for increasing density, and with an effect significant at the 0.05 level for decreasing density.

I therefore conclude that when the groat density is decreasing with two days at each level, the first day is higher than the equilibrium value for that density due presumably to the fact that the vole expects to find grains at a faster rate than it is actually finding them, and therefore makes an additional effort to satisfy its expectation as to how many should have been found. This effect is not sufficient to explain completely the differences found in the previous section between the periods of rising and of falling density: possibly there is a slower rise to the equilibrium level beyond the second day, for increasing or decreasing density, which has not been revealed due to the variability of the data and the limitation to two days at each density. Certainly, individual voles do not appear to conform to this general statement for the average vole, and a further understanding of carry-over effects would require more intensive investigation of the response of individual voles.

Quantitative Features

In this section, various features of the functional response curves for all voles will be described quantitatively. The periods of rising and of falling groat density will be treated independently, where appropriate. The results for all the features which will be discussed here are presented in Table 3.3.4.7-5 and reference will be made to this Table in the following discussion.

a) Plateau groat consumption

The table shows that the mean number of groats eaten by all voles at the plateau was 78. The range was quite large, from 48 to 134. Only in the one instance of session S2(IV) can we say that this value was influenced by the conditions of the experiment: it has been shown elsewhere (section 3.4.4.2) that overall response of this vole in its second experiment was lower than in its first (session S1(IV)), and that this is most likely due to the presence of wheat on the floor rather than in the nest. In the other cases there does not appear to be any significant relationship between the groat consumption and the percentage preference groats by weight; nor does the percentage preference for groats appear to be obviously related to other factors - the form of the wheat distribution (except in the instance mentioned), or the size of the experimental area. One

Table 3.3.4.7-5

Quantitative features of the functional response.

Session	Plateau groats eaten	% pref. for groats	Threshold density		Max.% groats found		Max. distance (feet)	
			Rise	Fall	Rise	Fall	Rise	Fall
S1 (I)	94	92	350	280	31	44	25	38
S2 (II)	49	83	107	101	53	63	52	52
S1 (III)	100	78	197	154	77	80	70	65
S1 (IV)	93	97	124	107	80	85	63	-
S2 (I)	79	96	114	128	76	71	56	56
S2 (IV)	48	52	102	147	50	44	41	42
S3 (I+II)	71	91	-	128	-	60	-	78
S3 (III+IV)	41	50	76	98	64	55	88	63
S4 (I-II)	55	68	170	128	37	63	50	64
S4 (III+IV)	55	61	328	143	34	46	35	56
S5 (II)	134	76	250	220	59	70	50	51
S5 (III)	86	86	130	134	66	69	53	52
S5 (IV)	72	77	140	140	59	71	44	44

would not expect the size of the experimental area to affect the plateau value if the higher densities used really did represent a plentiful supply of groats, since then it should not matter whether this supply is spread over double the area.

The mean percentage preference for groats at the plateau was determined by the method of multiplying the number of grains of wheat and groats taken by their mean weight. This overcomes difficulties when a large number of grains are put down, and small changes in the mean grain weight due to humidity changes can result in large errors if the weight of grain recovered is simply subtracted from the original weight. Using this method, the mean percentage preference for groats at the plateau for all voles was 82%, with a range from 61 to 97. These values would be expected from monitoring experiments on caged voles, and I therefore conclude that the experimental conditions associated with measuring the functional response does not have a marked effect on the vole's basis for maintaining a mixed diet when supplied with abundant food.

b) Threshold density

Although it was normally fairly easy to determine from the functional response curve the two density levels lying above and below the threshold density, the density at which the plateau is assumed to begin, I required a more precise measure as a basis for comparisons between voles. The assumption was made that the response could be approximated by two straight lines, a linear rise followed by a horizontal plateau, similar to the method used before for testing for a negatively-accelerated part of the curve. In this case, however, the slope of the linear rise was not determined by averaging all the values for the percentage of groats found; rather, the slope was determined from the ratio of the sum of all the values for number of groats found, divided by the sum of the corresponding density values. This produces a slope which is more strongly influenced by the larger values; it is thus less affected by the large sampling error at small groat densities, it biases the result in favour of those values which are closer to the point of intersection with the plateau, and the line produced is visually a better fit to the data.

The threshold value was calculated separately for the periods of rising and of falling groat density. This was done because I have shown earlier in this section that there is a difference in the response under the two sets of conditions, and since this effect is not seen in the plateau value, it must tend to affect the slope of the rise to the plateau, and therefore the estimate of the threshold density. This is confirmed by the results: the voles which showed the largest difference between the rising and the falling part of their response curve, S1(I), S1(III), S4(I+II), and S4(III+IV), show the largest difference between the two estimates of threshold density.

There are two features to note about these values for threshold density. The first is that there is a relationship between the threshold and the ad lib. groat consumption. This means that, between voles, the rate of search does not increase in proportion to plateau groat consumption; this will be considered later when I will discuss two indices of rate of search.

The second point is that the effect of putting a vole on double the area does not result in a proportionally higher threshold density, as would be expected if the vole's search rate was not affected by doubling the available area. Since for the sake of consistency the term 'density' had been used throughout to indicate the number of groats per <u>total</u> area, the threshold density for those voles on a double area should be twice as large as that for the other voles, if in fact it occurs at the same level of groats per unit area. The table, indicates that this is not so, as the threshold densities for the two groups are approximately the same. Part of the explanation lies in the fact that the voles on the double area appeared to have a lower ad lib. groat consumption than the other voles, and we have seen that this should, presumably independently, result in a threshold density lower than expected, but this does not account for all the discrepancy.

The two remaining sets of summary results included in the table, are both measures of the voles' maximum search rate. Both are considered separately for rising and falling groat densities. The first estimates the maximum percentage of available food found by the vole, by taking the arithmetic mean of the four highest values. Assuming that this is approximately equal to the percentage of the area covered by the vole, this measure indicates the effort that the vole is willing to put into searching for food at its most motivated. It can be seen that quite a high fraction of the available food is found, from over 30% up to 85%. It is also apparent that this index does not appear to be related to the vole's ad lib. groat consumption, and this explains why a positive relationship between threshold density and ad lib. groat consumption was found.

The other set of summary results considers the maximum distance travelled per day, again taking the four highest values for rising and falling groat density separately. These indicate that most voles are willing to travel between 40 feet and 70 feet per day through the brushes. If we take the average speed of a vole as 2 cm /sec. (section 5.5), then this means that between 20 minutes and 35 minutes at a maximum is spent per day in searching for groats. This is only say 2% of the day, so that it would appear that it is not the actual time involved which limits the vole's maximum searching effort.

How would we expect these two indices to change as the area is doubled? If the effort put in by the vole depended only on the number of grains per unit area, then the percentage of groats found should be halved, while the distance travelled should remain the same. Returning to the table, it can be seen that this is not so. The observed values for the double area are greater than those expected from the means of the single areas, though this is more marked in the case of the percentage of groats found, than in the distance measure. It therefore seems that the basic behavioural response of the vole is little changed by doubling the area available for groat searching: the response is basically determined by the number of grains encountered per unit distance covered, and not by the number available over the total area.

In view of this, it is hard to understand why the percentage of groats found are not lower on the double areas. It was shown elsewhere (section 3.4.4.6) that the ratio of distance travelled to percentage of groats found is fairly constant. Moreover, considering the data presented in the previous table, the ratio for the single areas is fairly constant, lying between 0.7 and 1.0, while for the double areas it ranges from 0.3 to 0.68. Possibly this is due to a difference in the reactive distance of these voles, either an intrinsic one or one produced by the different conditions. This seems unlikely, since the true densities used in these experiments were not so very different between the two sets of experiments. The alternative is that the ratio is affected by the density of vole tracks over the area, since the track density will be less if the same distance is covered over twice the area, and a lower track density will result in a smaller chance that two tracks will cover the same area. However, using the maximum four values for the two indices, there was no evidence that the ratio of percentage of groats found to distance travelled dropped off as distance increased for the single-area voles (Fig. 3.3.4.7-10). Also, it can be seen from this figure that even when the distance measures for the voles on the double area are divided by two, to make them comparable with the single-area voles, the points still lie above the corresponding points for the other voles.

Thus, of the possibilities put forward to explain these anomalous results, the only one that cannot be ruled out is that the apparent reactive distance of the vole is increased by the change of conditions. It is highly unlikely that the four voles used in the double areas each had a greater reactive distance than any of the eight used in the single areas - the

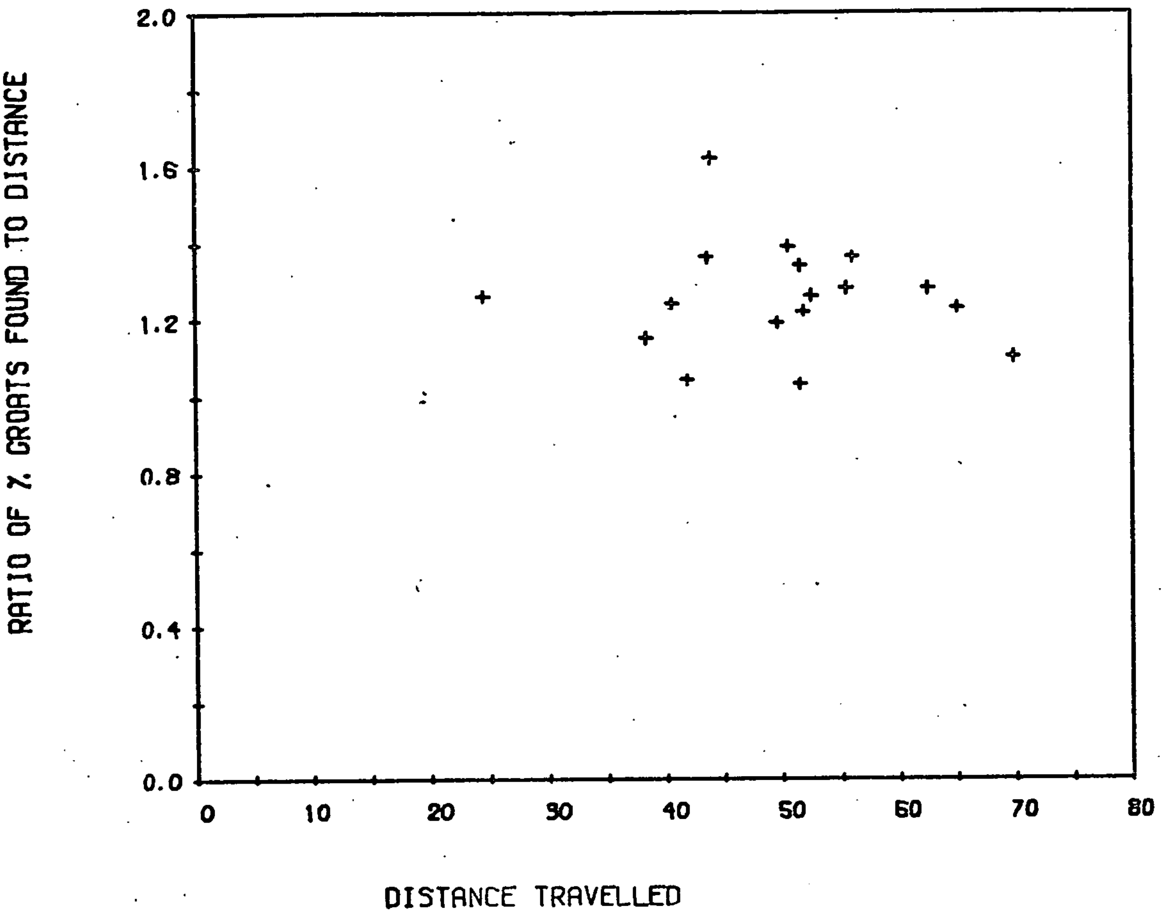


Fig. 3.3.4.7-10

Efficiency of finding groats related to distance travelled.

probability level is 0.004 that this could arise by chance. The possible effect of track density has been discounted above.

This discussion has shown that the quantitative measures of the functional response can be affected by the pattern of wheat distribution (session S2(IV)), and to some extent by the size of the experimental area. There still remains much variability in the various parameters of the functional response which can only be ascribed to inter-vole differences. This includes the measures of the threshold groat density, the plateau groat consumption, the maximum percentage of groats found and the maximum distance travelled, but not it would appear in the ratio of these two last parameters, indicating that the vole's reactive distance is more or less constant between animals.

In addition, however, there can also appear differences within a vole at different times. The only vole that was kept under the same conditions for two complete cycles was that used in sessions S1(I) and S2(I). It is clear from Table 3.3.4.7-4 that there are differences between the two sessions in most of the parameters. These differences are in the direction anticipated if the vole became used to the experimental conditions and was better able to exploit the area; that is, the threshold groat density is lower in the second case, and the maximum percentage of groats found and distance travelled is greater.

Section 4 Aspects of Feeding Behaviour

4.1 Introduction

The previous section discussed the description of functional response curves obtained for a number of voles, and the problem now is to analyse the mechanisms responsible for the shape of these curves. There are three methods available for doing this:

a) Deductions from the functional response experiments themselves. These were discussed in the previous section; the most obvious example was the fact that the reduction in numbers of groats eaten at low densities was largely due to the vole travelling smaller distances at these densities.

b) Deductions from general experiments designed for monitoring and describing the vole's feeding behaviour.

c) Analysis of experiments designed to study particular components of the feeding system and their inter-relationships (section 5).

The present section is concerned with the second of these approaches. It is the first stage of what Bellman calls "mathematical experimentation" (Bellman, 1962, Holling, 1965), and is the approach used by Holling (1965) in his analysis of the influence of the learning process on the functional response. To quote Holling, the approach "requires less information concerning cause and effect relations - just enough information to suggest a variety of different hypotheses...". It is not concerned with individual components of the feeding system, but rather aspects of the animal's behaviour which can be assumed to be derived from aggregates of components; hence, the qualitative relationships between components can be deduced.

The principal experimental method used in these studies was the daily monitoring experiment, in which various aspects of the vole's consumption, hoarding, and in some cases drinking, were recorded each day. Data derived in this way can be used both for determining static features, such as quantifying levels of consumption, classifying hoarding into various types, or determining the relation between consumption and body-weight. It can also be used for investigating dynamic relationships, such as the relation between amounts eaten on one day and on the next, or the relation between consumption and changes in body-weight. These dynamic features can in turn suggest mechanisms for the longer-term control of intake and preference.

Other methods used in this section include simple observations on searching and feeding voles, to obtain descriptions of their searching and eating behaviour; analysis of movements in and out of the nest in relation to hoarding behaviour; and analysis of data from event-recorders showing the fine-scale patterning of eating and drinking bouts.

4.2 Vole feeding behaviour

Fig. 4.2-1 illustrates the way in which the bank vole handles grains for eating. The grain on the photo is a groat grain, but the same posture is adopted for wheat.

The vole holds the grain in its front two paws, with one end, usually the endosperm end, facing upwards. The grain is then nibbled away in a rapid series of bites. When eating a groat grain, some voles occasionally left the last fragment,

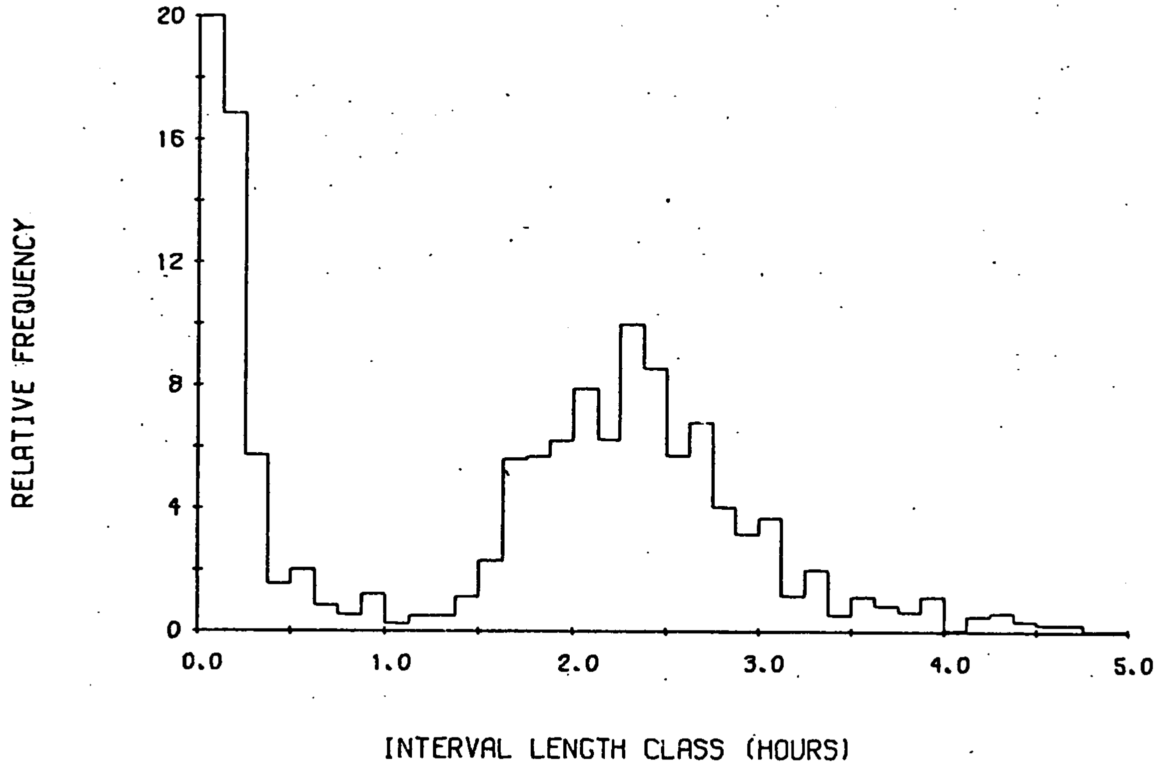
Fig. 4.2-1

Vole eating a groat grain.

which may be 10%-20% of the whole grain weight. More commonly, voles feeding on wheat might only eat a small part of the grain - mainly endosperm, discarding the remainder. Not all voles showed this pattern, and, of those which did, most would also eat some wheat grains completely during the same period. This means that "wheat" should be considered as two different food types, since the bulk of the grain clearly differs from the endosperm in terms of hardness and nutrient composition. Although a separate record was kept in most experiments of the number and weight of partly-chewed wheat, I have lumped the two together when referring to "weight of wheat eaten".

Under ad lib. conditions the vole typically feeds in a series of bouts. These bouts can be recognised by the fact that the intervals between taking grains within a bout are easily distinguishable from intervals between bouts. Fig. 4.2-2 shows the frequency distribution of interval lengths for two voles, using data obtained from the automatic feeding machine described in Appendix A3. In both cases, the results form a bimodal distribution. The valley between the two modes then provides a criterion for distinguishing between intra- and inter-bout intervals. There are usually between 8 and 12 bouts per day, giving an average inter-bout interval of 2 to 3 hours, as may be seen on these two examples.

Within a bout, the grains are eaten in rapid succession, with the next grain being taken usually in under 5 secs. from the end of the last grain. Often, the remnant of the last grain is still being chewed while the vole moves to pick up the next. The consistency of this pattern means that the interval between successive grains is fairly uniform, though it is more



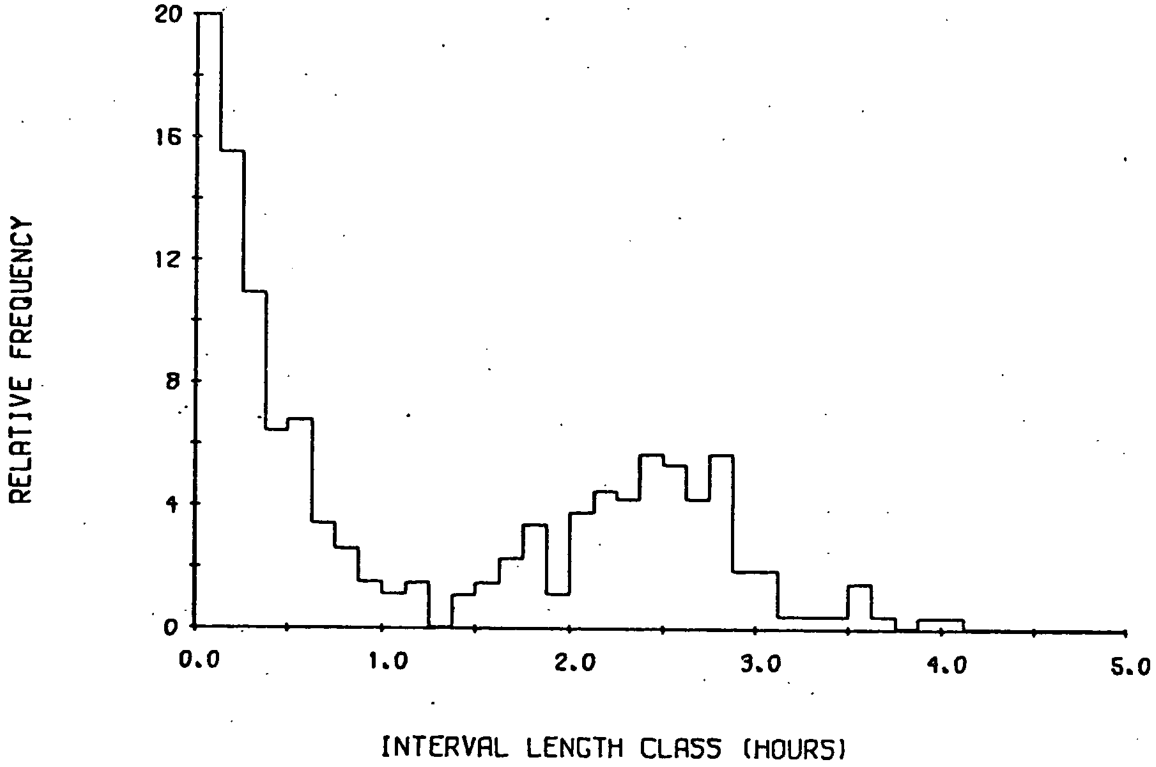


Fig. 4.2-2

Frequency distribution of all intervals between groat or wheat selection, for two voles.

uniform for groats than for wheat. Some examples of this are given in section 5.6, where this uniformity is used to derive an estimate of handling time for groats and wheat.

4.3 Vole searching behaviour

The searching behaviour of the bank vole was observed in the experimental arrangement used for measuring the vole's speed of movement (section 5.5). The vole could be observed from underneath travelling through blocks of brushes identical to those used in the functional response experiments (section 3.3).

The behaviour showed two distinct phases.

a) Forward movement. Normal movement through the brushes achieved by pushing against the floor and forcing a way through the brush bristles. Direction of travel is usually fairly straight. Grains encountered are eaten; if detected but not immediately accessible, the vole stops then forces its way towards the grain.

b) Probing. The vole is stationary and pushes its head 2-3 cm into the brushes to either or both sides. This occurs during forward movement at approximately 5 sec. intervals, or about every 10 cm, though it is a very variable element of behaviour. Detection of a grain during probing results in movement to the grain, as before.

It was not possible to resolve these two phases in the track records obtained from the functional response records. Therefore the index of distance travelled per day only indicates the forward movement component. This means that the estimate of reactive distance derived from these results (section 3.3.6) is a composite of the true reactive distance and the probing behaviour. Nor did the equipment used for recording the speed of movement of the vole (section 5.5) permit me to resolve the two phases, owing to errors in the operator following the vole's movement, and to the fact that the vole's co-ordinates were only obtained every 0.5 sec.

The daily pattern of the vole's searching behaviour in the brushes system was not recorded. There was no point in attaching a recording system to the vole's nest-box in the functional response experiments, since voles almost invariably nested under the brushes after the first few days. Nor could I observe its searching pattern for prolonged periods in the experimental arrangement designed for measuring speed of movement, since the area of brushes was too small, being only 1/4 or 1/8 of that used in the functional response experiments. However, Hill (1975) found that bank voles showed bouts in their visits to a feeding station in which the probability of finding a grain could be varied by the experimenter. Since this experiment was designed as an analogue of my functional response system (in which the vole's probability of finding a groat grain is a function of groat density), it is likely that the vole shows similar behaviour in the brushes system.

4.4 Consumption

4.4.1 Day-to-day stability

Voles, in common with most herbivores, show the ability to maintain their intake at a more-or-less constant level in the presence of an abundant food supply. The maintenance conditions for the voles invariably involved an ad lib. supply of food and water, and at no time were there any symptoms of obesity. The absence of a trend in the very long term, however, does not mean that there are no short-term fluctuations. In this section, I will investigate the day-to-day variability of consumption, and in the next I will consider evidence on the regulation of intake.

The measure of consumption used throughout refers to the total weight of groats and wheat consumed per day, without any correction for the moisture content for the two grain types (which in any case are very similar, being 14% for groats and 12% for wheat), or for differing digestibility, since this would involve an implicit assumption about total consumption from the vole's point of view. In all the experiments referred to here, the voles were kept in individual large cages, measuring 34 cm x 49 cm x 17 cm (height), under ambient conditions of temperature (approx. 20°C) and humidity, with an ad lib. supply of water. The two grain types, groats and wheat, were always presented separately, either in separate petri dishes placed next to each other or in a specially designed petri dish divided by hard-board partitions into four quadrants, with the same food type in opposite quadrants. This design was used to remove the possibility of any position effect influencing the vole's preference, though separate experiments discounted the importance of any such effect. When the two separate dishes were used (in the earlier experiments), the relative positions of the two dishes were kept the same from one day to the next, since the aim of these experiments was basically to examine day-to-day variability of consumption and preference, rather than to obtain the "true" values for these measures.

An idea of the day-to-day stability of consumption data can be obtained by considering the coefficient of variation, that is, the ratio of the standard deviation of the data to the mean; this standardises the measure of variability and permits comparisons to be made between voles. In the following discussion, the coefficient of variation is expressed as a percentage.

There were two experiments in which the consumption of the vole was monitored for a sufficiently long period of time to enable the coefficient of variation to be estimated. In the first, four voles were monitored for eighteen days, while the second involved twenty voles over sixteen days. All the values for the coefficient of variation for the first group were included in the range of values for the second group, so the two sets will be considered together.

The median value obtained was 13.3%, which means that, assuming normality of the data for the individual, 95% of the values for the average vole are likely to fall within approximately 25% of the vole's mean level of consumption. The quartile range for the coefficients of variation was 11.3% to 16%, and the overall range, from 8.6% to 27.3%. Although no formal test was carried out, to test the null hypothesis that all voles have the same coefficient of variation, the spread of values makes it unlikely, as does the fact that the distribution of values is markedly positively skewed, with several very high values, and this would not be expected if the values of the coefficient of variation were drawn from the same population. I therefore conclude that voles differ in the stability of their consumption from one day to the next.

Part of the variability of the data can be attributed to a sampling effect. Since voles tend to feed in bouts (Section 4.2), with about eight bouts per day, small variations in the regularity of bouts can mean that a different number of bouts are involved on different days, so that even if the size of each bout is constant, a slightly delayed bout could decrease the previous day's apparent consumption by 1/8 and increase the next days by the same amount, producing a 25% difference between the two values. Unfortunately, it is not possible to quantify the fraction of the coefficient of variation due to this, since this involves making assumptions about the variability of the inter-bout intervals, then generating an artificial sequence of bouts and sampling this at intervals of twenty-four hours. It is sufficient to say that while this may account for part of the day-to-day variability, there is still likely to be a remainder due to genuine differences in consumption between successive days.

The remaining variability could either be due to random variations in the level of intake between one day and the next, or else neighbouring days could bear a relationship to each other. In order to test for the presence of such a relationship, the data was analysed as a time series, using the technique of auto-correlation. This method involves correlating the data with itself lagged by successively-increasing number of time units. Thus, for a lag of one, the correlation coefficient is calculated between each item of data and the succeeding one, while for a lag of two it is calculated between each item and the next but one. Thus, if the correlation coefficient for a lag of one is significantly positive, it means that there is a positive relation between the amount of food eaten on one day and the amount eaten on the next.

Of the twenty-four voles tested, only three had significant correlation coefficients for a lag of one day. These three were significant at the one percent level, so that it is clear that this is not a chance result of calculating the correlation coefficient twenty-four times. In each case, the coefficient was positive, which means that each day bore a closer relationship to the next than would be expected by chance. The possibility that the positive correlation could be due to a trend in the data - a gradual increase or decrease of consumption over time - was discounted by the fact that the coefficient for high lag units became negative, a result which would not be found if such a trend were present.

It is possible that some of the remaining voles also showed a real effect, but that this was not discovered by the use of the arbitrary 95% confidence level. If this were so, then it would be expected that more of the voles should have had a positive correlation for a lag of one day than a negative one. In fact, the figures were thirteen positive to eight negative, which clearly does not depart significantly from 50/50, so it can be assumed that the remaining voles showed no effect.

It would appear that, for those three which did show a significant effect, this relationship tended to increase the apparent variability of the data, as measured by the coefficient ofvariation, since for these three the values were 27.3%, 17.2% and 16.2%, considerably higher than the median value of 13.3%. This is to be expected, since the addition of regular fluctuations to the vole's intake would be in addition to the inherent variability of the data.

It may therefore be concluded that the average vole shows considerable stability in its total daily consumption, with a true coefficient of variation rather less than the median value of 13.3% actually found, since this is subject to sampling error as well. It would also appear that, if regulation of intake is a dynamic process, responding to the physiological effects of past levels of intake, then this response takes place in a short period, generally less than a day, since for most voles there is no relationship between the amount eaten on successive days. For those voles which show a positive relationship between successive days, it can be deduced that this is due to a rather longer response time, so that there could be a lag of several days between the vole eating too much or too little and its becoming aware of the fact.

4.4.2 Regulation

In the previous section, it was deduced that the typical vole regulates its intake over a short time period, since for most there is no relation between the amount eaten on one day and the amount eaten on the next. In this section, another aspect of regulation of food intake will be considered. This does not consider the dynamic aspect of regulation, but rather tries to identify the parameter that an animal in a two-food situation attempts to regulate.

Five possible situations can be envisaged:

a) The vole tries to maintain a constant ratio between the amount eaten of the two types of foods. In Fig. 4.4.2-1, which represents hypothetical relationships between the amount of one food eaten per day and the amount of the other eaten per day, this possibility is represented by the line passing through the origin. In this case, the ratio of the amounts eaten shows less variability than the total amount eaten, so that the data points tend to lie along this line, with the slope representing the relative preference of one food over the other.

b) If the vole tends to maintain a constant intake irrespective of the relative amounts of the two foods eaten, then the diagonal line crossing the two axes should result, so that the more that is eaten of one food, the less there will be eaten of the other. If the two axes are in weight units, then the slope of the resultant line should be -45° if the two foods make equivalent contributions to the factor that the vole is attempting to regulate. If the slope differs significantly from -45°, then this indicates that the air-dry weights of the two foods are not

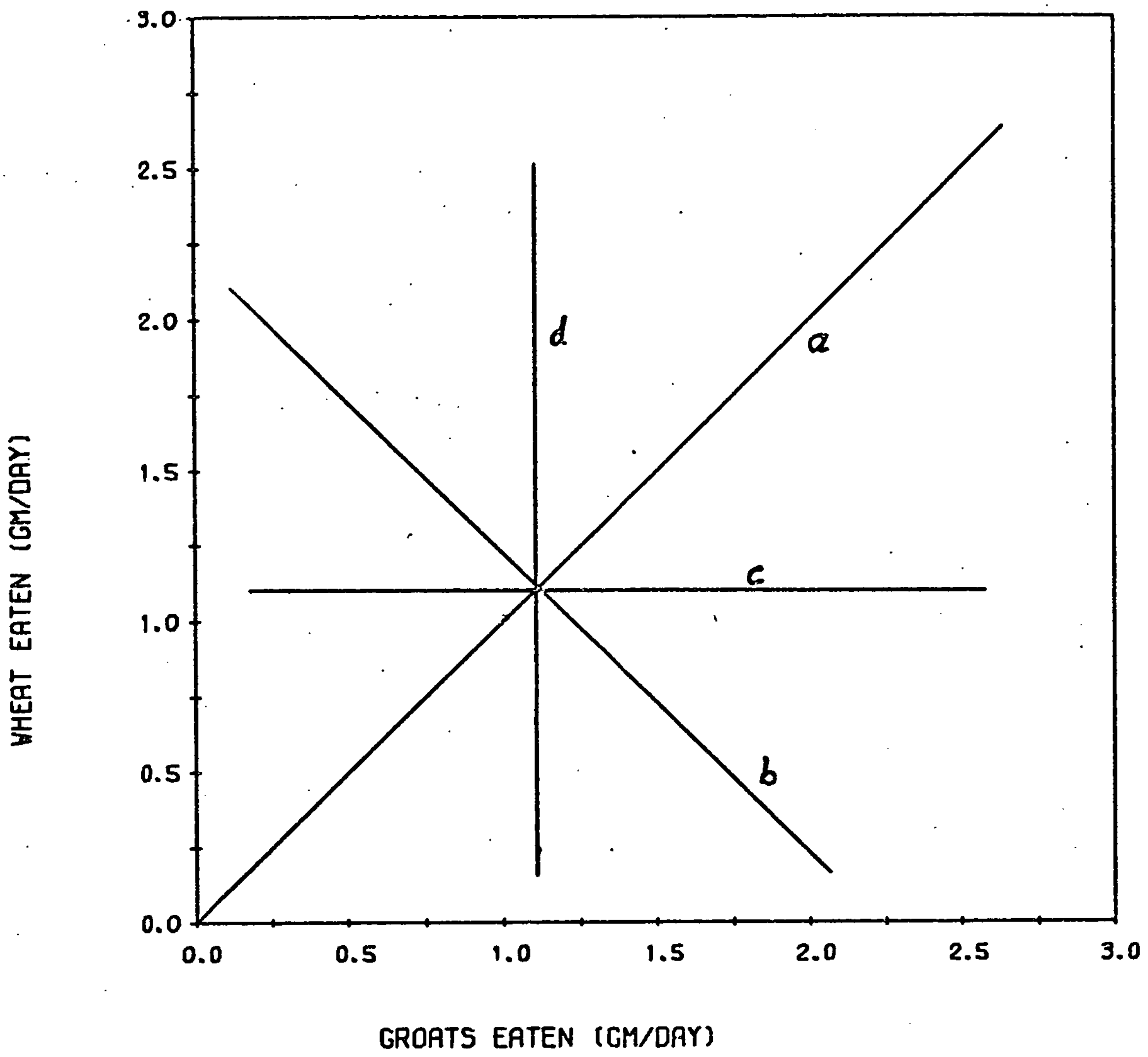


Fig. 4.4.2-1

Possible relationships between the weight of two foods eaten per day.

equivalent. This could be due to the differences in moisture content, differences in digestibility, or relative differences in composition of the nutrient or nutrients whose total intake the vole is trying to regulate.

c,d) If the vole tries to maintain a constant intake of one food type, and is not concerned about the exact amount eaten of the other type, then this would result in the data falling on a horizontal or vertical line. This would be most likely to apply if only one food contained an essential nutrient. Since voles can be maintained successfully on either groats or wheat for indefinite periods, we would not expect to find this type of relationship.

e) In a variety of situations where no one regulating factor had priority, no definite relationship would be detected.

Using the same twenty-four voles as before, it was found that nine of them showed a significant negative correlation between weight of groats and of wheat eaten,(2 at the 5% level, 3 at the 1% level, and 4 at the 0.1% level). In no case was there a significant positive correlation, and, although this would not be detected by the correlation coefficient, there was no evidence that the data could best be described by a vertical or horizontal line. I therefore conclude from this that the vole tends to regulate its intake primarily by the total amount of food eaten. This does not mean that the scatter of points along the diagonal line is necessarily due to random variation in its attempt to satisfy a fixed reference level for preference; it is also possible that this reference level for preference is changing over the course of the experiment. But we can conclude that the reference level for total consumption is more important in that either it remains more constant over a period of days, or the vole is better able to assess the discrepancy between actual and desired levels for consumption than for preference.

The problem of determining the slope of the diagonal is complicated by the fact that the regression coefficient linking the amount of groats to the amount of wheat eaten depends on which variable is taken as the independent variable: ideally the regression coefficient for wheat on groats should be the reciprocal of the coefficient for groats on wheat. In fact, the actual values departed from this ideal, so an average value for the amount of wheat eaten over amount of groats was obtained by averaging the one coefficient and the reciprocal of the other. Using this method, it was found that, of the six values used, four had a slope lying between 0.66 and 0.72, while the other two had values of 1.09 and 0.97. These last two indicate that for these two voles, a unit weight of groats and of wheat contributed equally to the regulating variable. In the case of the other four, the value for the slope of less than one means that, for every gram less of groats, the vole eats only an additional 2/3 gm of wheat. This is a surprising result, since it means that one gramme of wheat contributes more to the regulating factor than one gramme of groats, and this despite the fact that wheat appears to have a lower digestibility (section 5.3). Possibly this result is due to the fact that the experiments were conducted in an ad lib. situation, so that the changes in the ratio of wheat to groats eaten were not determined by experimental manipulation. Also, the vole's response on any one day, in terms of total weight eaten, may not represent the equilibrium response for that particular ratio of groats to wheat. Certainly, when voles are kept on either groats or wheat alone for lengthy periods, those on wheat eat a greater weight per day. Furthermore, in the functional response experiments, where the amount of groats available was limiting, the total weight eaten either remained constant or increased as a higher proportion of wheat was eaten.

To conclude this section, it appears that, under ad lib. conditions where there is no restriction on either the ratio of two foods that the vole can choose or on the total weight eaten, the vole appears to regulate the total weight eaten to a larger extent than the ratio of the two foods, or the amount eaten of either food individually. This can be due either to a more stable internal reference level for the desired level of intake, or to a more accurate mechanism for assessing the error between actual and desired levels. The interpretation of the results in terms of the relative worth of the two foods in satisfying the desired level seems to suggest that, in some cases, a given weight of wheat is worth more than the same weight of groats. This is in contrast to the results obtained in other experiments, and would not in any case be expected in view of the lower digestibility of the wheat. It seems likely that the discrepancy is a result of the fact that the varying ratio of groats to wheat eaten was generated by the vole itself.

4.4.3 Factors influencing consumption

The previous two sections have considered factors influencing consumption within individual voles. In this section, I shall consider some factors which could account for some of the variability in consumption rates between voles.

a) Body weight

The consumption of the bank vole could be influenced by its body-weight, as has commonly been found with other species (Kleiber, 1947; McNab, 1963). The underlying reason for the importance of considering body-weight has to do with the relationship between surface area and volume of the homeothermic animal as its size increases; energy intake does not need to increase in proportion to tissue volume, since a given increase in volume results in a less-than-proportional increase in surface area.

The data was collected from a series of observations on the consumption and body-weight of a group of initially thirty-six voles for their first fifty days in captivity. The data was collected at five times, giving four periods for which consumption and body-weight changes could be estimated. These periods were not of the same length, and for the last two periods, the number of voles used was reduced to seventeen, since some were required in other experiments. Table 4.4.3-1 summarise the information on length of each period and number of voles of each sex used, as well as the food or foods on which each vole was kept. The voles were kept individually in either large or small cages, containing a nest-

Table 4.4.3-1

Summary statistics from the monitoring of body-weight and consumption.
(All weights in gms)

	Period 1	Period 2	Period 3	Period 4
No. of days	13-16	17-20	11	4
No. of voles				
Male/female	23/13	20/13	11/6	10/6
Groats/wheat/both	14/14/8	13/13/7	7/10/0	6/10/0
Initial body-weight	19.1	19.8	18.0	17.2
Change in body-weight per day	+0.04	-0.09	-0.06	-0.18
Change in body-weight per day (as % of body-weight)	.24	-.48	-.27	-.99
Eat per day	3.48	2.54	2.52	2.81
Eat per day (as % of body-weight)	18.4	13.0	14.3	16.4

box with bedding, some wood-wool for cover, and an ad lib. water supply, and kept at an ambient temperature of about 20°C.

The parameters calculated from the basic data included:

a) the body-weight at the start of a period

b) the change in body-weight per day

c) the total amount eaten per day

d) the change in body-weight per day per gm initial body-weight, and

e) the amount eaten per day per gm initial body-weight.

In Table 4.4.3-1, mean values for these parameters are presented for each period. The analysis consisted of correlation and regression analysis using these parameters. Although each period was analysed separately, the results presented here are for all periods lumped together, giving 102 cases. Although this is strictly speaking not statistically valid, because of the lack of independence of the data for the same vole on successive periods, the results obtained in this way agree with the separate results, though some of these had not reached the level of formal significance.

The statistics describing the relationships between the main factors are summarised in Table 4.4.3-2, showing the correlation coefficient, the probability of obtaining such a result by chance, the coefficient and constant for the regression equation, the standard deviation of the estimate, and the standard error of the regression coefficient. It can be seen that, although the correlation coefficient is quite low, the significance level is very high, in view of the large number of cases, though clearly a large amount of the variance remains unexplained.

Table 4.4.3-2

Relationships between consumption and body-weight

	Eat per day / Body-weight	Eat per day (% of BW) / Body-weight	Change in BW / Eat per day
Correlation coefficient	.28	-.31	.38
Significance level	0.01	0.01	0.001
Regression coefficient	.074	.441	0.070
Constant	1.52	23.95	0.25
S.D. (estimate)	.75	3.96	0.13
S.E. (regression coefficient)	.025	.135	.017

The relationship between consumption per day and body-weight is that expected from numerous studies on other species. The fact that there is a positive off-set on the Y-axis, i.e. the regression line indicates a positive value for consumption at zero body-weight, agrees with the commonly-held idea that the relationship can be described by an equation of the form

$$C = a.B^{d},$$

where: C = consumption (gm/day)

B = body-weight (gm)

a,d = constants

The value of d is normally taken to be between approximately 0.75 (McNab, 1963; Rosenzweig and Sterner, 1970). However, in view of the variability of the data, and the fact that the consumption levels were not those for stable body-weights (Table 4.4.3-1 shows that mean body-weights changed considerably over the course of the experiment, and Table 4.4.3-2 shows that the change in body-weight is correlated with consumption), it was not possible to fit this equation to the data.

Fig. 4.4.3-2 shows a graph of consumption per unit body-weight against body-weight, for the first period. The negative correlation is that which would be expected from the theoretical analysis. Although this should also be a curvilinear relationship, tending asymptotically to zero, the general trend does tend to confirm the theoretical basis for the relationship between consumption and body-weight. This theory predicts that as body-weight increases, then the ratio of surface

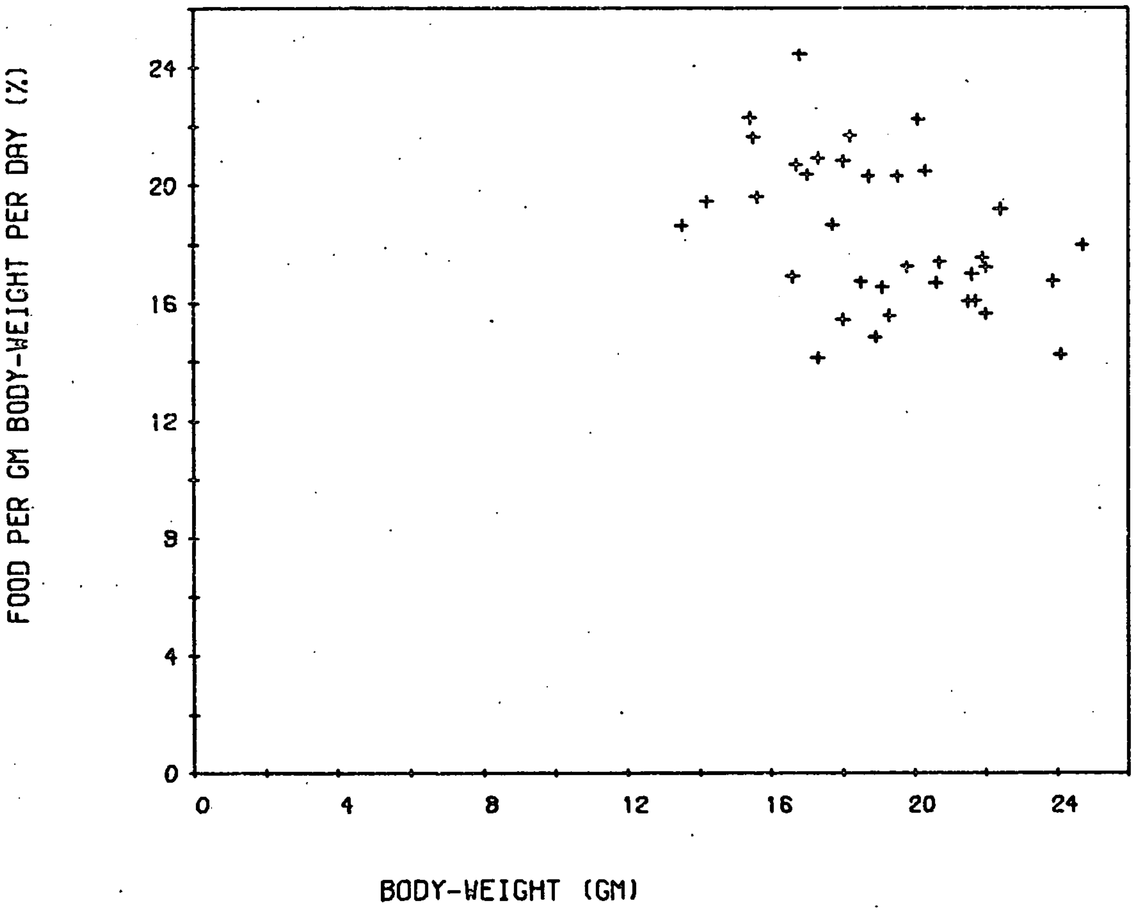


Fig. 4.4.3-1

Relationship between consumption per gm body-weight and body-weight.

area to body-weight decreases, the rate of heat loss per unit body-weight also decreases, so less food is therefore needed per unit body-weight.

b) Sex

Some of the remaining variability in the data for daily consumption could be due to differences in sex. However, this was tested both for the individual periods and for the grouped data, using the Mann-Whitney U-test, and in no case was there a significant difference between the sexes.

c) Food type

The data was also tested to see if there was a difference in total consumption between those voles fed only groats and those fed only on wheat. There was significant difference between the two; the mean daily consumption for voles on groat only was 2.43 gm, while for those fed only on wheat it was 3.18 gm, giving a ratio of 1:1.3. Although this could be partly due to the fact that voles fed on groats lost more weight over the course of the experiment (0.066 gm/per day) than those fed on wheat (0.037 gm/per day), the difference between these two values is not significant, due to the variability of the data on change in body-weight. From the results presented below a much larger change in body-weight would be expected if the air-dry unit weight of both foods were equivalent nutritionally.

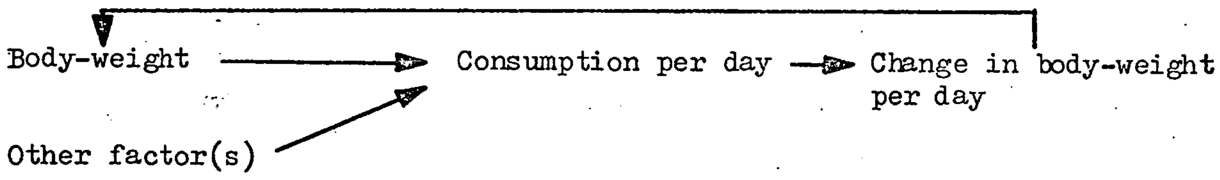
d) Temporal changes

A further source of variability appeared in the form of differences between the successive periods of the experiment. This is apparent by reference back to Table 4.3.3-1, and it can be seen that the values for body-weight, body-weight change, and consumption per day are larger in the first period than subsequently. Although the positive body-weight changes in the first period could be attributed to the voles recovering from the trauma of being trapped, with this requiring a higher level of consumption, it is less easy to see why there should be a consistent drop in body-weight after this. It could be that, although it was proved that voles can survive more or less indefinitely on one food type, this is nevertheless a sub-optimal situation, with the vole's body-weight levelling-out at a lower level than on an optimal diet.

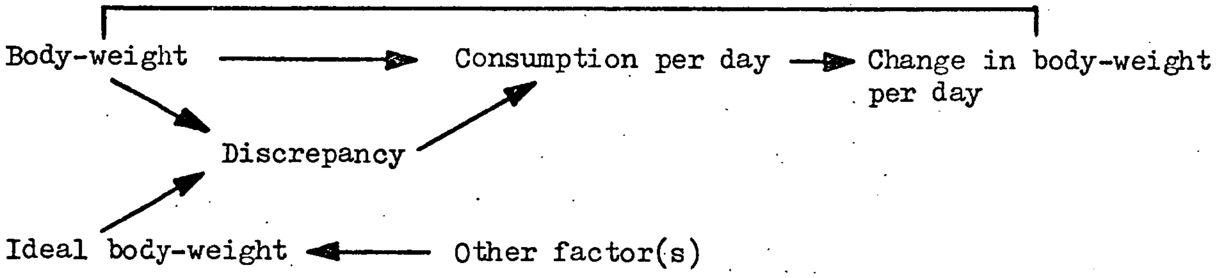
The results shown in Table 4.4.3-2 also demonstrate that there is a positive relationship between daily consumption and daily change in body-weight. This is not a spurious relationship produced by a hypothetical link between consumption and body-weight, and body-weight and rate of body-weight change, since results (not shown) indicate that this latter relationship is, if anything, weakly negative.

This result is important in demonstrating that, even under apparently constant conditions, there are variations in the intake of a vole which cannot be attributed to a slowness in adjusting intake to the vole's requirements as indicated by its body-weight, since the variations in intake are sufficiently large as to cause changes in body-weight. This means that for any particular vole on a given type of food, the level of consumption is not simply a function of its current body-weight plus a random element. Rather, these results are compatible with either of the following two models:

a) Consumption is a function of body-weight and some other independent factor(s), which could refer to environmental variations or, as we have seen, to long-term physiological effects resulting from prolonged feeding on one type of food.



b) As well as having an ideal level of intake determined at least in part by the current body-weight, the vole could have an ideal body-weight, which itself could be a function of other factors, including the physiological effects mentioned above. Then the discrepancy between current body-weight and this ideal could itself affect the level of consumption.



Whatever the mechanism, it is clear that there are long-term changes in a vole's feeding motivation. If an attempt was being made to model the vole's feeding behaviour over a period of weeks or months, then the mechanisms involved would have to be examined.

In the present study, however, the main interest is in the short-term feeding behaviour, so that consumption can be assumed to be constant in the short run.

4.4.4 Relation to effort expended

In the previous section, the results of monitoring experiments were examined to determine some of the factors affecting the vole's daily consumption. Some of these, such as the nature of the main food type, need to be considered in any model of vole feeding. Others only act slowly over long periods of time, and can be ignored in a study of the vole's short-term behaviour. These could include the response to slowly-changing external factors, a gradual physiological response, or acclimitisation, to sub-optimal conditions, and the varying of intake to adjust the body-weight. In this section, I will consider the possible effect of effort expenditure on the vole's consumption, as this is a factor which can operate in the short-term under conditions where the vole can vary the amount of effort that it puts into searching for a preferred food, such as was found in the functional response experiments.

It has been shown for many species that large changes in the rates of metabolism and consumption can be brought about by artificially imposed regimes of high activity (Hart, 1952). The question that arises here is whether the range of activity shown in these experiments is large enough to result in significant changes in the vole's metabolism, and if so whether these changes are reflected in a day-to-day adjustment of consumption.

I will use the data collected in the functional response experiments described in Section 3. Distance travelled will be used as a measure of the vole's effort expenditure, and the total weight of food eaten will be calculated from data on the number of grains eaten and their mean weight, rather than by subtracting the weight of food recovered from the weight put down, since this latter method is very sensitive to small humidity changes in the seeds when large numbers of seeds are involved.

In view of the possibility that there may be long-term, independent changes in distance travelled and total eaten, it is not justifiable to test the significance of an assumed relationship by calculating the correlation coefficient. Therefore, the data was inspected graphically by plotting total weight eaten against distance. In some cases for example, (Fig. 4.4.4-1a) consumption appears to be independent of the distance travelled, while in others (for example, Fig. 4.4.4-1b) a relationship is clearly apparent. Further work would be needed to determine whether this relationship is a spurious one (resulting from gradual changes in the vole during the course of the experiment), whether it is genuine but resulting from changes in the ratio of wheat to groats eaten at different densities, or whether it reflects a genuine increase of food intake to compensate for increased effort expenditure.

However, it would be thought that such a relationship, if found in some voles, should be found in all, since it is unlikely that there will be large differences between voles in the technique of penetrating the brushes.

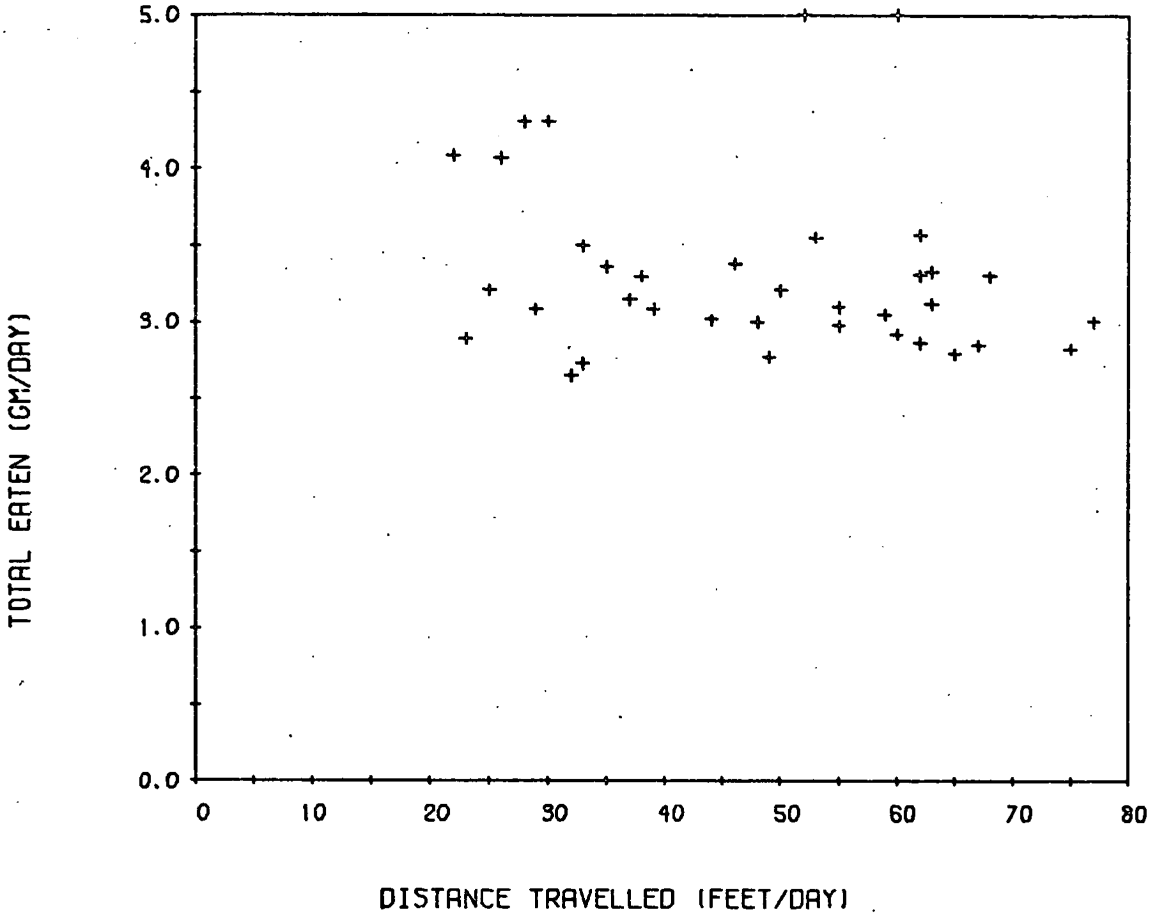


Fig. 4.4.4-1a

Relationship between total amount eaten and distance travelled, for session S1 (III).

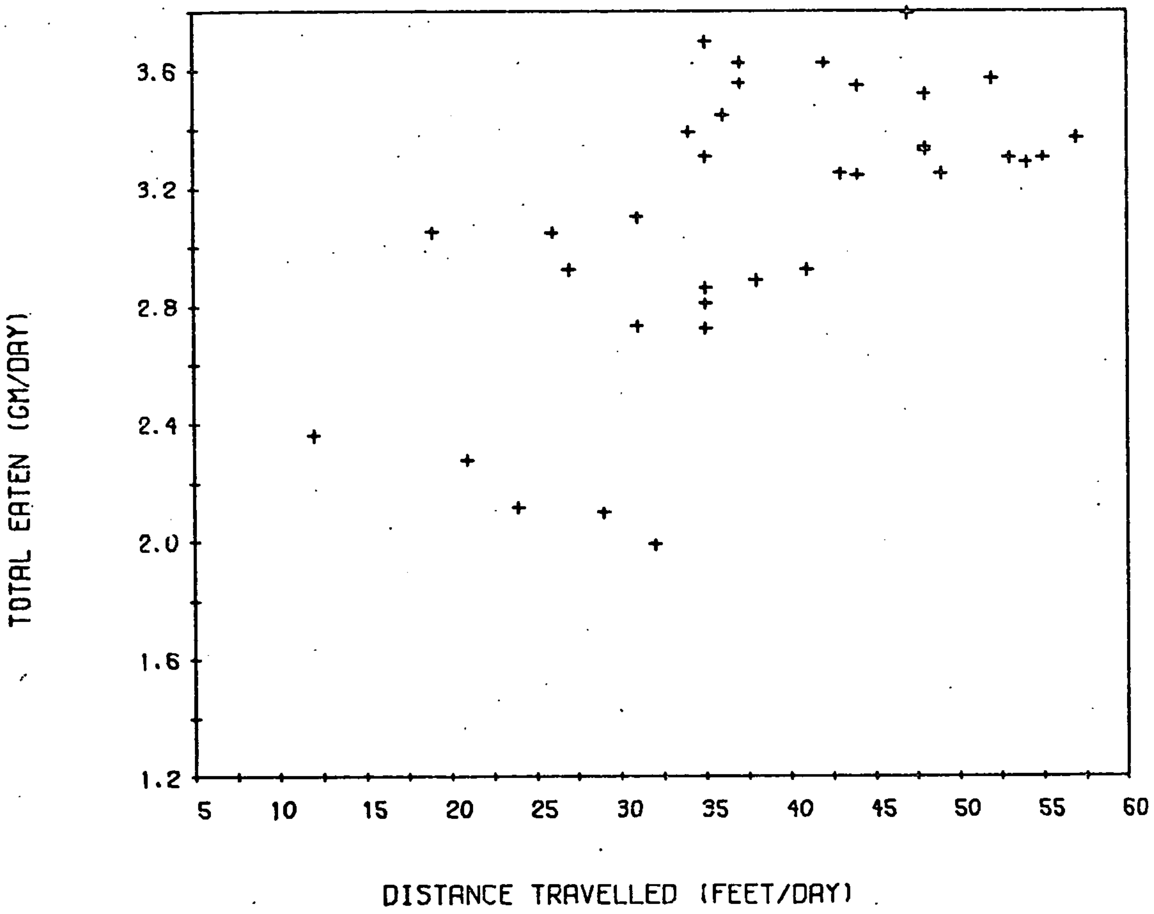


Fig. 4.4.4-1b

As for preceding Figure, for session S5 (III)

If this conclusion is correct, it considerably simplifies the analysis of the functional response system. The alternative would require the modelling of a long-term hunger component (see section 5.2), which could respond to changes in the metabolic rate as a result of searching, and thereby influence the start-searching/stop-searching thresholds.

4.5 Food preference

4.5.1 Basis of preference

The relative preference that an animal shows for one food item over one or more others can be expressed in two ways. On the one hand, the preference can be expressed in terms of the relative numbers of the different food items taken. For obvious reasons, this approach has been readily adopted by those investigating predator-type feeding animals; for example, Ivlev (1961) expresses the food selection, or electivity, of carp in terms of the relative numbers of prey items consumed, and this approach is frequently used by those studying the feeding behaviour of insectivorous birds (e.g. Tinbergen, 1960; Royama, 1970). Alternatively, preference may be expressed in terms of the relative weights of the different foods consumed, either as found by the animal or converted to dry weight. This approach is more common amongst those studying the feeding of some herbivores whose food cannot be readily classified into discrete items (Arnold, 1964), and in laboratory studies by those primarily interested in the physiology of feeding (Drozdz, 1967). In either case, the method used seems to have been selected more for its convenience than out of any conviction that the method chosen most closely represents the inherent basis of preference.

Both approaches reflect a facet of the selection mechanism. On the behavioural level, selection often takes place in discrete steps, either because the prey is discrete or because the animal feeds in separate and potentially independent bites. On the physiological level, it is readily accepted that the composition of a mixed diet reflects the nutritional needs of the animal. So it can be seen that the method used for representing preference is related to that part of the selection process which is being investigated.

The present study involves an investigation at both levels, since on the one hand I am concerned with the selection of individual grains, as in the functional response experiments (Section 3), or in considering the sequence of selection (Section 5). On the other hand, I have looked at the stability and regulation of preference, and the effect on subsequent selection of limitation to one food type for a period. It is therefore of some interest to determine whether the basis for preference - i.e. the internal reference level which the vole seeks to achieve - operates in terms of the number of units taken or on the weight eaten.

I thought at first that the problem could be resolved by comparing the variability of the percentage preference for groats calculated in the two ways, in terms of number of grains and weight of grains. The reasoning behind this was that the method which the vole itself uses in regulating its intake should show less variability. A suitable measure of relative variability would be the coefficient of variation (the ratio of standard deviation to the mean), since this standardises for different means. However, it can be shown that the result obtained, giving a lower coefficient of variation for preference based on numbers, is an artefact resulting from the fact that I was finding the coefficient of variation of a ratio and that groats was the preferred food.

As an alternative approach, an experiment was set up in which voles were presented, in successive periods of five days, with a choice between groats and either small wheat grains or large wheat grains. All the wheat came from the same stock, but the larger had a mean grain weight of approximately twice that of the smaller grains.

In an initial series, six voles were given a choice between the two types of wheat alone for a period of thirteen days. The results of this experiment are summarised in Table 4.5.1-1, and show that there is a large difference between voles in the median preference for small wheat, and that within individuals the quartile range is quite large. These results are expressed in

Table 4.5.1-1

Median values for percentage preference (by numbers) of small wheat vs. large wheat, with quartile limits.

Median	Quartile limits
39	30 - 54
54	43 - 61
74+	65 - 84
77	49 - 84
78+	66 - 87
84+	75 - 95

Data arranged in order of increasing median value.

+ Indicates that, at the 5% level of significance, more values are above or below the 50% level than expected by chance.

terms of relative numbers eaten, since there is little reason to assume physiological feed-back determining this relative preference. The three cases which differ significantly from 50%, on the basis of the Chi^2 test, all show a greater preference for the small grains.

In the main experiment, eight voles were used. Their consumption was recorded every five days, and a choice between groats and small wheat in one period alternated with a choice between groats and large wheat in the next.

The results obtained are rather ambiguous. In the case of one vole, the amount of wheat eaten decreased at every change from large wheat to small, and vice-versa; moreover, the mean daily consumption of large wheat was 0.63 gm, almost exactly twice the mean daily consumption of small wheat, at 0.29 gm. This is just the pattern to be expected if the number of grains eaten was the basis for preference. However, in the case of other voles, there is no pattern in the transitions from large wheat to small or vice-versa, and the mean weights eaten per day of the two types are not significantly different. In yet others, the pattern of transitions is virtually the reverse, and the mean daily weight eaten of the large wheat is significantly smaller than for the small wheat. It therefore appears that even in a groats/wheat situation, the two wheat types are not equivalent in either terms of numbers or of weight, and that preference differences between the two wheat types remain. Only if it could be shown that the weight of small wheat eaten was consistently equal to, or consistently half of, the weight of the large wheat, could these results be confidently used to indicate the basis for preference.

It does, therefore, seem likely that the basis of preference is ultimately physiological. In the first place, the results relating to the first of the two experiments shows that the variability of preference between the two wheat types, as indicated by the quartile limits is much greater than usually found in groat/wheat situations. This could reasonably be due to the fact that the physiological differences between two sizes of wheat are much smaller than between two grain species. Also, in the following pages I will present the results of auto-correlation studies on preferences of groats over wheat on successive days, which show in some cases a carry-over effect from one day to the next, implying a more stable physiological control of relative intakes. Finally, in section 5.3, where I deal with the problem of specific hunger, the effect of limitation to one grain type on subsequent selection also suggests that a physiological rather than a behavioural basis is involved in determining preference.

4.5.2 Differences between voles

Whatever the basis for preference within voles, it is of interest to look at the normal range of values shown by voles in their preference of groats over wheat, and the differences between them. In all further discussion, preference will be expressed in terms of weight units, as follows:

Percentage preference of groats over wheat (% pref. groats) =

$$100 \times \frac{\text{Weight of groats eaten}}{\text{Total weight eaten}}$$

The results presented here are drawn from the monitoring experiment involving twenty voles described in section 4.4.1. The voles had been maintained in captivity for several months under approximately the same conditions as were used in the experiment, with an ad lib. supply of groats, wheat and water, and in the same type of large cages.

In view of the occasional presence of an unusually large or small value, and to remove the need of applying the arcsine transform to normalise the data, the results are expressed as the median value for each vole. Confidence limits for the median were derived from a table produced by Nair (1940) and reproduced in Campbell (1967). For n=16, the fourth value from each end of the ranked data gives the confidence limits at 97.9%, while the fifth value gives the limits at approximately 93%: the latter level of significance was used here, since a rigorous test of the data was not being made, and so there is now a 7% chance that apparent differences between medians are not significant.

The median values with their 93% confidence limits are shown in Fig. 4.5.2-1, in order of increasing median % pref. groats. From this it is clear that all voles tend to prefer groats over wheat, since all the median values are greater than 50%. It can also be seen that, typically, each vole occupies a relatively small proportion of the spread shown by all voles, with the exception of one vole.

The confidence limits of the median can be used as the basis for a test of the significance of a difference between two medians, since, in this case, there is a 93% chance that the difference is significant if one median falls outside the confidence limits for another. Thus, each vole can be compared with every other vole by seeing whether the median value of the one falls outside the median range of the other. The results for all comparisons can then be summarised in the form of a matrix, with each element representing one comparison. This table need not be symmetrical, since the median range of vole i may overlap the median of j, while the reverse need not be true. In fact, only the one vole with a large median range affected the symmetry of the table. It was found that 72% of the comparisons were significant at the 93% level. These results show that each vole has a specific and restricted preference level.

On the right of Fig. 4.5.2-1, the median values are collected in a frequency distribution based on intervals of 5%. It can be seen that the distribution is fairly symmetrical around 70-75%. The same pattern is found if mean values for % pref. groats are used instead of medians - in fact, the two values only differ by an average of 1.5%. It was my impression that one tended to find a higher proportion of voles with % pref. groats

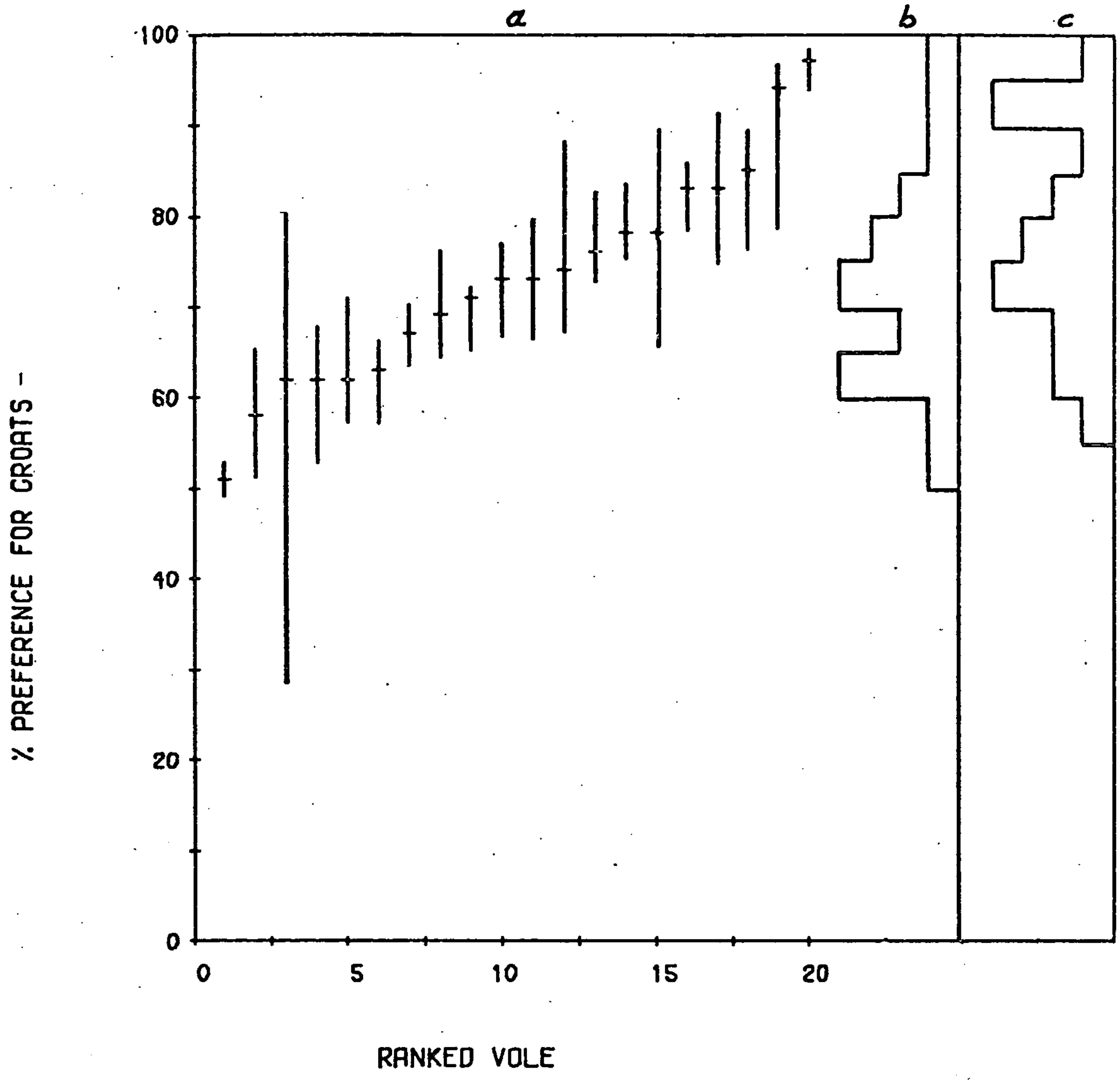


Fig. 4.5.2-1

a) Vole's ranked by median % preference for groats, with 95% confidence limits for median.

b,c) Frequency distribution of median % preference for groats, for this group and another group.

over 90%, and it could be that this particular group - which all had the same history - was slightly atypical: the right-hand frequency distribution shows the distribution of mean % pref. groats for another group of 20 voles, but although the median value for this group is some 5% points higher and there are five instead of two values above a preference level, the difference between the two groups is not significant. It is likely that the impression was due to being over-impressed by those occasions on which virtually no wheat was taken.

In the interpretation of these results, as with any time-series data, the values for each vole suffer from lack of independence. This problem is not overcome by the use of non-parametric statistics, and, since in some cases there was evidence for a trend in the values over time, it is in principle possible for the % pref. groats for all values to cover the same range over a period of months.

But we are justified in saying that, in the short term, an individual vole shows a high degree of stability in its preference, as evidenced by the fact that its average value tends to differ significantly from that of other voles.

In conclusion, it is clear that voles tend as a group to prefer groats to wheat, with individuals being quite narrow in their preference range. This tells us nothing about why a particular vole has a specific preference for groats, but does indicate that any explanation put forward must be compatible with both the difference between members of the same species, and with the limited range shown by individuals.

4.5.3 Day-to-day stability

The previous section showed that, over a period of sixteen days, the average preference level of the vole can be defined within quite a narrow range. This implies that the vole is able to regulate the proportion of groats and wheat taken, and in this section I will show whether time series analysis of the day-to-day stability of preference levels can tell us anything about the temporal nature of this regulation.

Just as the technique of auto-correlation was used in section 4.4.1 to investigate the day-to-day stability of consumption levels, it can in a similar way be used here to find out what relationship there is between the preference level on one day and that on preceding days. The results could fall into three classes:
a) no significant correlations for any lag value - regulation of proportion of foods taken takes place mainly within days, and day-to-day variation is mainly random variation;
b) small lag values produce positive correlations - neighbouring days tend to have the same preference levels, and regulation takes place over periods of more than a few days;
c) negative correlation for a lag of one day - regulation takes place between one day and the next, so that one day's deviation from the ideal preference level is corrected on the next.

The analysis was done on the same two groups of voles as were used in section 4.4.1, with one group of four voles monitored daily for eighteen days and another group of twenty voles monitored daily for sixteen days. There was ad lib. groats, wheat and water in all cases, and the presentation of the two food types was designed to minimise the effect of possible position preferences on the percentage preference for groats (% pref. groats), either by keeping the two food dishes in the same position from one day to the next, or by using the specially-designed food dish which presented both foods in close proximity. Both methods are more fully described in 4.4.1.

Interpretation of auto-correlation results is complicated by the fact that here the normal methods for determining the significance of a correlation coefficient are not valid. The analysis therefore needs to rest on the detection of pattern in a set of results. This pattern can either be found between voles, so that if several animals show the same pattern of auto-correlation coefficients, then more confidence can be placed upon the results of an individual. Alternatively, the set of auto-correlation coefficients for an individual may show a distinct pattern: if neighbouring coefficients tend to be similar, then it is more likely that they result from a genuine effect; and if the auto-correlation coefficients follow a regular cycle when plotted against lag number, then it is highly likely that this results from a cyclic pattern in the original data, with a period the same as for the coefficients themselves.

The results for the twenty-four voles varied from those which showed no obvious pattern up to the maximum lag value of ten days (this maximum being set by the fact that there were only sixteen - eighteen days data for each vole), to those which showed a very distinct pattern. Since I am not trying to show how the 'typical' vole behaves, or test a particular hypothesis, but simply to investigate the range of forms that the day-to-day stability of preference can take, it is not necessary to classify the intermediate voles.

Fig. 4.5.3-1 shows the auto-correlation results for seven voles selected from the group of twenty for both the clearness of their individual pattern and the series that they form together. It can be seen that this series show all three forms of pattern described above. First, there is a degree of consistency between different voles; for example, voles 5C and 5A both show a gradual drop in the auto-correlation coefficient followed by a rise for lags of nine and ten days, and no vole showed a pattern which was the reverse of this. Second, it can be seen that the changes in the coefficient with increasing lag are fairly smooth; this is not an artefact of the method, since no such pattern is observed if the sixteen values are randomly re-assorted. Third, it can be seen that in some cases the coefficient shows a definite periodicity, and it is possible that the bottom three voles would show the same feature if followed for a longer time. Again, this pattern is not observed with randomly re-assorted data. Further evidence for the significance of the cyclic behaviour of the coefficient comes from the fact that in every case the phase positioning of the cycle is consistent with it beginning at a peak.

The random re-assortment of the data referred to above was done by using a computer program to re-assign randomly each of the sixteen values for percentage preference of groats to one of the sixteen days. This was then done seven times for each vole, and for all twenty voles. In Fig. 4.5.3-2a,b I have plotted all seven runs for two of the voles already considered in Fig. 4.5.3-1 - voles 5K and 5A - and it can be seen that no pattern is apparent

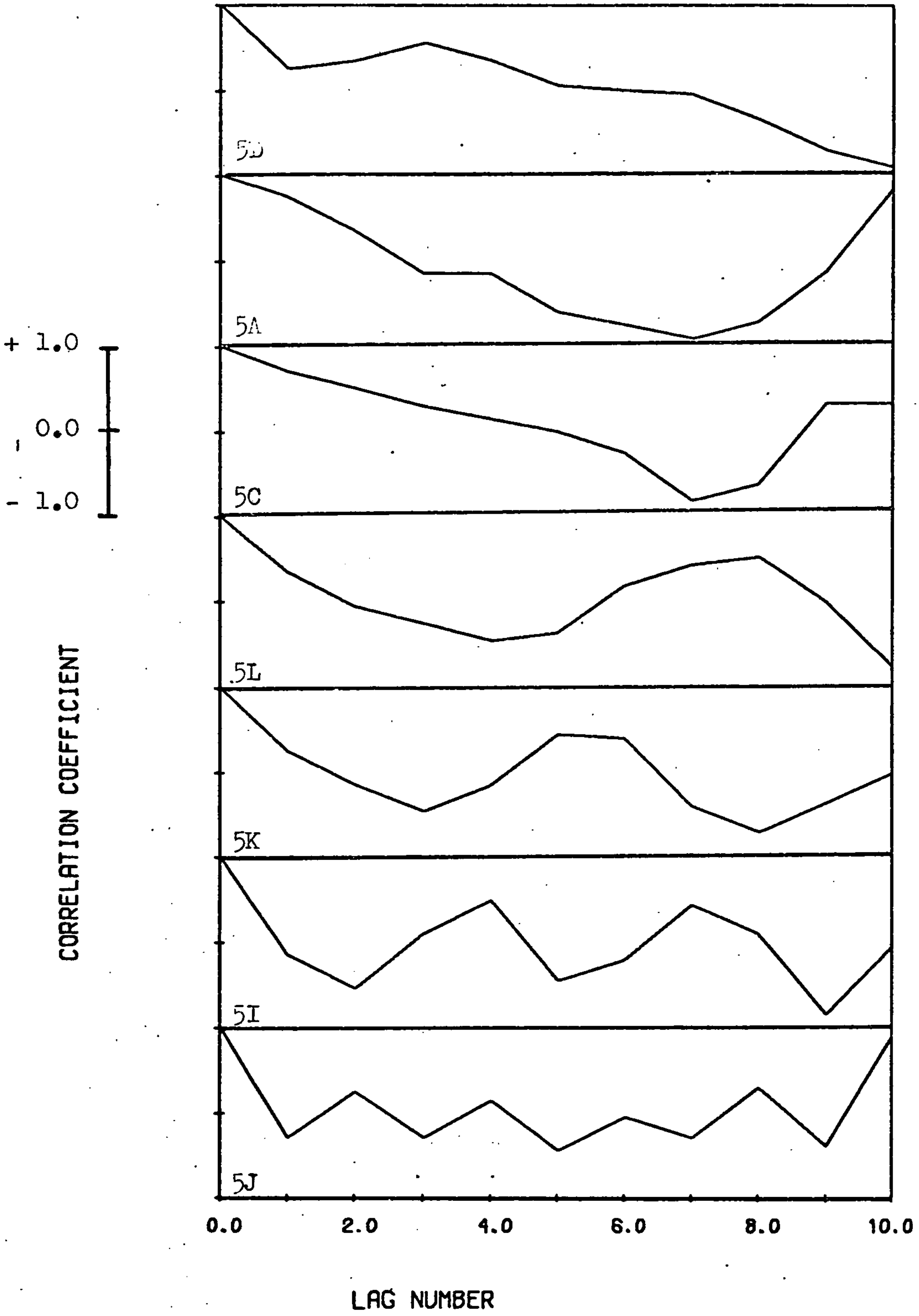


Fig. 4.5.3-1

Autocorrelation patterns in groat preference for seven voles.

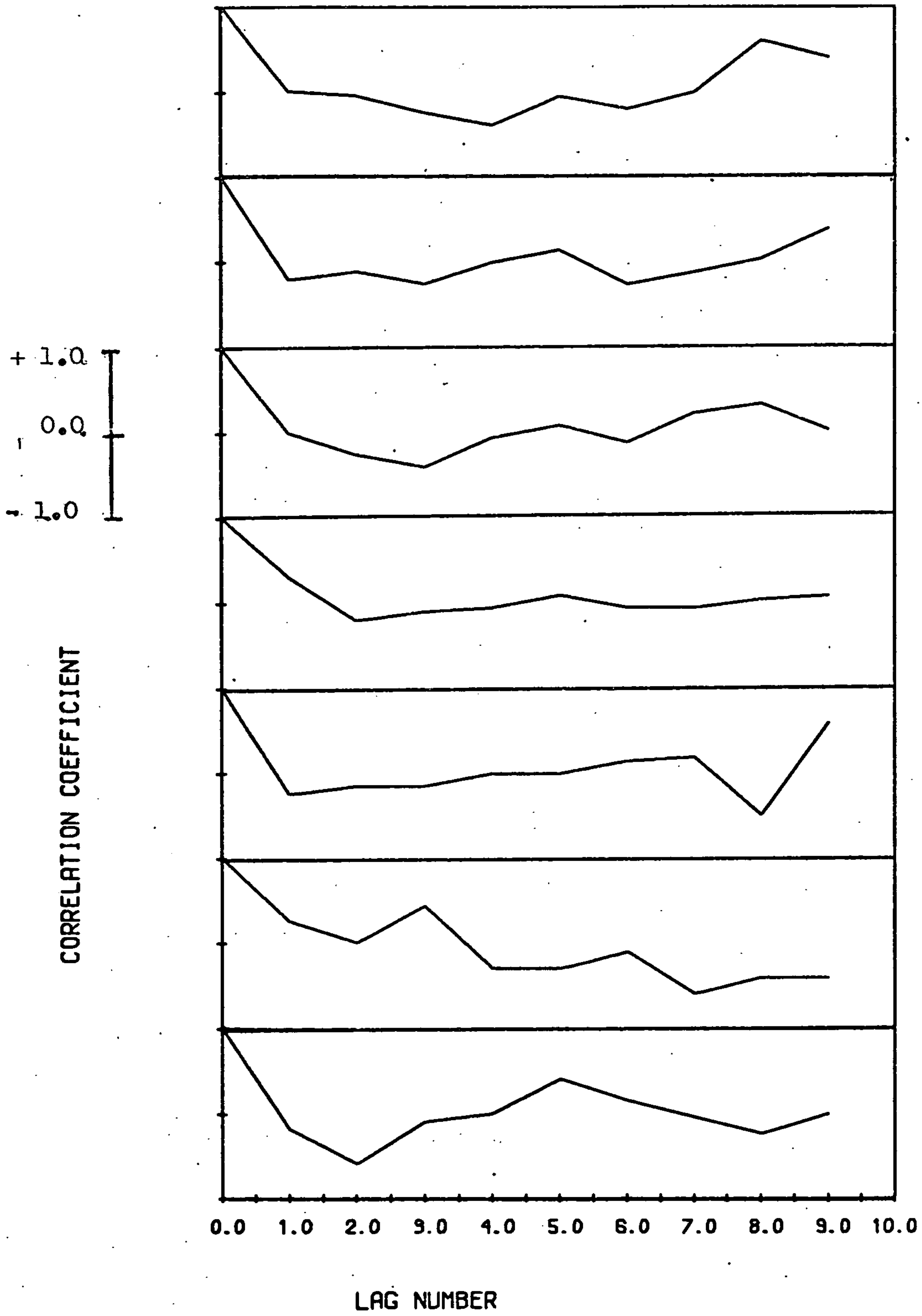


Fig. 4.5.3-2a

Lack of pattern in autocorrelation analysis of randomly reassorted data for groat preference.

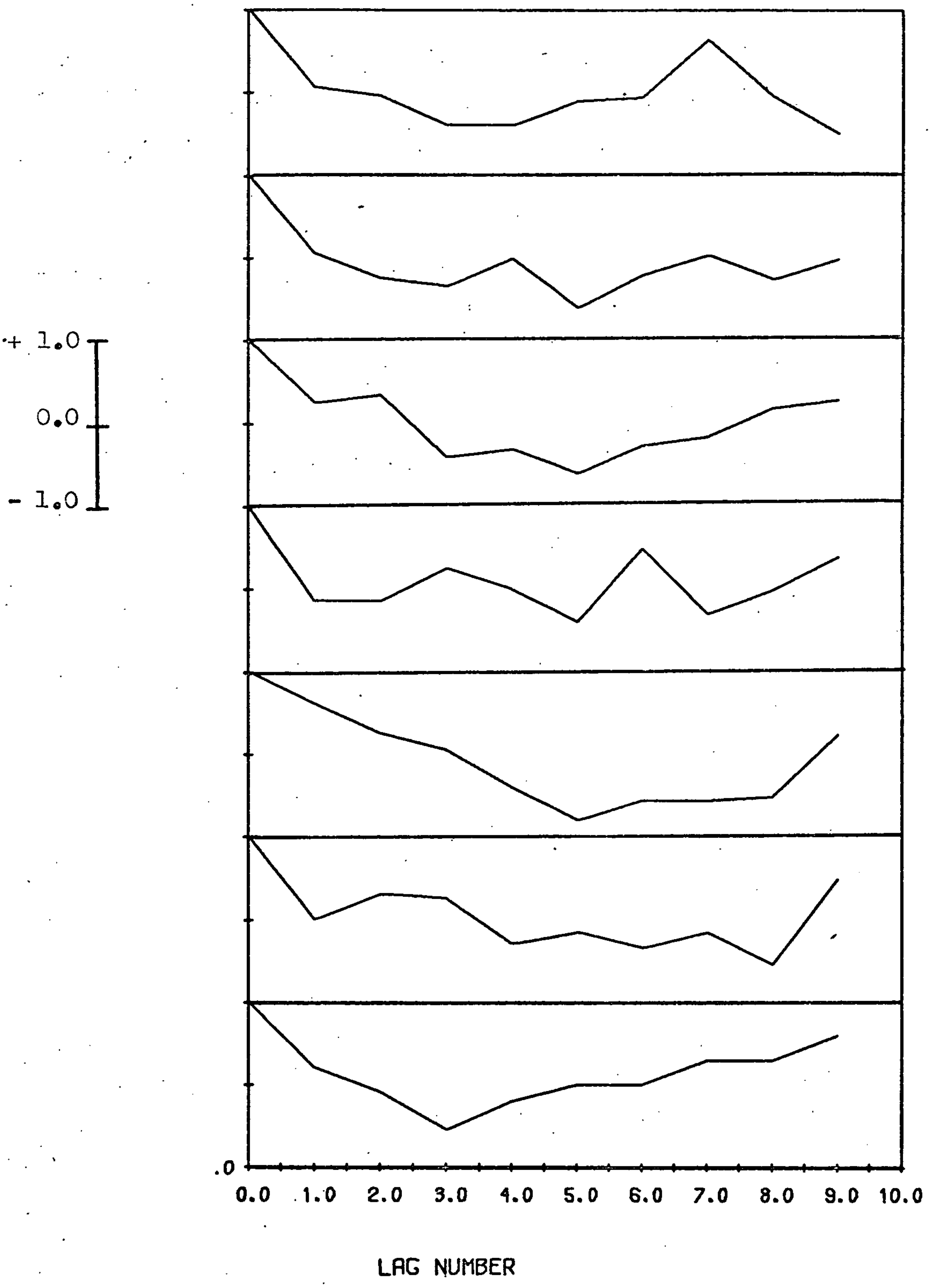


Fig. 4.5.3-2b

As for preceding Figure.

using the re-assorted data.

These results show clearly that voles differ in their day-to-day stability of their preference for groats over wheat. Those which show no pattern with the auto-correlation analysis have daily preference values which vary randomly around some mean value. This could indicate dynamic regulation of their relative consumption of groats and wheat within the day, an absence of dynamic regulation of selectivity at all, or else a close linkage between the physiological optimum ratio of the two foods and the behavioural mechanism responsible for the selection of food.

An explanation of the cycles shown by the other voles need not necessarily be related to the idea of adjustment of selectivity to satisfy some constant reference level. It could be, for example, that the reference level itself fluctuates in this manner, and that these results merely show that selectivity closely follows the changes in the preference reference level. In this case, the factor(s) causing the reference level to vary would also have to be cyclic. No such cycles were detected in total consumption, and besides there appears to be no correlation between an animal's total consumption and its preference for groats. It is not related to environmental factors, since for any one group of voles the experiment was conducted at the same time in the same room, so that all cycles should have the same period. In the same way, this rules out the oestrous cycle, which in bank voles is fairly constant, with a period of about 3 days (Southern, 1964).

Thus, it is likely that cycles in the auto-correlation coefficient, indicating a tendency for the actual preference values to show a cycle of the same period, result from attempts to adjust selectivity to some reference preference level and compensation for departures from the reference level. In this sense, voles appear to behave as under-damped servo-control systems, with a discrepancy from the desired reference level causing over-compensation and too high a level of selection of the other food. If a vole could control its relative intake with complete accuracy, then a single discrepancy should produce fluctuations in actual preference which eventually settle down to the ideal level; but if, as seems likely, there are sampling errors in selecting individual grains, then the vole will be constantly correcting for past errors. This explains why this pattern can still be observed even though the voles had been under the experimental conditions for several weeks previously.

4.5.4 Regulation

It was shown in the previous two sections that, in maintaining a mixed diet, voles tend to take a fairly constant ratio of the two foods (4.5.2), and that this ratio shows a high degree of constancy from one day to the next, implying dynamic regulation of the ratio (4.5.3). This does not mean, however, that in eating the two foods this ratio is the principle thing that the vole is trying to stabilise. It was shown in Section 4.4.2 that the primary objective of the vole could be to regulate total consumption, the consumption of groats, the consumption of wheat, or the ratio of the two. Information on which is most important cannot be obtained from the temporal patterning of the consumption data, but a plot of weight of groats eaten versus weight of wheat eaten could yield one of four relationships, depending on which of the above possibilities in fact operates (see Fig. 4.4.2-1).

This analysis has already been done in Section 4.4.2, and showed clearly that in every case where a significant relationship was found between the weights of the two foods eaten, it was a negative one, agreeing with the postulate that regulation of total consumption is the primary objective, since in this case increased consumption of groats causes less wheat to be eaten, and vice-versa. Departures from the expected regression coefficient of -1.0 could be explained by differences in the nutritional value and digestability of the two foods.

Thus, it can be seen that, within a day, the vole principally attempts to regulate its total consumption, rather than the ratio of the two food types or the weight eaten of either one. This agrees with the auto-correlation results, which showed very few cases of pattern in the auto-correlation values for total consumption, and only three cases with a significant positive auto-correlation coefficient for a lag of one day, implying that any regulation takes place within the day; while the auto-correlation results for the percentage preference for groats showed a pattern of positive auto-correlation coefficients for small lags and negative ones for higher lags, implying regulation of preference over a period of several days. It seems then that it is a much easier matter for a vole to monitor the discrepancy between desired and actual levels of consumption than the discrepancy between the desired and actual ratios of the two foods. This is probably because this latter process depends on the monitoring of more subtle effects. In evolutionary terms, it is more important for an animal's survival to obtain food to satisfy its energy requirements, especially when it is a small animal like the vole with a high ratio of surface area to body-weight and therefore a high metabolic rate, than to obtain essential nutrients in the optimum ratio.

4.5.5 Response to single-food conditions.

The previous sections have considered various aspects of a vole's preference under ad lib. conditions for both foods. But the functional response situation is characterised by occasional periods of low density of at least one food. Since it seems likely that physiological feed-back is important in determining preference, it seems likely that a temporary shortage of one food may affect subsequent preferences when both foods are plentiful. In this section I shall consider the extreme case of this, that is, the effect that complete deprivation of one food has on preference levels. Only medium and long-term effects will be considered, in which preference levels are determined from daily consumption values: consideration of short-term effects will be delayed till section 5.3, where the whole process is considered as a component of the functional response mechanism, under the heading of specific hunger.

This problem has been considered before from two points-of-view. On the one hand, Southern (1954) saw this as a problem in conditioning, that is, whether limitation to one food type tended to increase subsequent consumption of this food relative to others when a choice was again presented. Using three foods, and with house-mice as the experimental animal, he operated a sequence of limitation to one food for seven to ten days followed by unlimited supply of the three foods for six to seven days, then limitation of the next food and so on. These results showed that even when the limitation to one food was for such a short period and the animals had already had experience of all three foods, quite definite evidence of conditioning, or habituation, occurred. For example, the consumption of bread-crumbs was consistently less than 10% of the total until the mice were fed on this exclusively, after which it rose to 35%. In one case, several days passed before the previously-exclusive food rose to its maximum level of relative consumption, and during this time the relative consumption of the other two foods fell. This could suggest that deprivation of these two foods resulted in their initially-increased consumption.

This last finding is characteristic of the second type of approach to diet restriction. Many workers see the deprivation of one food as a disturbance in an internal homeostatic system, which should be compensated for by increased consumption of the deprived food when the choice is restored. This effect would be in a direction opposite to that arising from conditioning to one food.

a) Long-term restriction to one food

The first experiment was designed to reveal the presence of any conditioning in addition to short-term compensation effects. Ten voles were used, and from the date of capture for the next two months, five were maintained on groats alone and five on wheat alone. The voles were all kept in small cages, with ad lib. water, and bedding. The animals were kept under ambient conditions of temperature (approx. 20°C) and humidity, and on a 0900 - 1700 light regime.

The voles were then presented with an ad lib. supply of both types of grain. As it was important to eliminate any possibility of position preference, since it was the actual initial value for preference as well as the temporal trend which was of interest, the specially-designed petri-dish was used, in which the same food type was placed in opposite quadrants of the same dish.

The initial behaviour of the voles was quite exceptional. Normally, after removing the left-over food and putting down the new supply, voles are rarely seen within the first ten minutes. But when the two foods were provided, four out of the five voles which had been on wheat alone went direct to the groats, and two out of the five other voles went direct to the wheat. None of the observed voles were seen to take the food to which they had been limited.

Food intake was then monitored after four hours. Fig. 4.5.5-1 shows the relationship between the weight of groats and the weight of wheat eaten during this period for those voles fed only on groats (X), and those fed only on wheat (+). Two features are apparent: the first is that all the voles fed on

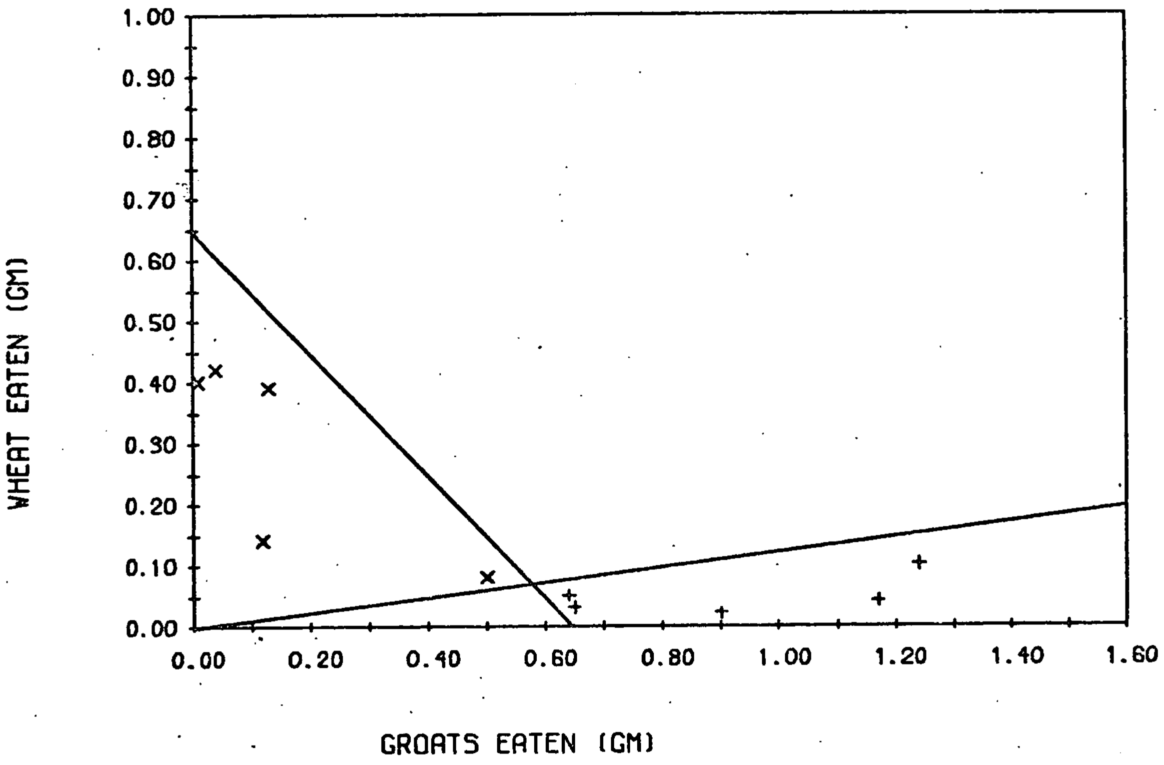


Fig. 4.5.5-1

Weight of groats and wheat eaten following end of:

× : restriction to groats

+ : restriction to wheat

wheat have a higher relative preference for groats than any vole fed on groats, and second that all these voles ate more in this period than those fed on groats. Both these are highly unlikely according to the null hypothesis that there is no difference between voles fed on groats and those fed on wheat.

It can thus be seen that after limitation to one food voles show a marked preference for the alternative food, and that this is apparent as soon as the alternative food is presented, even though the voles have had no previous experience of it. It also appears that those fed only on wheat show a more marked swing to groats than vice-versa, both in terms of its relative consumption and in terms of the absolute amount eaten. The first point is not surprising, since voles normally show a preference for groats, but the second point indicates either that absence of groats caused a greater nutritional deficit, or that groats are more readily consumed for a given deficit. This seems more likely, since groats are the softer and more easily chewed of the two grain types.

The pattern of longer-term adjustment to the two foods is shown in Fig. 4.5.5-2 , in which all the values for percentage preference of groats are shown for all voles of both groups. Readings were taken daily for this period of fourteen days except for the last six days, which are represented by an average value.

The most obvious feature of this graph is again the very pronounced initial preference for the alternative food. Those voles previously fed on groats rapidly tend to a higher level for % pref. groats over the first few days; from the sixth day on, these values remain virtually unchanged. Those voles which had

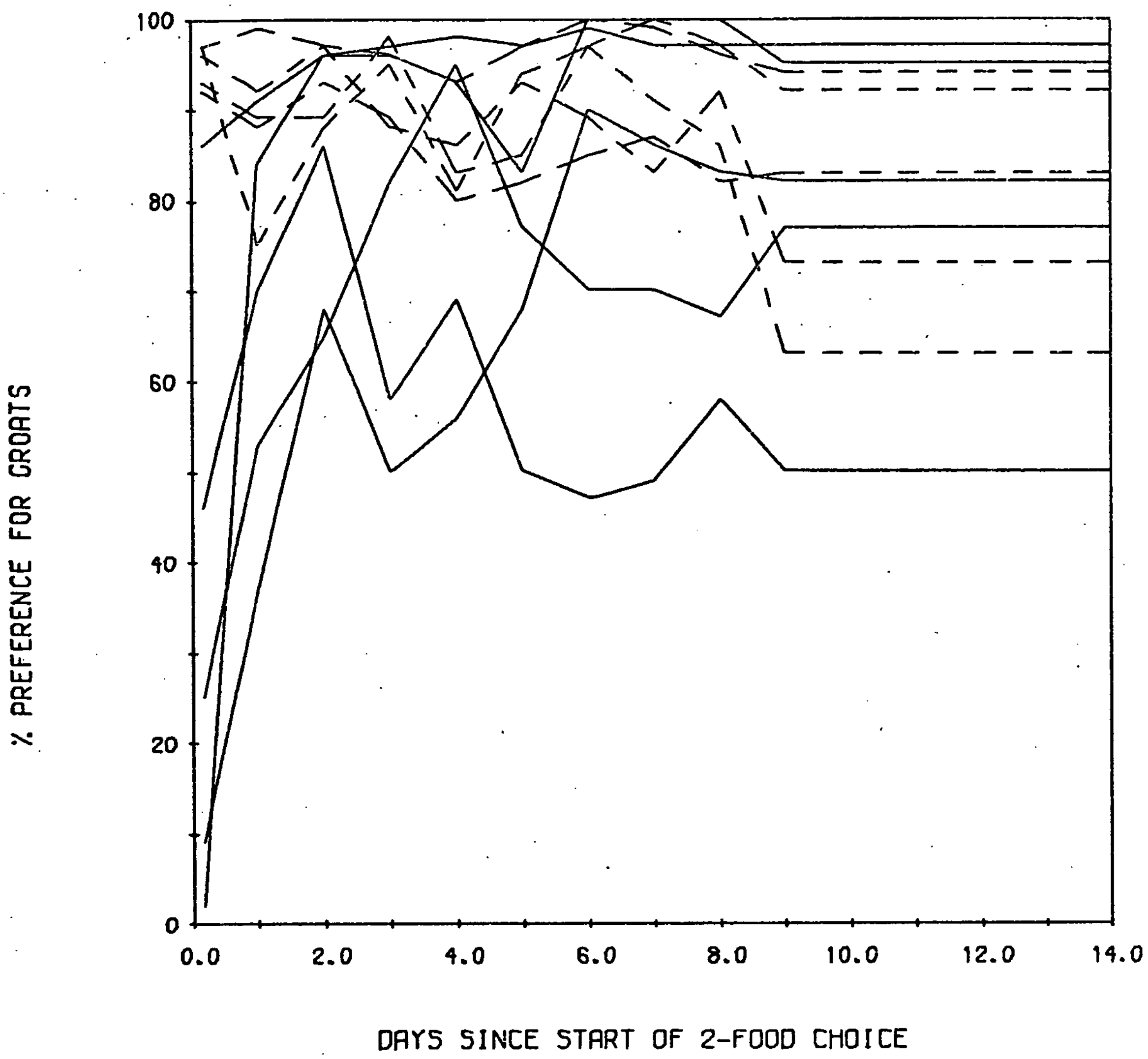


Fig. 4.5.5-2

Percentage preference for groats following end of:

——— : restriction to groats

– – – : restriction to wheat

been fed only on wheat do not show the same marked changes. Although the final level for three of these voles is lower than the previous daily values, the significance of this is not very clear, since it is difficult formally to test for any trend over this period. It remains possible that for those three voles with the lower final value, the decline over the first eight days is genuine though it is not possible to test it statistically.

It is clear that there is no basis for separating the two groups at the end of the fourteen days. We can therefore assume that by this time the voles have settled down to their stable preference level, and that the effect of the initial limitation to one food is no longer important.

The results of this experiment provide no evidence for any conditioning to the food to which the vole had been restricted for two months. Rather, the reverse is the case. Both groups of voles showed an exceptional eagerness to start feeding on the alternate food as soon as it was presented. Those fed only on wheat showed an initial high preference for groats; the significance of the subsequent drop is difficult to assess, and the values in any case are typical of voles which have always had a choice of the two foods. These voles did, however, initially eat the groats at a much higher rate than their equilibrium level, and this could be a reflection of their increased need for groats in the early stages of the two-food situation. Those voles fed on groats did not show much higher rates of consumption when wheat was also presented, but they did show preference levels for wheat which were much further away from their equilibrium level, settling down to a stable level of preference after approximately six days. These results all suggest that limitation to one food results in nutritional deficiencies, and that the presentation of an additional food type is immediately recognised as a means to modify the balance of nutrients provided by the one food alone. The period of adjustment appears to be fairly short, since the differences between the two groups have disappeared by the fourteen days.

Although Holling (1965) recognised the possibility of this type of response to restriction of choice, the model that he produces to account for the vertebrate functional response in fact assumes the opposite mechanism, namely that the shorter the experience of a particular food type, the less willing the animal is to eat it. Although this was obviously formulated for the situation of food scarcity, it was not expressed in terms of willingness to search for a particular food type, but rather, of willingness to eat an encountered food item, and is thus relevant to the ad lib. situation. A model based on the animal's willingness to search for food would still be compatible with Holling's learning and forgetting curves, and in addition would not contradict the findings described above.

b) Medium-term restriction to one food

In addition to the above experiment, another experiment was devised to investigate the effect of shorter periods of limitation to one food on subsequent preference. Twelve voles were kept under standard conditions for twenty-seven days. For the first six days, the voles were allowed to adjust to the experimental situation, ad lib. groats and wheat were available, and the voles were monitored every day. Following this, periods of limitation to wheat only for one, two or three days were randomly assigned to eight of the voles, with the other four only being assigned one period of one day and there-after being kept on both foods, to act as controls against the possibility of trends in the preference for groats; in fact, no such trend was apparent from the data. After a period of limitation to wheat, three days were given on the mixed diet before another period of limitation was imposed. If there is an effect following limitation, and if this period of three days is not long enough for the vole to recover from it, then this would still be apparent as a trend in the values over these three days.

The analyses that will be discussed here were all done on the lumped data, not distinguishing between periods of limitation of one, two or three days, since the paucity of the data and its variability did not permit of analysing each separately. The results of the analyses are presented in Table (4.5.5-1).

Comparison of the percentage preference for groats on the day prior to the limitation to wheat with the day following the limitation showed a tendency for the preference to increase over this period. A Chi^2 analysis of the number of rises and falls in this preference yielded a value significant at the 10% level, and the 95% confidence limits for the median of the percentage points difference between the two values cover the range -1 to 16, indicating that there is a small chance that the true median is

Table 4.5.5-1

Changes in % preference for groats following restriction to wheat for 1, 2 or 3 days.

Changes between:

	Last day before restriction		First day following restriction		Second day following restriction		Third day following restriction
Number of rises		18		5		12	
Number of falls		9		23		16	
Chi^2		3.0		11.6		0.6	
Median difference (% points)		5		-5		-	
95% conf. limits for median		(-1,16)		(-2,-9)		-	

negative, and that the preference for groats fell over the period of limitation, though it is of course much more likely that the preference for groats increases.

If this effect is significant, and the vole compensates for a period of limitation to wheat by increasing its consumption of groats when given the opportunity, then it would be expected that this increased consumption would be temporary, and subsequent days should show a drop in the preference level towards the normal value. The Table shows that there were in fact a much larger number of decreases in the preference for groats over the first two days after the limitation than there were increases, and that this effect is significant at the 0.1% level. As expected the 95% confidence limits for the median value of the percentage points change between these two days both fall below zero, covering the range -2 to -9, which confirms the Chi^2 results, and indicates a significant drop in the preference for groats.

Comparison of the second and third days after the limitation shows no effect at all, with a Chi^2 value of 0.6. It therefore seems that the effect of limitation to wheat lasted for only one day, and that the vole has attained its normal preference level by the second day on a mixed diet.

It is surprising that the effect over the period of limitation is so much smaller than over the two days following it. However, it was shown in Section 4.5.3 that there may be little connection between the preference level on one day and that several days later under ad lib. conditions. Thus, it could be that the low level of significance for over this period is due to the fact that there are changes in the vole's preference level not necessarily related to the effect of a restricted diet over several days. Conversely, the highly significant results for the first two days following limitation could in part be due to the fact that two consecutive days are being compared, so that most of the difference will not be the result of independent fluctuations.

These results confirm the findings of the first experiment in this section, and indicate that limitation to one food tends to increase the consumption of the alternative food when the choice is restored. This effect is mainly restricted to the first day of restoration of the mixed diet, which means that experiments where consumption is measured daily are not the best way for studying consumption patterns following the limitation. Analysis on a much finer time scale will be left till section 5.3, where the effect of limitation to one pattern on the actual sequence of selection within a bout will be studied.

4.6 Hoarding

The phenomenon of hoarding is common amongst small herbivorous mammal species (Richford, 1974). Although different species show hoarding which ranges from a localised single hoard near the home to many scattered hoards of which some may not be found again, it seems clear that the basic hoarding response is of survival value in providing a supply of food to last over the winter. The factors stimulating hoarding are generally assumed to be abiotic environmental factors - decreasing temperature or decreasing photoperiod - though it could also be a response to an abundant food supply.

The primary foods hoarded are the reproductive parts of plants seeds and nuts - and quite large quantities can be involved: Shaw (1934) found hoards of up to 33 litres of seed for the giant kangaroo nut (Dipodomys ingens). It therefore follows that hoarding can have a large impact on the plant community, either to the benefit of the hoarded species, as when it helps in seed dispersal, or to its detriment, as when seeds are removed to a place unsuitable for germination, quite apart from the fact that seeds would stand a greater chance of being consumed if they are hoarded.

The implications for the hoarding animal are not simply that it now has a food supply during periods of scarcity, but also in its possible effect on all features of the feeding response of the animal during the period of hoarding and of increasing food scarcity. First, hoarding affects the effective density of the hoarded food, both at the time of hoarding but more especially later, since it changes a widely-distributed food supply into a compact, readily found one, and since it removes that food from consumption by other animals. Second, the strategy adopted by the feeding animal as the densities of other foods change could be affected by the presence or absence of a supply of hoarded food. It is thus necessary to include hoarding in a study of an animal's functional response.

In the context of the present studies, however, the shape of the functional response curves described in section 3 are not likely to have been affected by food hoarding. Although a certain amount of hoarding of groats as well as wheat took place in cages (4.6.2), hoarding in the functional response experiments consisted almost entirely of wheat, which was always abundant and easily accessible in any case. When hoarding of groats did occur, only under conditions of the highest groat densities, it was of no benefit to the vole on subsequent periods of low groat density since all hoarded food was removed each day.

4.6.1 Types of hoarding by voles

The areas used for my experimental animals were quite small compared with the natural situation, either being large cages measuring 30 cm by 50 cm, or the areas used in the functional response experiments. Since voles were often observed to take food back to the nest to eat it, and since it is possible that some of the grains taken back for eating are then left, it is possible that not all grains found to have been removed from their original place were hoarded, but could rather have been taken for eating. In this section, I will first show that grains were eaten in the nest, and then analyse the data to see if we can distinguish between hoarded grains and those taken for eating on the basis of the weight apparently hoarded per day.

The eating of grains in the nest was demonstrated in an experiment in which oats, rather than the huskless groats, were used. This meant that the site of de-husking and eating grains could be found from the remaining husk, and the number of grains eaten from the known mean weight of husk per oat grain, which was found to be 12.9 mg. The method could also be used for wheat grains selected to still have part of the husk, and in this case the mean husk weight was 4.6 mg.

Though the experiment was designed to test the effect of other factors on hoarding, as will be discussed in subsequent sections, the results show that eating of grains in the nest does take place, that this can happen both with groats and wheat, and that it can be affected by changing conditions. The results are shown for one vole in Fig. 4.6.1-1 in which the estimated number of grains eaten outside the nest and inside, and the number of grains found in the nest, are shown for both groats and wheat.

There are several features to note in this graph. First, a low amount of grain eating in the nest took place throughout the experiment. Second, both hoarding and eating in the nest was dramatically increased when the cover was removed. This effect decayed rapidly, and was very similar for both the wheat and groats.

These results suggest that, under normal conditions, a vole either has one or two feeding bouts a day in the nest, or eats one or two grains in the nest during each bout. Observations on voles feeding in the automatic feeding machines strongly supports the latter idea, since it was very common to find a vole eating all grains but the last near the given supply point, and then taking the last grain to a covered spot to eat it. This could be the optimum solution to the problem of minimising the time exposed to predators, since if it went back to the nest to eat every grain then travelling time could increase the time exposed. Rosenzweig and Sterner (1970) have considered this

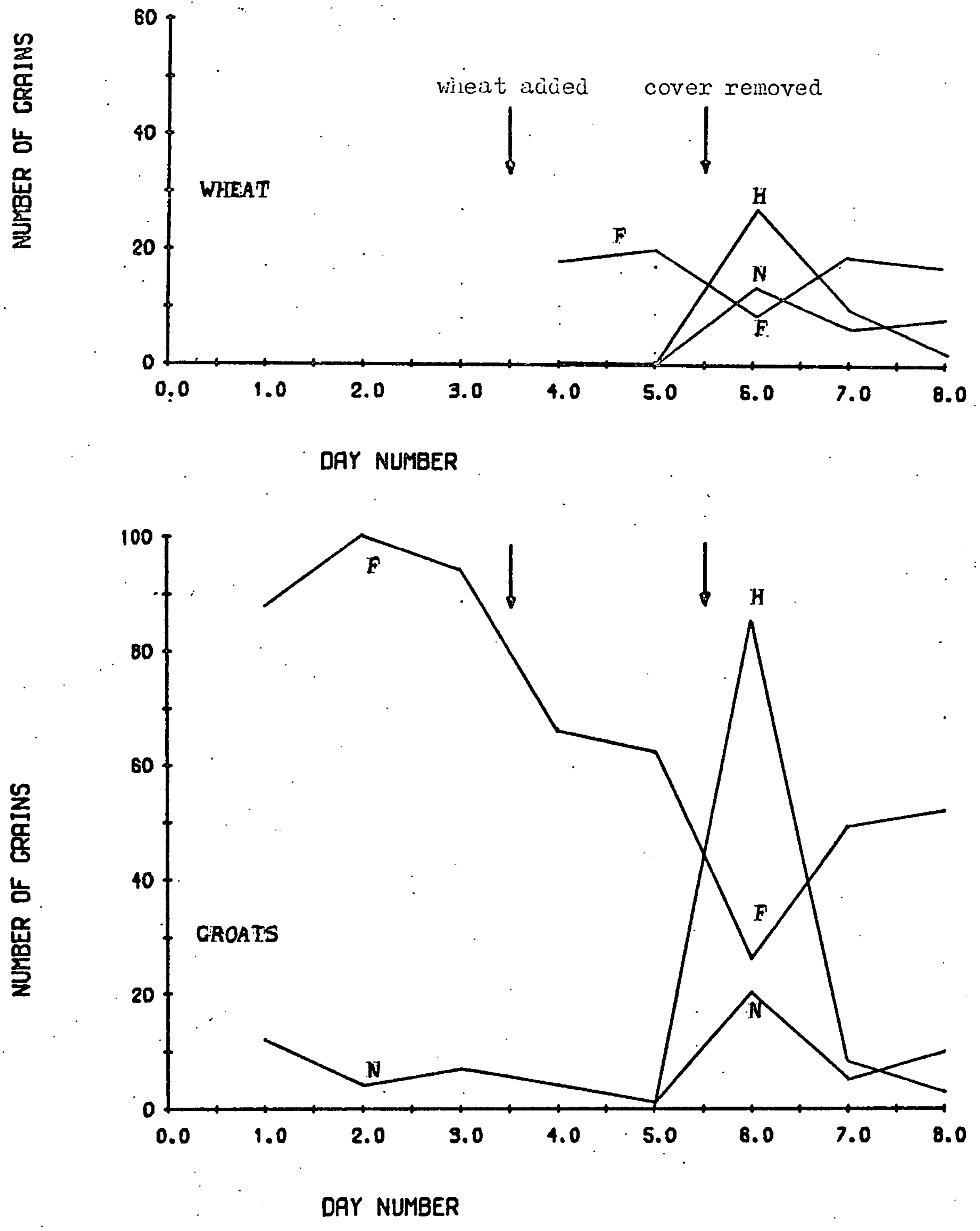


Fig. 4.6.1-1

Pattern of consumption and hoarding in relation to cover.

F - Food eaten on floor
N - Food eaten on nest
H - Food hoarded

problem in relation to husking grain.

The similar increases in hoarding and nest eating when cover was removed, and their similar decay, imply that both are governed by the same mechanism. If this is so then the hoarding seen here would not be so much preparation for periods of food scarcity as a new solution to the problem of predation, modified by the vole's changing assessment of the risk involved in eating food where it is found. Although hoarding decreases in this vole as it becomes used to the lack of cover, this need not happen with all voles, and so a similar explanation could explain the sustained hoarding level of other voles.

In order to see whether it was possible to detect differences in the hoarding levels of different voles, which could then possibly be explained in terms of different mechanisms operating at the different levels, data for twenty voles monitored over the same period of nine days was analysed. In view of the higher hoarding levels at the start of the experiment, (see section 4.6.4), the first two days were discarded (though they only affect the conclusions quantitatively), and a mean of the data for the remaining seven days calculated to give a daily value for total hoarding (wheat and groats together).

This data was then ranked, and the data for each vole plotted against its rank number. This approach was adopted rather than plotting the frequency distribution of weight hoarded, since the cluster of values at the lower end of the scale made this latter approach impractical. From Fig. 4.6.1-2 it can be seen that there is a fairly smooth rise from zero hoarding up to the maximum levels of 5.0 - 6.0 gm/day. There is evidence of slight discontinuities, that is, regions of sharper

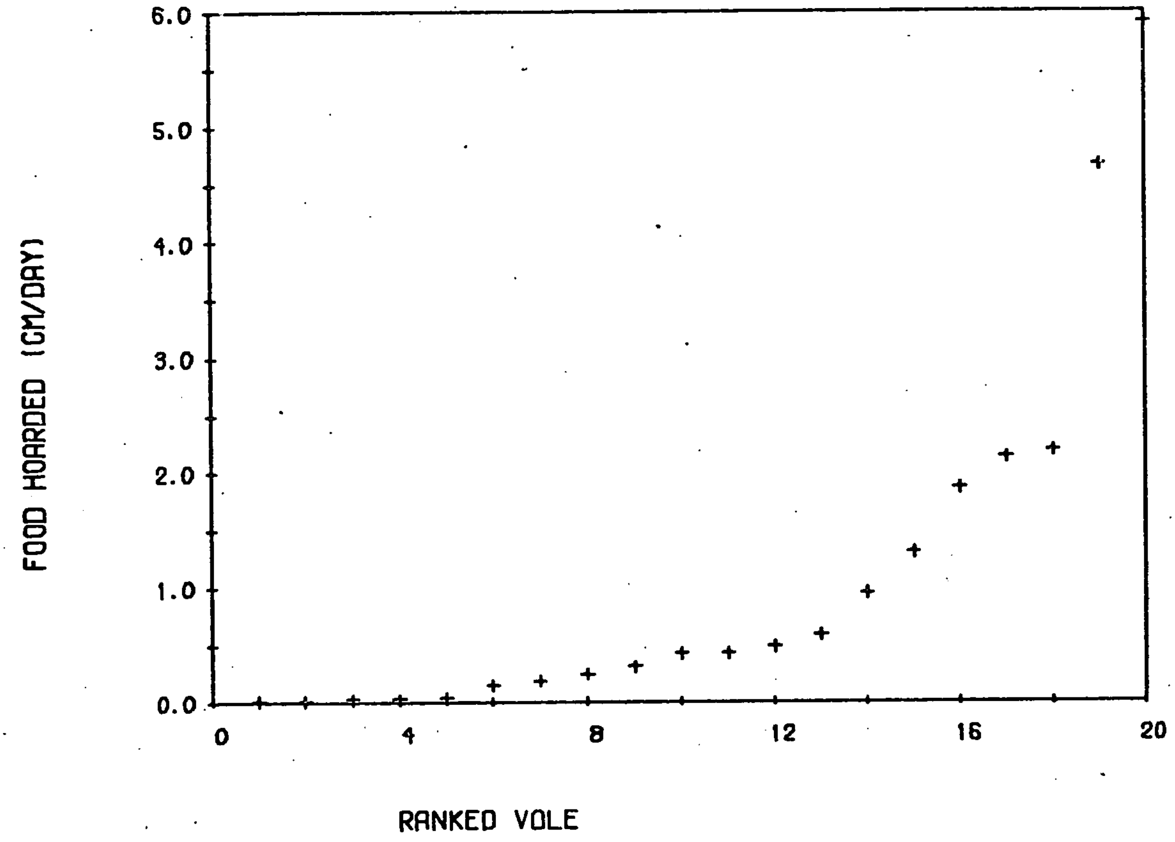


Fig. 4.6.1-2

Voles ranked by amount of food hoarded per day.

rise in the graph, at approximately 0.8 gm and 3.0 gm, but it is hard to assess their significance. On plotting the log of the values (Fig.4.6.1-3), it can be seen that except for the lower four voles, the data falls on a straight line: the two apparent discontinuities are still present but minimal, and there is no basis for splitting the voles into low hoarders and high hoarders. There is though a difference between those which hoard and those which do not hoard at all.

These results indicate that: voles are either hoarders or non-hoarders; the same mechanism controls hoarding in all hoarders, and that this varies in an exponential manner; these results do not enable us to say if different voles hoard for different reasons.

4.6.2 Hoarding preference

In this section, I shall consider the relative proportions of the two available foods hoarded by the bank vole. The conclusion of other workers, based mainly on results obtained from the rat, is that an animal tends to hoard food which can help to relieve a nutrient deficiency (Gross and Cohn, 1954; Fisher and Cohn, 1955). Bindra (1947b) found that rats deprived alternatively of food and water tended to hoard that of which they had been deprived. Although I did not specifically check this relationship in the vole, it is clearly not the whole explanation of hoarding in this species, since all animals whose hoarding was monitored had an ad lib. supply of both food types.

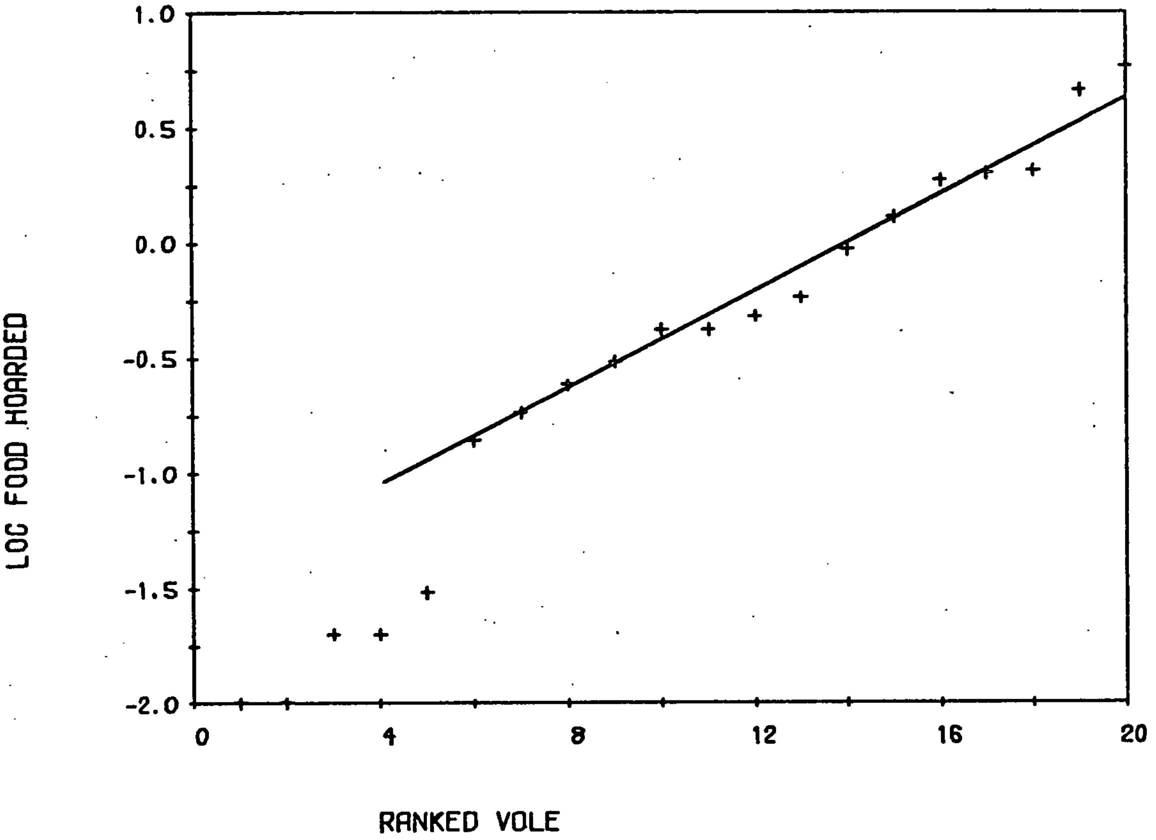


Fig. 4.6.1-3

Log transformation of hoarding data for ranked voles.

The analysis presented here was based on the same group of voles introduced in section 4.6.1. Again, the data obtained from the first two days was rejected, in view of the initial effects discussed in section 4.6.4. For the remaining seven days, the total weights eaten and hoarded for both wheat and groats were found, and the percentage preference groats then calculated for both activities. Of the twenty voles, seven hoarded less than 0.1 gm/day, and were excluded on the grounds that the discrete nature of grains made the ratio of groats to total very variable. The results for the remaining thirteen voles are presented in Fig. 4.6.2-1, showing the relationship between % pref. groats for eating and hoarding.

The data show a positive correlation (r=0.54, df=11) which is virtually at the 5% level of significance of 0.55. This indicates that the higher a vole's preference for groats for eating, the higher its preference for hoarding groats. This indeed implies that part at least of the mechanism determining hoarding preference is related to the nutrient status of the two foods, and that voles with a need for a higher proportion of groats in their diet show a corresponding increase in the proportion of groats in the hoarded food.

However, it is also very clear from the figure that individual voles differ markedly in their percentage preference for groats for eating and hoarding, and that the nature of this difference is similar for all voles, with the data points clustered in the region of high % pref. groats for eating and low % pref. groats for hoarding. This can be interpreted in two ways. First, it could be thought that the distinction

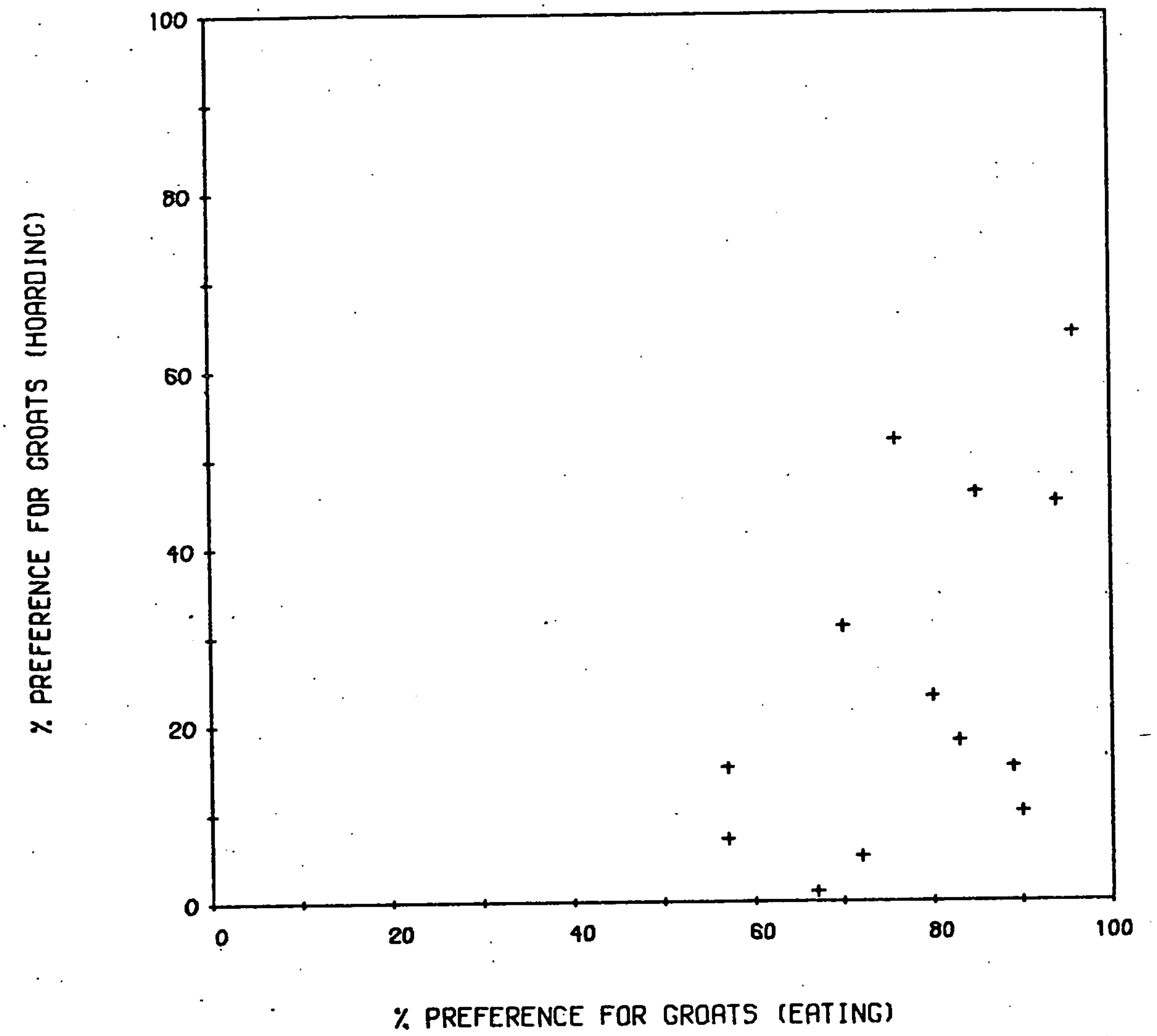


Fig. 4.6.2-1

Relationship between preference for hoarding and for eating groats.

between hoarding and eating activities is erroneous, and that the true separation should be between collecting and eating, with hoarded food appearing as that collected food which is not eaten. Then, if both foods are collected equally, and there is a preference for groats at the eating stage, then the hoarded food should have a higher proportion of wheat. This is an attractive idea, but has to be rejected on two counts. If it were correct, there should be a negative correlation between the % pref. groats for eating and hoarding, and not the positive one described above. Also, the weight hoarded is rarely equal to the weight eaten in a given period, and this theory predicts that in this case the hoard should not contain any of the preferred food for eating, which is obviously not so.

The alternative explanation is that hoarding and eating are separate activities, and that the criteria by which a vole assesses the relative value of the two grain types is different for hoarding. Ewer (1968) identified one possible factor, when he found that rats tend to eat smaller items of a food type and hoard the larger ones. This is a good strategy for an animal to adopt, since it involves a lower expenditure of energy per unit weight hoarded. If this is so, we would expect that a similar preference should be shown when the vole is given a choice between small wheat grains and large ones. Data to test this was available from another experiment, in which five voles were monitored for thirteen days with only small and large wheat grains available, the former being approximately half the weight of the latter. An average value for the percentage preference for small wheat was obtained from the totals of the two types hoarded over the thirteen days, with these results:

36%, 41%, 54%, 57%, 58%.

Here, despite a size difference as great as between groats and wheat, there is no evidence that the larger food is preferred. Indeed, if the preference value is based on number of grains rather than weights, all the values are greater than 50%. Thus, it does not seem that size in itself determines hoarding preferences.

4.6.3 Factors influencing hoarding

If hoarding is not only a means of building up a store of food for winter, but also an indication of what the vole judges to be its optimum strategy in terms of minimising exposure to predators and minimising effort expended, as suggested in section 4.6.3, then it is likely to be affected by factors other than seasonal ones and food density. Richford (1974) has revealed two factors which can influence the hoarding level of the bank vole for a given type of food. First, hoarding of food was much greater when the food was spread on bare floor than when it was underneath cover - the cover used was in fact the same blocks of brushes which had been used in my functional response experiments (section 3). This effect was greater on the first day of removal of cover than thereafter. Second, if the hoarded food was not removed every day, the rate of hoarding dropped off till it reached approximately zero, and the size of the hoard then remained constant.

This second finding is of some relevance to the type of conditions that I used in the functional experiments. In these, I always removed any hoarded food, for three reasons. First, it was felt that this made for greater uniformity between days. Second, hoarding of a preferred food would clearly affect the conditions of the experiment when this food was set to a lower density. Third, it was impossible to return a hoard in an undisturbed condition after counting and weighing, especially when the hoard had been under the brushes. But the above results do show that this approach may have kept hoarding at a higher level than if the hoard had been left.

The effect of cover on the level of hoarding was also demonstrated in two situations with my voles. The first was an early experiment conducted in the room used for the functional response experiments, and one frame of wood-chippings was used for cover - see Appendix A1 for details. Several hundred grains of groats and wheat were placed under the cover on the first day of the experiment (though the vole had been in the experimental area for several days previously), and the time spent out of the nest was recorded using a treadle device linked to an event recorder. On the following day, the cover was removed, hoarded grains were returned to the floor, and additional groats added to make up for those consumed. Although the experiment was only conducted for two days, and the results for the second day almost certainly do not represent the equilibrium level of hoarding in the absence of cover, the results tell us rather more than the simple hoarding levels for the two days, and can thus indicate the differing vole strategy.

The results are given in Table 4.6.3-1, showing the numbers of grains hoarded, the number of sorties, the total time outside the nest, and derived statistics. It can be seen that when the cover was removed, there was a large increase in the hoarding of both foods, but that this increase was much larger in the case of the preferred groats. This is parallelled by an increase in the number of sorties on this day, but this was proportionally less than the increase in grains hoarded, since the values for the mean number of grains carried per trip show that many more were carried per trip when the cover was removed. This can either be interpreted to show that some of the trips are not associated with hoarding when the cover was down, or that more grains are actually carried back to the nest with each trip when the cover is removed. Inspection of the event recorder record indicates that the latter is more likely, but either case shows a change in the vole's strategy. It can also be seen that the total time spent outside the nest was much less when the cover was removed, and that the difference between the mean length per sortie was even more marked, being decreased by approximately 87% when the cover was lifted.

4.6.4 Temporal patterns in hoarding

I shall consider the manner in which hoarding activity can be patterned in relation to time at two levels. First, hoarding can be studied on a day-to-day basis, and this is useful for indicating trends over time and day-to-day variations. Second,

Table 4.6.3-1

Hoarding and activity data for one vole on two days, with and without cover.

		Day 1 (cover)	Day 2 (no cover)
Hoarding :	Groats	1	340
	Wheat	36	109
	Total	37	449
Activity :	Number of sorties	83	156
	Time outside nest (mins.)	35	8.3
	Grains per sortie	0.45	2.88
	Mean length of sortie (secs.)	25	3.2

a small amount of data on the pattern of hoarding within a day, on a minute-to-minute basis, will be examined for indications it can give on the hoarding mechanism.

Most studies of hoarding have shown that, for a given animal, it is a very variable activity, and easily influenced by 'emotional' factors and the conditions of the experiment. Thus, it has been commonly found with rats that it is influenced by the length of time since introduction to a new experimental arrangement (Bindra, 1947b; Bindra, 1948a; Morgan, 1947). In these cases, the animals are reported to hoard little when first introduced and then to increase their level of hoarding as they become accustomed to their surroundings. Richford (1974) claims to have found a similar effect in the bank vole, though his results were obtained from voles whose experimental conditions was being manipulated to test their effect on hoarding.

However, my results, obtained from several experiments on voles, failed to confirm these findings, and indeed most showed precisely the opposite effect, with voles tending to hoard much more when first introduced into new surroundings. These findings are illustrated by the results of one monitoring experiment, in which the consumption and hoarding of twenty voles was monitored daily for sixteen days. Fig. 4.6.4-1 shows the total weight hoarded per day for the seven voles which hoarded more than an arbitrary level of 0.3 gm/day. Five of these voles show marked higher level of hoarding at the start of the period of introduction into new cages; one vole only shows high levels of hoarding after eight days, despite an initial burst on the second and third days; and the other vole shows two sporadic bursts of hoarding. The results from other monitoring experiments were

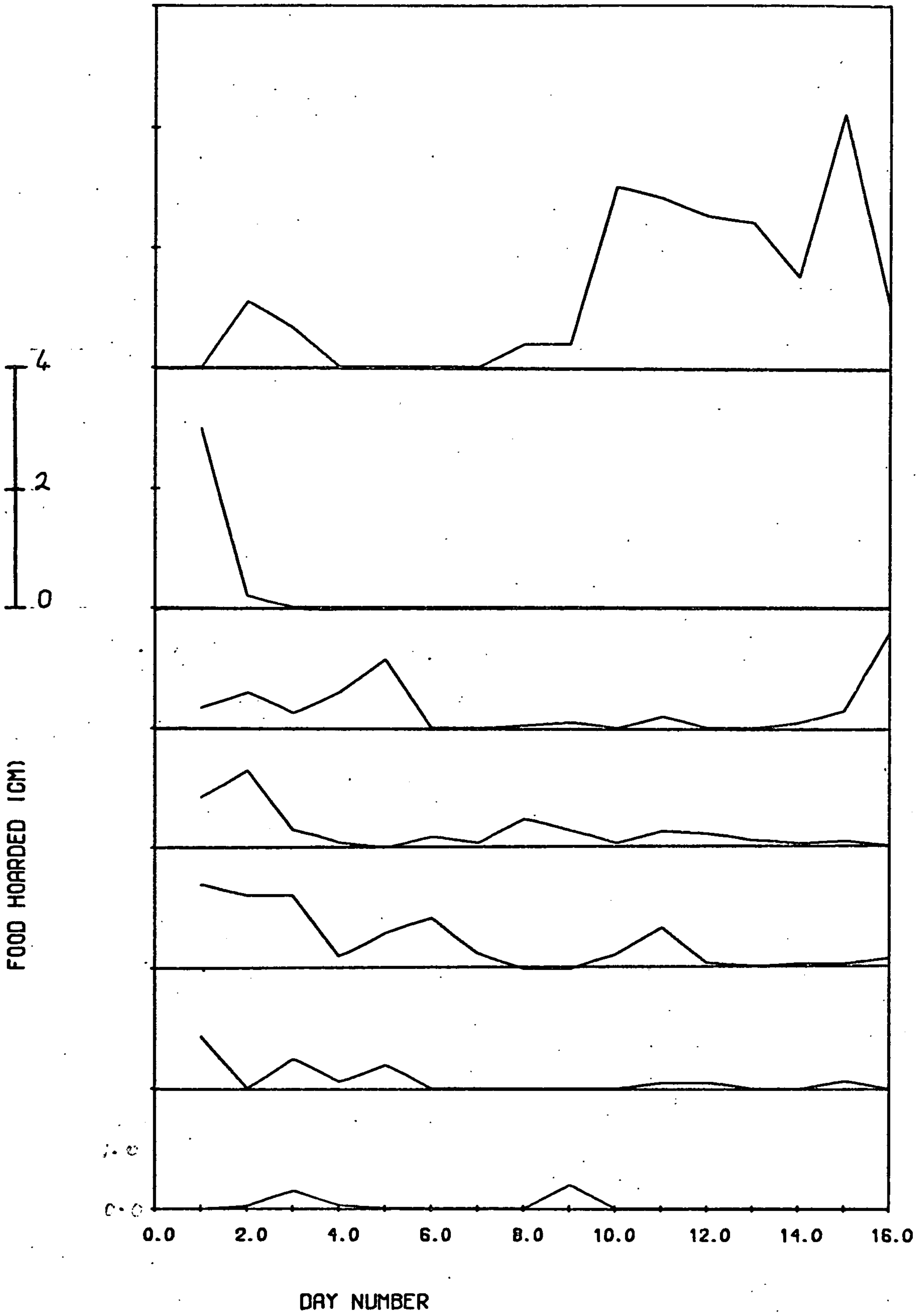


Fig. 4.6.4-1

Hoarding pattern for seven voles.

examined and showed similar patterns, with most voles hoarding most on the first few days, and a few only starting to hoard after an initial low period. Even in these few cases, it is often more plausible to explain the results as a burst of hoarding lasting from one to several days, rather than as a rise to some equilibrium level of hoarding after adjustment to the conditions.

The feature, shown by the one vole above, of sporadic hoarding seemed to be a common aspect of hoarding, whether voles do or do not show the initial high levels of hoarding. Figure 4.6.4-2 illustrates three other examples, selected from another monitoring experiment involving twelve voles over thirteen days. In these cases, there is little evidence of trend over time, but the amount hoarded per day fluctuates over a large range and apparently randomly. Since there can be around twenty to thirty grains per gram, quite large numbers of grains are being moved on those days of heavy hoarding activity.

Some idea of the reason for these fluctuations can be obtained from an analysis on a finer scale of hoarding activity. The event recorder record of movements into and out of the nest for the vole first mentioned in section 4.6.3 was inspected. On the second day, when cover was removed, hoarding was increased, and less time spent out of the nest, it was found that hoarding takes place in well-defined bouts. The turn-around time was very fast, so fast in fact that the two traces for return into the nest and subsequent exit could not be distinguished on this time scale. Time outside the nest to pick up hoarded food was approximately 0.5

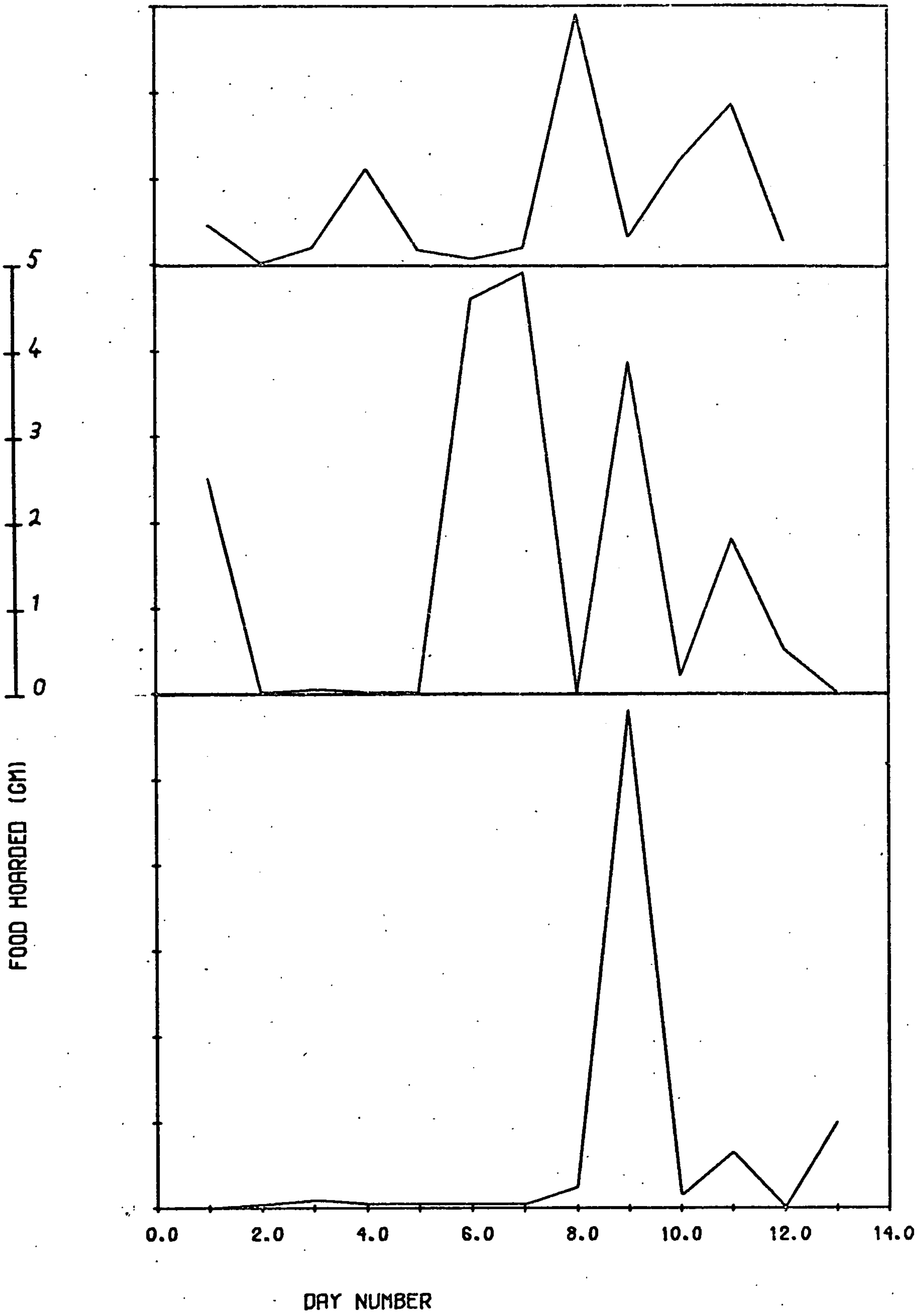


Fig. 4.6.4-2

Hoarding pattern for three voles.

minutes (the time-base mark was made once per minute), and during this time an average of approximately three grains was picked up and carried to the nest. These results imply that the unit of hoarding is the hoarding bout rather than the individual grain. This helps to explain the range of variation in the daily hoard size, since the vole could in fact have a constant probability of starting a hoarding bout at any moment of time. Then, if a bout was begun, it continued until a large number of grains had been collected.

An alternative explanation could arise from Richford's observation that hoarding decreased if the hoard was not removed every day; if the hoard was then removed, the level of hoarding increased. It might be that with some voles, the estimation of current hoard size would come not only from feed-back from the actual hoard, but also from the experience of having recently hoarded. In this case, the latter effect would cause less hoarding after a period of high hoarding activity, until the vole became aware of the discrepancy between estimated and actual hoard size, when hoarding would again be triggered.

This variability in daily hoarding levels arising from the discrete nature of the hoarding bout has certain implications for an analysis of the functional response of a hoarding-type animal. If time spent hoarding competes with time needed to find food for eating, then this would vary on different days. Second, if contact with certain types of food in the course of hoarding affected the probability of the animal searching for that type, then this also could influence the proportions taken of the different food types, all other things being equal. Finally, the animal could update its awareness of the relative abundance of different food types on those days in which it collected food for hoarding. However, none of these effects appeared to influence the functional response results obtained in section 3, since, although hoarding did take place, it was almost invariably the super-abundant wheat which was hoarded, so that none of the above three effects should be apparent.

4.7 Drinking

In all the experiments described herein, water was always present in an ad lib. supply. This appears to be in keeping with other experimental investigations of the functional response, in which no mention is made of water availability as an experimental variable (Holling, 1965; Smith and Dawkins, 1971). If one is only interested in a description of the functional response itself, then it does not matter if part of this response is mediated through effects of changing food conditions on the response, since water is not limiting. If, however, one is also interested in investigating the components of the functional response, then one needs to make the assumption that no aspect of thirst is a significant component in the response mechanism. If either changes in the experimental conditions have a direct effect on drinking, or if they have an effect through changes in feeding levels, and then if these changes in drinking have an effect on eating patterns, then drinking would need to be considered as a component of the functional response, since it would need to be included if a realistic, rather than an empirical, description were to result.

No experiments were conducted to investigate the importance of these possible links. It seems unlikely that changes in the experimental conditions themselves would affect drinking, since water was always readily available, and the main experimental variable was the amount of groats present. It is possible that changes in the response variables (amounts eaten of the two foods, and distance travelled) could affect drinking). However, distance travelled did not appear to affect consumption (section 4.4.5), so it seems unlikely that there will be an effect on drinking. And, although changes in total consumption are known to affect drinking (Kutscher, 1969), I know of no evidence to suggest that changes in the relative proportions eaten of two acceptable foods affects the level of drinking. Finally, it is well known that there is a connection in the remaining link, from levels of drinking back to feeding (Collier, 1969). Thus, any direct or indirect effect on changes in groat density on drinking would tend to be passed on to the control of consumption.

In the following sections, various aspects of drinking will be discussed and related to eating behaviour.

4.7.1 Relation of drinking to other factors

In this section, I shall consider the results obtained from a monitoring experiment in which the body-weight, groat and wheat consumption, and water consumption were measured for two periods of eleven days and four days for a group of seventeen voles. Water consumption was not measured daily for the reason that a certain amount of water dripped out of the water bottle each time it was replaced after weighing, and, as the amount lost was fairly variable, a longer period between weighings would reduce the relative importance of this error. The voles had been in captivity for a month, and the cages used were the same small ones in which they had been placed from the date of capture, though cleaned out at the start of this period.

Controls for water loss through dripping and evaporation were obtained by setting up four bottles over the four-day period. These gave values for water loss of between 0.4 to 0.6 gm/day. The average value of 0.5 gm/day was applied to all values, and on average reduced the estimate of water consumption by about 8%.

One point of interest is the extent to which a vole regulates its intake of water, as compared with its intake of food. One way of considering this is to plot the mean daily intake for one period with the mean value for the next period for all voles: if complete regulation is exercised and each vole has its own optimum level, then the points should fall on the 45° line. In Fig. 4.7.1-1a the data is presented in this way for drinking, and also for eating and the ratio of food to drink (Fig. 4.7.1-1b,c). It can be seen that in all three cases there is a good correlation between the two sets of data, which implies that the individual vole is fairly consistent in all three of these indices.

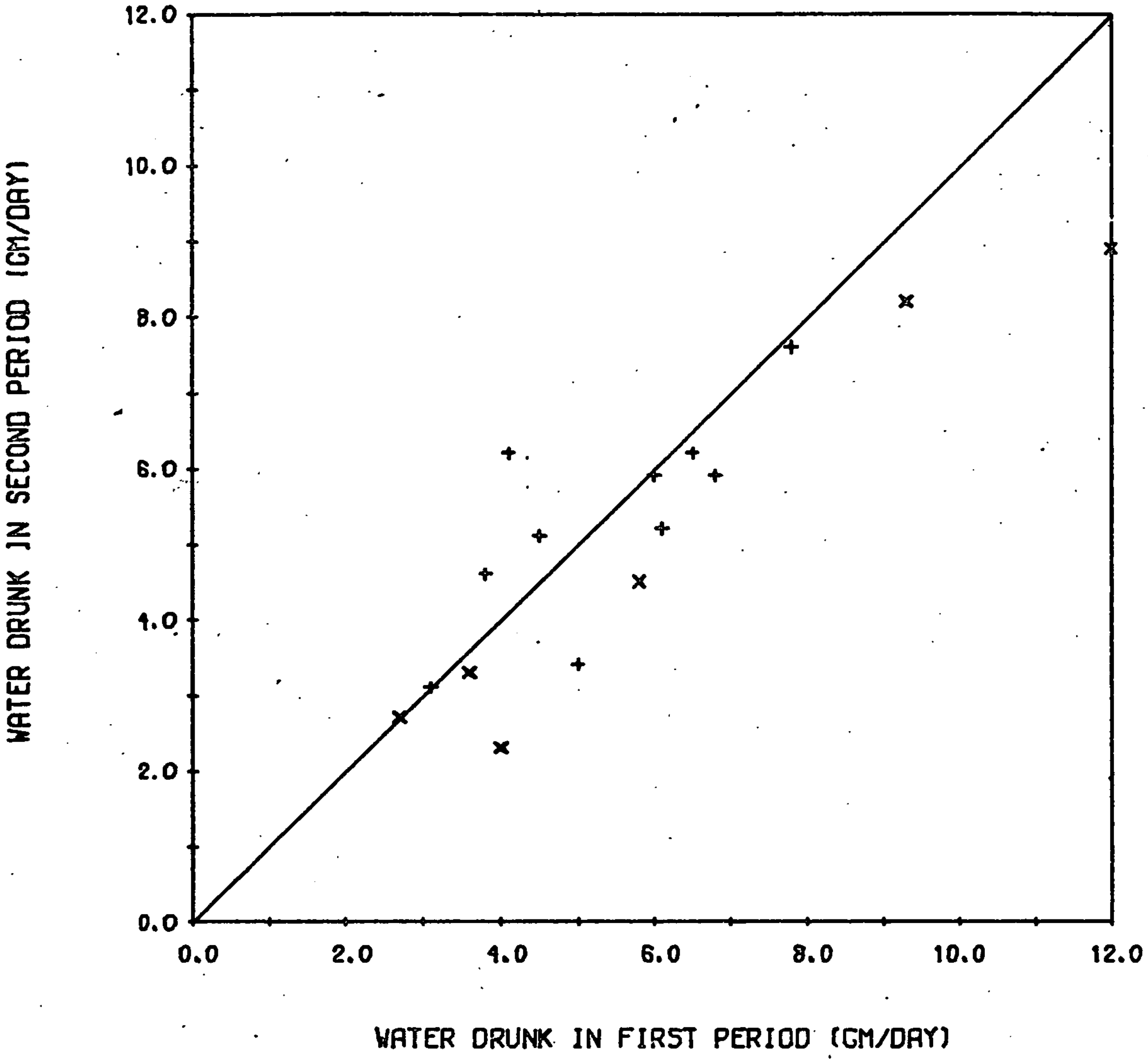


Fig. 4.7.1-1a

Relationship between water intake during one period and during the next, for voles fed on:-

× : Groats only
\+ : Wheat only

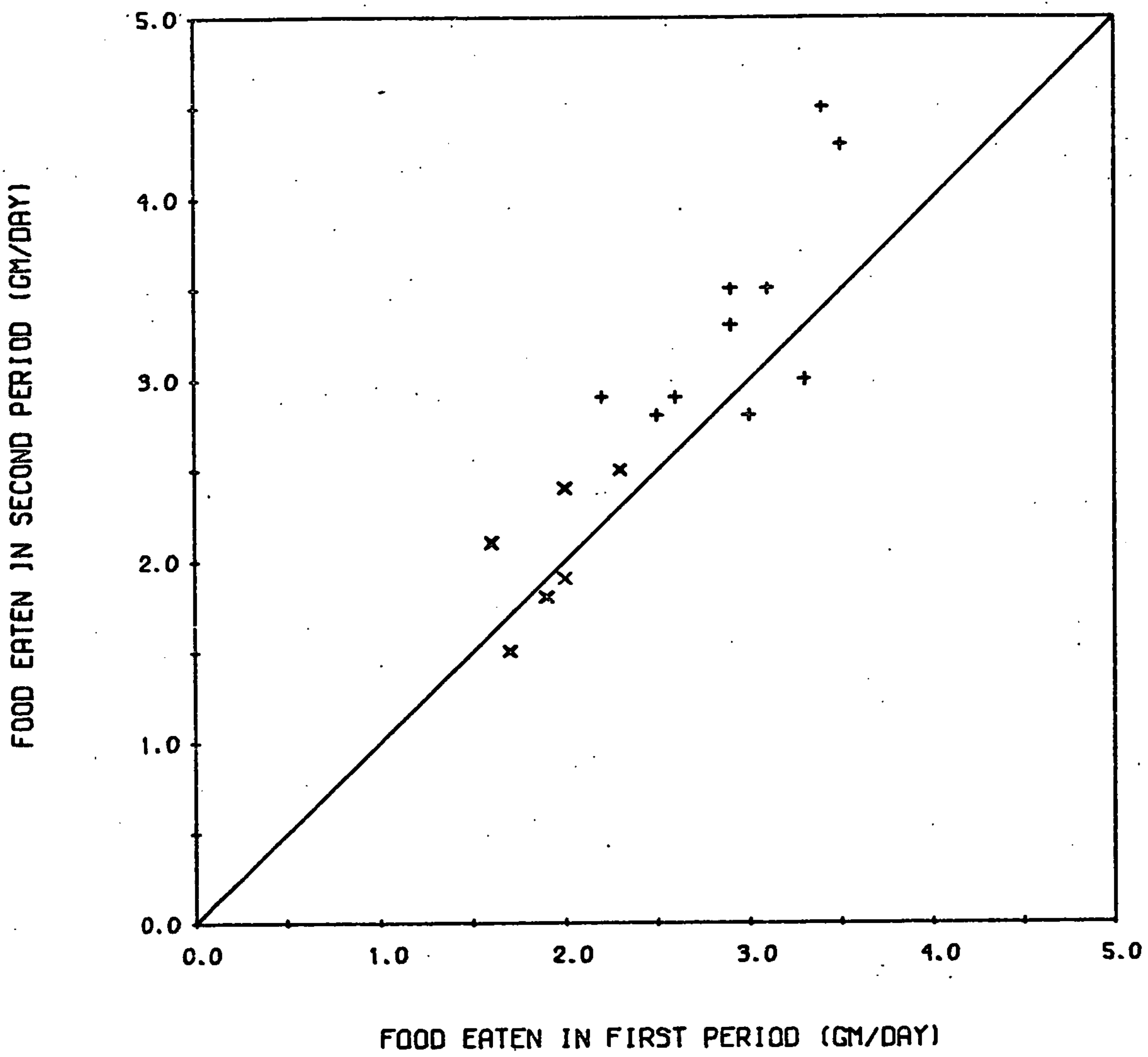


Fig. 4.7.1-1b

Relationship between food consumption during one period and during the next, for voles fed on:

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+ : Wheat only

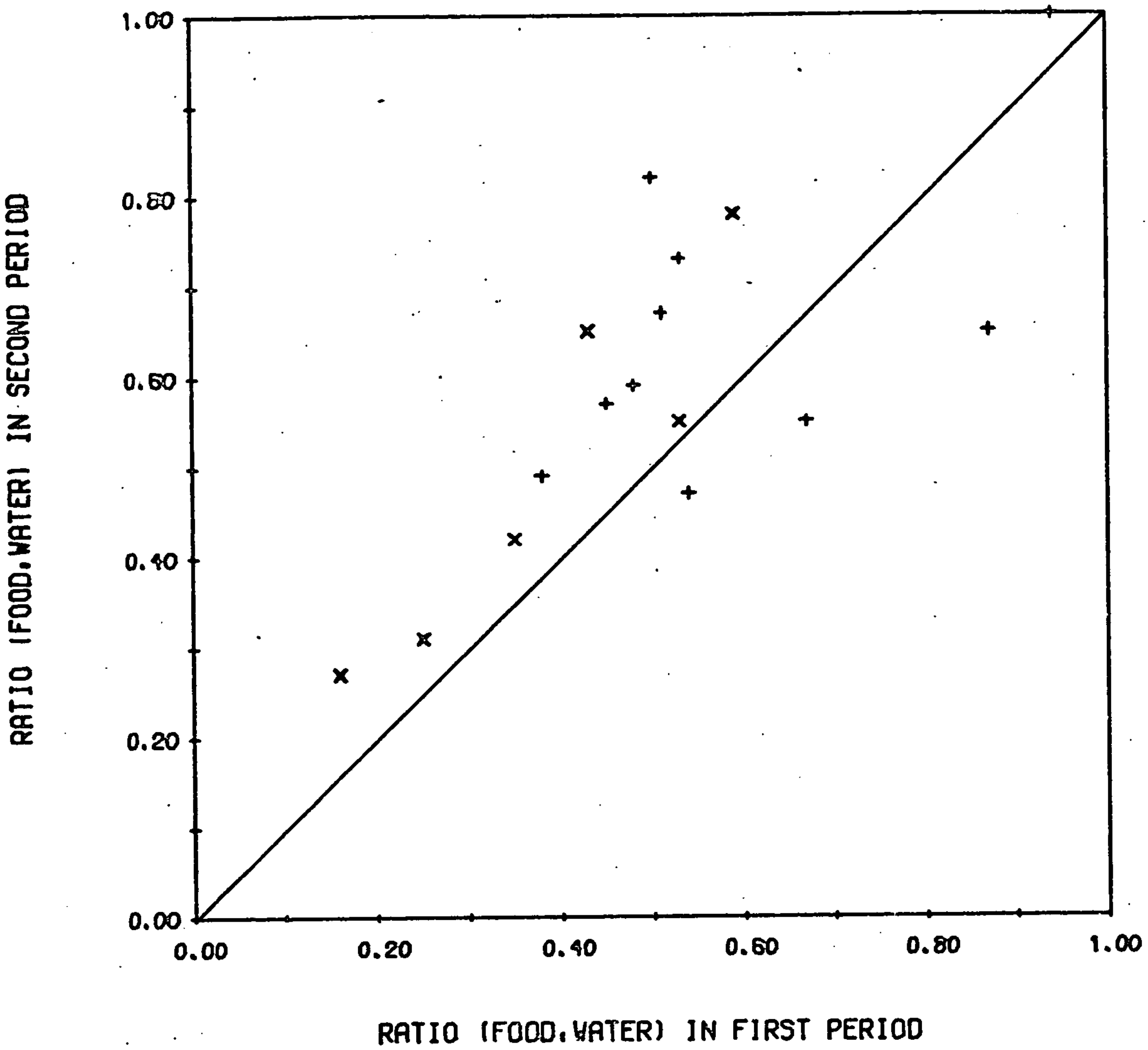


Fig. 4.7.1-1c

Relationship between ratio of food to water intake during one period and during the next, for voles fed on:

× : Groats only
+ : Wheat only

It can be seen that there is a slight drop in drinking between the two periods, and a rise in food consumption; consequently, the food/drink index shows a marked rise over the two periods. This indicates that drinking and eating rates can be varied to some extent independently, and that their ratio is fairly plastic. It would also appear that drinking is rather more variable than eating, both in terms of the range shown by the group of voles, and also for each vole, since the points are more scattered around the middle line for the drinking data.

The fact that individual voles still tended to show a certain degree of consistency between the two periods for their ratio of food to water, as indicated by Fig.4.7.1-1c, does not in itself mean that the ratio is more or less the same for all voles. Indeed, it can be seen from this graph that ratio of food to drink varies from 0.2 to 1.0. In Fig. 4.7.1-2, the average amount of water drunk for each vole for the two periods is plotted against the average amount of groats or wheat eaten over the same period. It can be seen that there is no evidence that voles show the same ratio of food to water despite their differences in the absolute amounts of food and water taken. There is slight evidence to suggest that voles feeding on groats alone tend to drink more than those feeding on wheat alone, but this is clearly affected by three voles which have unusually high intakes of water. These results suggest that although individuals tend to have a fairly constant ratio of food to drink, the population at large shows large variability between individuals in the ratio of daily food and water intake.

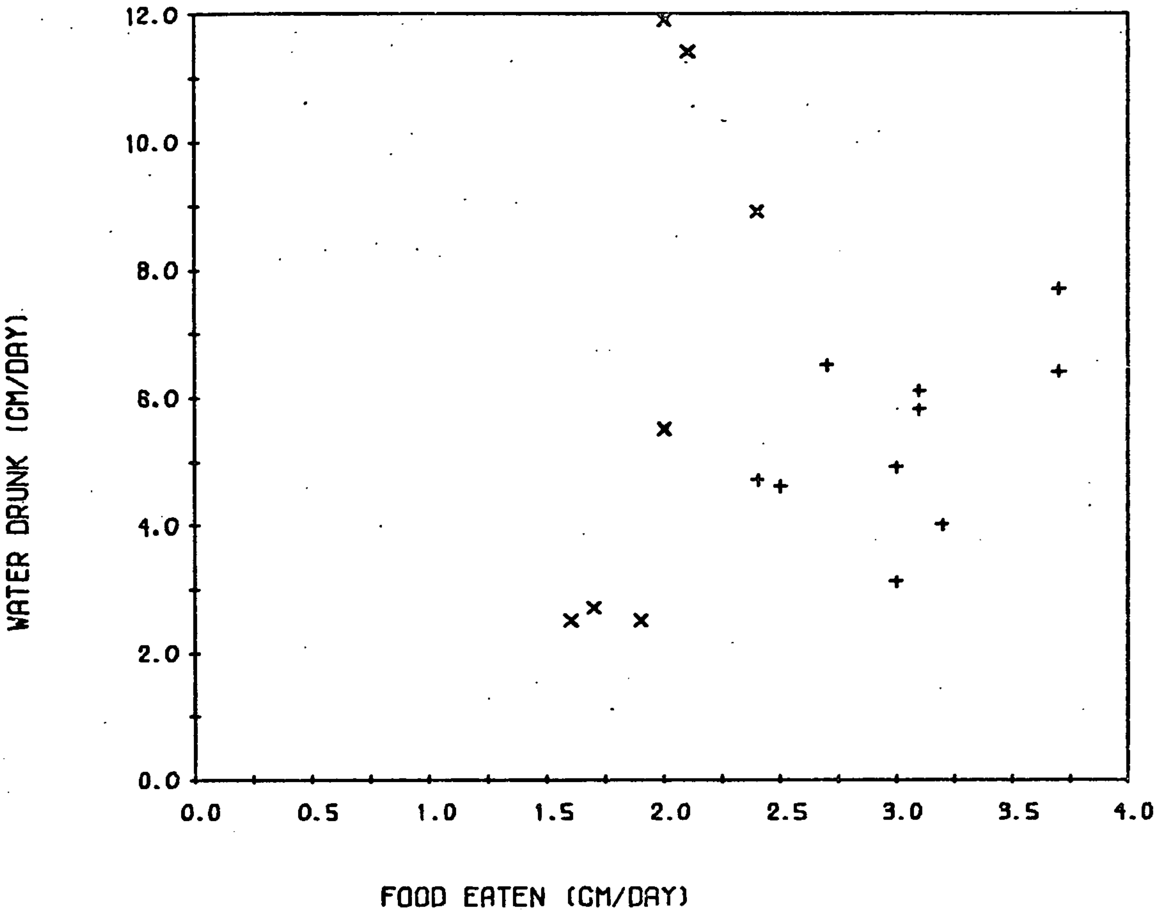


Fig. 4.7.1-2

Relationship between water and food intake for voles feeding on:

× : Groats only

+ : Wheat only

This indication that voles are fairly specific in their ratio of food to water intake is confirmed by the work of Collier (1969) with rats who found that forced decreases in water intake resulted in a reduction in food intake; he suggested that the main mechanism may operate through changes in the body-weight caused by the water deprivation, with food intake decreasing in order to conserve the same ratio of calorific content to body-weight, though it would seem from my feeding records that the decrease in consumption occurs much faster than predicted by this hypothesis when water accidentally ran out. Kutscher (1969) found similar results with rats, hamsters, guinea-pigs, and gerbils after five days deprivation of water, with the decrease being about 50% for gerbils and 80-95% for the rest. However, the restriction or deprivation of food has less clear-cut results on water intake, with most species showing a decrease in water consumption as food restriction started followed by a several-fold rise above normal.

From this, it can be concluded that if a vole experiences a shortage of water in the wild, then this would affect the functional response; this seems unlikely, since Watts (1968) found that bank voles mainly eat moist foods - green plants and fruit - during the period March - October. If all good quality food is in short supply, then it is possible that the effect of this shortage acting through the drinking system would have to be taken into account in developing a realistic model of the animal's functional response under these conditions, though again it is a long way from the harsh conditions of enforced deprivation to those encountered in the animal's natural habitat. It is not possible to make any conclusions from the available data on the effect of the changing diet composition on thirst-mediated effects on the functional response system.

4.7.2 Temporal patterning of drinking

In view of the fact that drinking could potentially need to be considered as a component of the functional response, and in view of the possibilities raised in the previous section, it was felt to be useful to investigate one aspect of the drinking mechanism, its temporal patterning in relation to eating bouts. A further reason is that, in section 5.2 I will discuss possible sub-components of the hunger system, of which one, the short-term component, can be most easily thought of as operating on the level of the stomach; how realistic this is may be affected by the pattern of drinking bouts.

The method involved the use of the automatic feeding machines, described in Appendix A3. In order to incorporate a measure of drinking on the event-recorder record, a sensitive voltage amplifier was used to detect the presence of a vole bridging the gap between a piece of wire gauze in the bottom of the cage and the water bottle. Input terminals to the amplifier were attached to both the gauze and the inside of the water bottle, and the circuit responded to the change in resistance across these two terminals as the vole drank. The amplifier fed its output into both the channels on the event recorder reserved for the particular vole, so that the drinking marks could be distinguished from the selection of groats or wheat, while at the same time being easily comparable with those associated with eating. The circuit diagram for the apparatus is included in Appendix A3. It should perhaps be noted at this stage that there was no evidence that the vole could detect the very small voltage across the wire gauze and the water bottle, and, in view of this low voltage and the vole's high body resistance, the current flowing through the vole would have been very small indeed. No vole was observed to pull back on making contact, and the patterning of drinking in relation to eating did not appear to change with time.

Data for one vole obtained over a continuous period of four days will be presented here; the records for other voles showed a similar pattern, and their data was not lifted.

It was clear from the record that there was a strong tendency for a feeding bout to be closely followed by a drinking bout, followed by perhaps another drinking bout and then the next feeding bout approximately two to three hours after the start of the first. In order to abstract this data, the frequency distribution of interval lengths were obtained for the four possible types of transition between an eating event (E), and a drinking event (D). The four possible transition classes are thus (E - E), (E - D), (D - E), and (D - D). An eating event was defined as the taking of a grain of either groats or of wheat, while a drinking event was defined as an uninterrupted drinking trace. Although this latter definition may be thought to give rise to the occasional ambiguous event, it was in practice found that there were no breaks in a drinking event of approximately 0.1 cm (equivalent to c. 30 secs.) which could have been difficult to classify.

The results are shown in Fig. 4.7.2-1, which shows the frequency distribution of interval lengths for the four transition types, up to sixty minutes: longer intervals are lumped in the end column. It can be seen that virtually all the (E - E) transitions occur under five minutes, showing that the eating bout is a definite entity and with its intervals determined largely by the time taken to eat one grain. A similar pattern, though less marked, is shown for the (E - D) transitions, with most of the intervals being less than five minutes, though with a much higher proportion being greater than this value. The (D - E) transitions show a strikingly different pattern, with only one third of the intervals being less than thirty minutes, with the rest longer than one hour. Finally, the (D - D) transitions differ from the others in showing no definite modal value.

These results give a clear picture of the patterning of eating and drinking. The basic pattern appears to be one of a meal comprising an initial feeding period, when grains are eaten in fairly rapid succession, and a terminal drinking session. The mechanism initiating the start of drinking is clearly different from that causing another grain to be taken, since the interval between the last grain and the start of drinking is relatively long. Following drinking, the vole may occasionally have another drinking session or eat more grains within the hour; more commonly, the meal is followed by a long interval of about two hours, before the start of the next

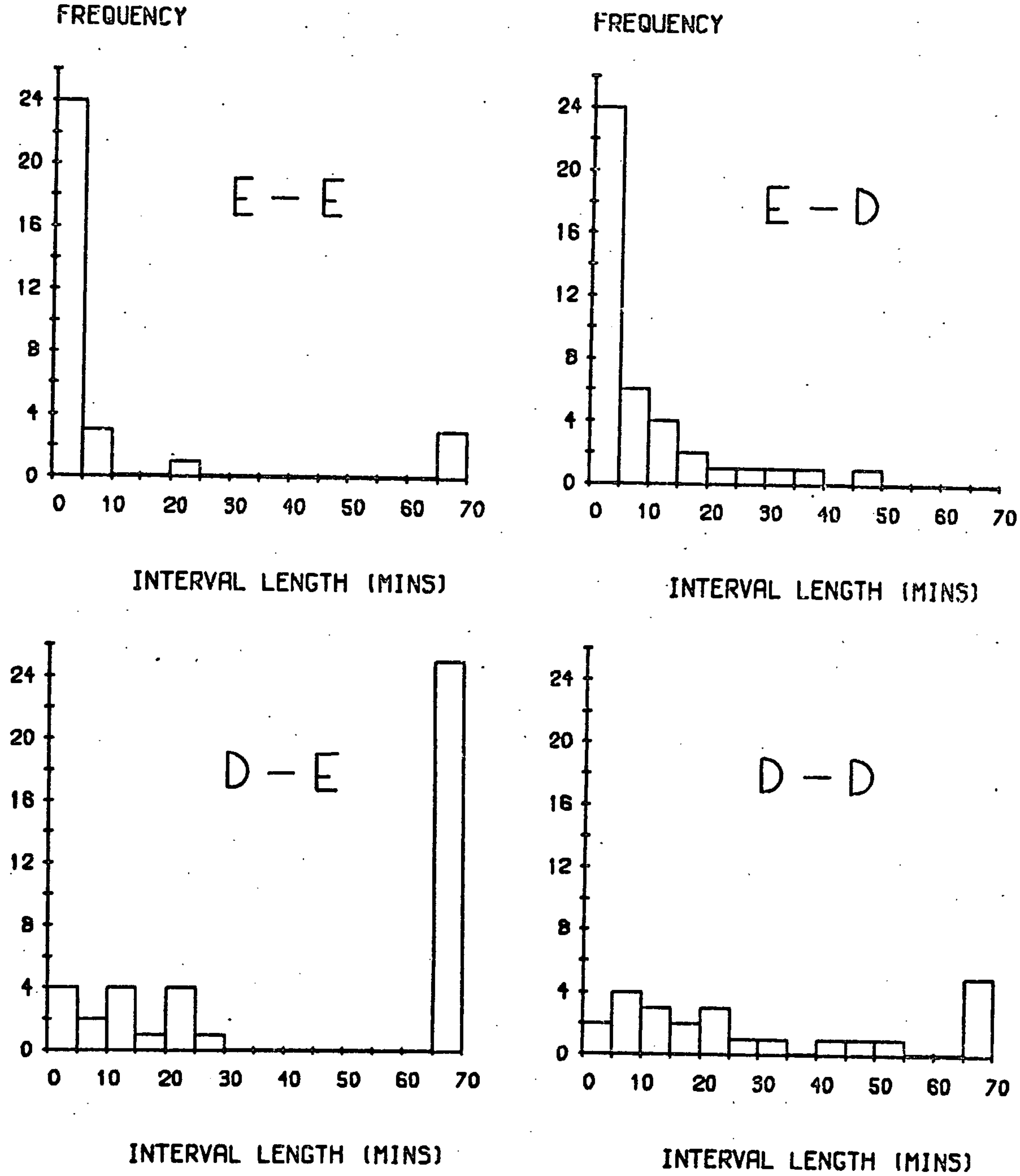


Fig. 4.7.2-1

Frequency distribution of interval lengths for the transitions:

E - E	Eat - Eat
E - D	Eat - Drink
D - E	Drink - Eat
D - D	Drink - Drink

meal.

These results mean that any model of short-term hunger based on a hydraulic analogy, with the stomach filling up with food to some maximum level and then emptying at some rate, is bound to be an incorrect representation of the actual process. The reason for this is that there is clearly room left in the short-term component after the end of a feeding bout, since drinking can still take place. However, such a model is still a useful way of representing the hunger system; it could be interpreted in terms of the maximum amount of food the stomach can hold, leaving a reserve for the water that will soon be ingested; or such a model could be seen as representing the animal's perceptual awareness of the amount of food that it has recently ingested, depending not only on stretching of the stomach but also on oral and pharyngeal sensors. In this case, such a model would be perfectly compatible with the above findings on the patterning of drinking in relation to the eating bout.

Section 5 Analysis of the Functional Response

5.1 The analysis of components

The value of analysing a complex ecological situation, like the functional response of an animal to food density, in terms of its components was discussed in Section 2. In this Section I will be considering in more detail what is meant by a "component", listing those components which are required for an adequate analysis of the functional response, and then considering each component in detail, either on the basis of direct experimentation (experimental component analysis - Holling, 1963), or by inferrence from facts relating to the physiology and behaviour of voles and other animals.

The term component is used in both a general and in a specific sense. Its use in the general sense is useful in determining the basic factors which may be thought to influence a process. Thus, we can say that learning is an important component without specifying the precise nature of this component. Alternatively, the term can be used in a more precise way. For example, the speed of movement of the animal is a component of the functional response system which is represented by a single variable and can be readily measured. A component does not, however, have to be represented by a single variable: for example, it will be argued in section 5.2 that at least three variables are needed to represent the component of hunger.

Two types of components can be recognised (see Fig.5.1-1). First, there are those which have a direct effect on the animal's feeding response. For example, the speed of movement directly affects the rate of search, which is important in terms of the

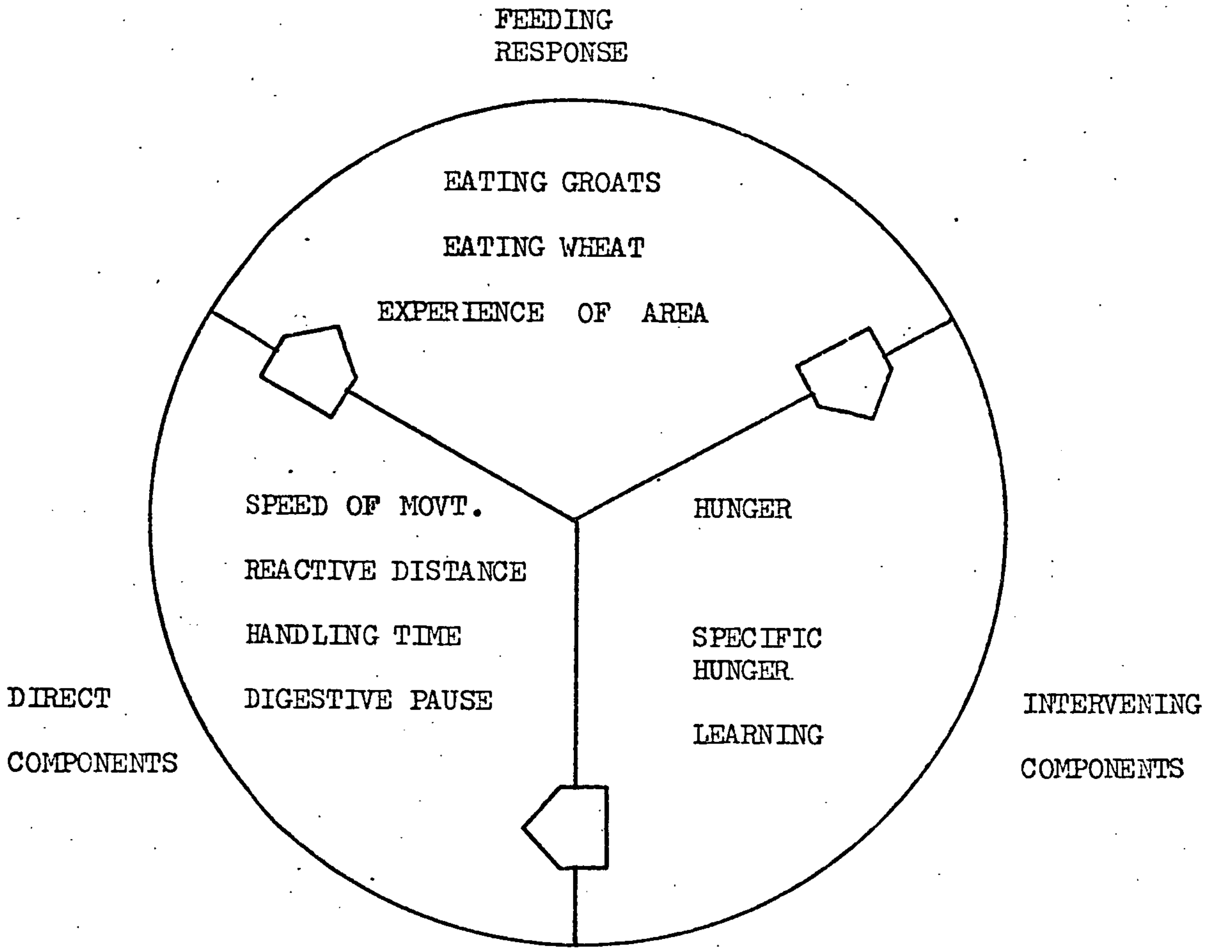


Fig. 5.1-1

Inter-relationships of the feeding response.

success in finding a specific food type.

The second type operate indirectly on the feeding response, by affecting the direct components. Since the system would not be very realistic if we assumed that all of the direct components had constant values, it is necessary to assume that other components mediate between the animal's past eating history, and those direct components which affect its future feeding pattern. Hinde (1966) has suggested that the word "drive" used to represent a motivational state, can be used in this context, and Tolman (1932) has suggested that drive may be represented by an intervening variable, intervening between the independent variables - the preceding conditions - and dependent variables, which are the various measures of the animal's subsequent activity. If we remove the restriction of a single variable, then we can talk of an intervening component, which may include several variables.

In general, the variables of an intervening component are state variables, that is their value specifies the state of the system and is not a time function (Patten, 1971). This is because the intervening component is used to accumulate the consequences of past eating history, so that a compartment approach is reasonable. The variable of a direct component, on the other hand, need not be of this type; thus the speed of movement component only has meaning in time.

There are two further types of variable that can be associated with the intervening components. The first is the threshold: this is needed in conjunction with a variable of an intervening component in order to produce the discontinuous activity characteristic of an animal's feeding behaviour even when there are no externally introduced discontinuities in the form of, for example, contacts between feeder and food (Holling, 1965). Second, there is the rate variable, which is needed to define the decay characteristics of a state variable in an intervening component: hunger increases in the absence of food, and what has been learnt is gradually forgotten.

The derivation of the important components in the functional response system closely follows that of Holling (1966). The starting point is the equation

$N = a.D.T.$ where: a = rate of successful search

D = food density

T = time searching

N = number of food items eaten

The right-hand variables can be further sub-divided:

a ... rate of successful search:

i - speed of movement of searching animal,

ii - size of reactive distance of searching animal.

T ... time spent searching:

i - time needed for other activities,

ii - handling time for each food item eaten,

iii - time spent in a "digestive pause" during which the animal is not hungry enough to search for food.

iv - total time available.

This analysis of components is considerably simpler than that presented by Holling (1965). First, capture success is ignored, since it represents the product of recognition success, pursuit success and strike success, all of which are assumed to have the value of 1.0 for a vole feeding on static food items which it recognises by smell. Second, "time spent pursuing and subduing a prey" can similarly be safely ignored in the present context. Third, Holling's division between time exposed to prey and handling time $(N = a.D.(T-H.N))$ is not preserved, since he then proceeds to make the time spent in the digestive pause part of the handling time (H), and it is convenient to regard this as a linear function of number of prey eaten. In addition, I shall further assume that the full day is potentially available for searching and feeding, so that the "time needed for other activities" comes out of the time spent in the digestive pause. This is in keeping with the normal understanding of competing activities (McFarland, 1969) and means that feeding over-rides other activities when its motivation is at a certain level. Thus, the total time spent searching per day is then (in hours):

Twenty-four
minus: Total time spent handling food
minus: Time in digestive pause

The above derivation is for the single-food situation. When two or more foods are involved, it is not possible to use the basic equation for both food types separately, making all variables specific to the particular food type, since it is not possible to assume that the alternative food type will not be eaten if encountered during the time spent searching for the one type. However, it is possible to say that the number eaten of each type per day will be a function of the set of direct components listed above. This is satisfactory for our purposes, since the formal equation is used as a key into the components that we must consider; it is not to be expected that the eventual synthesis of the components will necessarily fit into the formal equation.

A minimum of three intervening components are required to account for known features of the vole's feeding behaviour as described in Sections 3 and 4. The first of these is a hunger component. This is needed both to generate the type of feeding in bouts characteristic of the vole, and to enable the vole to respond to changes in its over-all level of nutrition as one food becomes more scarce. The hunger component takes as input the food eaten, without regard to food type except in so far as different foods may differ in a common characteristic; for example, the digestibility of groats and wheat may be different, so different amounts would be assimilated for a given amount eaten.

Second, it is known that an animal's past experience of particular foods affects its pattern of selection when given an ad lib. choice. In some cases, this may show itself as a preference for the specific food to which the animal was exposed (Southern, 1954), in which case the animal is said to be conditioned to a specific food. Much more frequently, however, it is found that limitation to a particular food, or deprivation of another, causes the animal to show an increased preference for the restricted food, that is, the animal shows a specific hunger (Young, 1949) for this food. This was shown for the bank vole in section 4.5.5. This effect has to be considered in the context of the functional response, where a period of restriction to one food type may be followed by an abundant supply of two foods. It also provides an argument against using the random density schedule used by Holling (1965), in his study of the functional response of the deer mouse, since a specific hunger for the food whose density is being changed (arising from a day at low density) could be carried over to a period of higher density, and distort the results. Further, this distortion would tend to produce an S-shaped functional response curve, since a day at low density would be more likely to be preceded by a day at higher density: this means that the animal's specific hunger for the food would be less than if it has been kept at the low density for several days.

The need for a learning component was revealed by the results from the functional response experiments (section 3). It will be remembered that there were differences in the vole's response to a given density level depending upon the antecedent conditions. For example, the distance travelled during a period of zero density of groats following a high groat density is high on the first day and much lower on subsequent days. Also, the response curve for decreasing groat density tended to be higher than for increasing density. It is not possible to explain these effects in terms of the other components; in particular, the specific hunger component would produce results opposite in direction to those which need explaining.

5.2 Hunger

5.2.1 Introduction

In this section, I shall deal with the first of the three postulated intervening components in the functional response system.

This is the hunger component, and is considered first because of its potential effect on most other components of the system.

To describe the hunger system as a component does not mean that it need be defined by the value of one variable, although it could be so. I cannot agree with Holling's (1965) assumption that the hunger system of the deer mouse is structurally the same as that of the preying mantid. Clearly, there is no reason why two such diverse species should have identical mechanisms; we would on the contrary expect that the difference between poikilothermy and homoiothermy, and the differences in phylogeny, could result in quite diverse mechanisms for regulating intake. Indeed, Holling himself finds evidence to suggest that a single-variable representation of hunger is inadequate even for the preying mantid, since there is evidence for depression of intake after the longer periods of deprivation.

The potential importance of the hunger component is three-fold. First, it is the component which is most directly affected by the results of the animal's feeding response, and is therefore well placed to provide feed-back on the current success of the feeding animal in satisfying its requirements. Second, it is likely to affect several components of the response; for example, Holling (1966) showed that the reactive distance of the preying mantid increases as it becomes more hungry, and it has been demonstrated with rats that the speed of movement increases as hunger increases (Reynolds and Pavlik, 1960). Third, in all but the simplest of models of the functional response system, we cannot assume that all time not actually spent handling food or in other fixed activities is actually devoted to searching for food; rather, we need to assume that for some of the time the animal is "not hungry enough" to search for food, a phrase whose meaning will be expanded later. Therefore, the animal will not be searching for food during the whole time that it could, and this will ddpend on its past feeding history, in turn a function of the densities of the available foods. The way in which hunger levels switch on and switch off food searching will thus affect the relative times that the animal can devote to searching for the available food types, and thus have an effect on the functional response.

It is now possible to attempt a definition of the term "hunger". We can represent the hunger system by a model of those processes which operate on the physiological level between the intake of food and those factors, influenced by this intake, which in turn can affect the intake level. The model need not be physiologically accurate, rather that it is an empirical description which can account for the observed relationships between intake and the levels of the other factors. The inclusion of the term "physiological level" rules out possible learning processes which can also monitor intake and affect subsequent intake; and the definition does not exclude specific hunger, in which the relative intake of more than one food affects their subsequent selection, since it is possible to envisage that this operates within the hunger system. Discussion of specific hunger will, however, be left till section 5.3.

Although the model does not have to be an exact analogue of the actual physiological system, it is desirable to make the model tie in as closely as possible with known physiological facts. By thus increasing the realism of the model, it becomes easier to expand the model to account for additional information on feeding behaviour, or to take into account additional physiological information. An example of a model which cannot be expanded in this way is Wiepkema's model (1971) for the operation of positive and negative feed-backs in the hunger system. His model is expressed in terms of the frequency of transitions from the feeding state to the feeding and non-feeding state, and vice-versa, and on closer inspection appears to be just one way of describing a small proportion of behavioural information on feeding. The model as expressed cannot be used to investigate further properties of the hunger system, it is unlikely to reflect the mechanisms which start and stop eating, and it is difficult to expand to include additional information, either behavioural or physiological.

I shall first consider the known facts about the physiology of the hunger system, drawing mainly from work on the rat. This will be followed by the development of a model for hunger which is compatible with these facts, and which also takes into account information on the feeding behaviour of animals. Following this, I will attempt to trace the movement of food through the vole, as one way of viewing the hunger mechanism.

5.2.1.1 Physiological aspects of hunger

The investigation of the physiological mechanisms underlying feeding behaviour have been extensively studied, with the rat forming the main experimental animal, though on occasion the other animals have been used: for example, the skipjack tuna (Magnuson, 1969), the Barbary dove (McFarland, 1964), the laboratory mouse (Wiepkema, 1970), the dog (Lorber et al, 1950), and man (Janowitz and Ivy, 1949).

The basics techniques have either involved interference with a physiological component and observing the consequent changes in feeding behaviour, or the monitoring of one or more physiological variables in relation to feeding activity. Neither technique may provide much information of use in the construction of a model of the hunger system. In the first case, the absence of an effect on feeding behaviour does not mean that the component interfered with is not important; this component could be vital under normal conditions, but easily be by-passed when removed from the system. An example of this process could be found in a hypothetical study of driving habits: if a driver was prevented from obtaining information on his speed from peripheral vision, and no difference in driving was found when he was forced to rely on the speedometer, then it may be (erroneously) concluded that peripheral vision is not important in regulating speed. Conversely, the presence of an effect does not mean that the component involved is normally important. For example, the effect of inflating a small balloon in a rat's stomach in reducing intake has been suggested to be due to nausea rather than the simulation of satiation (Miller, 1957).

The results of monitoring experiments are also inconclusive. For example, Steffens (1969) has shown that blood glucose levels in the rat rise within minutes of the start of a meal, much faster than would be expected from the normal digestive process. This could - correctly - be interpreted as indicating that blood glucose levels in themselves are not crucial in regulating intake. However, it is possible that, while the onset of a meal triggers glucose release into the blood, this occurs at a known rate and the progress of meal digestion can still be monitored. Alternatively, we can imagine that in terms of evolutionary history, a correspondence can be built up between intake and its consequences. If this is so, it means that to some extent the dependence on monitoring glucose levels in the blood could be lessened, provided that food can be adequately assessed for its potential contribution to blood glucose and that discrepancies can be monitored. These possibilities are only proposed as a warning that undue weight should not be given to a study of any particular aspect of the hunger system, else evidence can be produced both to discount any particular aspect and to show its importance.

The possibility that animals can learn to associate the stimuli presented by food with their metabolic properties has also been suggested by LeMagnen (1969), and Stevenson (1969). The implication is that normally the stimuli have become secondarily correlated with the primary metabolic aspects of feeding; removal of one aspect, by experimental manipulation, should continue to result in regulation for an indefinite period, if the metabolic properties can still be monitored by the animal, or for a short period only if the animal can only respond to the food's stimuli.

With these points in mind, we can consider the investigations into the various levels at which regulation can take place. Morgane (1969), in his introduction to a symposium on the "Neural Regulation of Food and Water Intake", suggests that the problem can be considered on four levels:

a) oro-pharyngeal; peripheral sensory.
b) gastro-intestinal; peripheral sensory and metabolic monitoring.
c) blood nutrient; metabolic monitoring.
d) tissue status (body reserves); metabolic monitoring.

Several studies have indicated that oro-pharyngeal factors do contribute to a feeling of satiation. These studies have involved the use of fistulated animals, in which tubes are attached to one or both ends of the severed oesophagous, so that ingested food does not reach the stomach, (sham feeding), or food can be introduced into the stomach without passing through the mouth. Lorber et al (1950) found that sham feeding in dogs caused an immediate stop in gastric motor activity (a correlate of hunger), and Berkun et al (1952) found that rats were willing to eat less when they had been pre-fed with milk ingested normally than when the same quantity was introduced directly into the stomach. Although this effect could be due to the actual act of ingesting tending to reduce hunger, it is more likely that taste receptors are involved, since Miller (1957) has shown that the addition of saccharin to food only reduces hunger when the food is ingested, and has no effect when the mouth is by-passed.

However, although oro-pharyngeal factors may have an effect, this appears to be mainly on the short-term level, and even then it does not offer a complete explanation; Janowitz and Grossman (1949) have shown that the amount "consumed" during sham feeding is much greater than normal. In the long-term, Epstein and Teitelbaum (1962) have shown that rats can regulate their intake for two to six weeks when fed through gastric tubes, which bypassed the mouth and pharynx. They even modified their intake to adjust for changes in the dilution of the food and the size of the food portion.

The above findings imply that gastric effects may be of some importance in regulating intake, since this is the only other level which can be assumed to respond fast enough to influence meal patterns. The importance of the stomach has been confirmed in several studies, and these have shown that actual bulk in the stomach acts as a satiety stimulus (Smith and Duffy, 1957), and that food nutritive quality is also assessed: Berkun et al (1952) have shown that milk injected directly into the stomach causes a greater reduction in hunger (as measured by a consumatory response) than the same volume of saline solution. Similarly, Adolph (1947) has shown that short-term patterns of intake are varied to allow for differences in the nutritive worth of the food, and that this regulation occurs faster than would be expected if the animal only responded when the change in nutritive worth of the food affected longer-term food reserves in the body. Further evidence for the role of the stomach comes from Hoebel (1969), who found that stomach distension reduced the self-stimulation of the lateral hypothalamus by animals with an electrode implant; stimulation of this region is normally equivalent to the presentation of an appetising item of food. de Ruiter and Beukema (1963) have also identified a gastric factor regulating intake in the three-spined stickleback.

The need for some factor that operates on a longer time scale than the oro-pharangeal or gastro-intestinal is indicated by studies which show that an animal can compensate for a food deficit over more than just one feeding bout. This means that the "memory" of the deficit is retained independently of those variables immediately affected by the intake of food.

The role of blood composition, and specifically blood glucose, in regulating consumption is a matter of some controversy. Logically, this factor is well placed to mediate between the intake and digestion of food on the one hand, and the state of the body reserves on the other.

Glucose receptors have been identified in the hypothalamus (e.g. Cross, 1964; Mayer, 1955), and in the liver (Niijima, 1969), and it would seem unlikely that these should only be concerned with controlling the transfer between the blood and the body reserves. The main lines of evidence are indirect; for example, Bash's (1939) demonstration that bits of stomach transplanted to other parts of the body show contractions indicates that the blood carries the necessary factor, though this need not be glucose. Coppock and Chambers (1954) found that rats tended to keep their heads longer in a certain position if rewarded by a glucose injection. Le Magnen (1969) has interpreted his findings on the way in which food deprivation affects the pattern of meal bouts as indicating a systemic effect as being important.

On the other hand, attempts to influence meal pattern by direct manipulation of blood glucose levels have not been very successful. Siegel and Dorman (1954) injected rats with blood from hungry or from satiated rats, and could detect no difference in subsequent feeding behaviour. Similarly, Smith and Duffy (1957) could find no evidence that blood glucose levels affect hunger. Steffens (1969), quoted earlier, indeed suggested that the changes in blood glucose levels bear little relation to the normal course of digestion and assimilation, as glucose levels rise at the very start of a meal. This indicates that it is not the direct changes in the glucose levels which are monitored, even if the animal did allow for the release of a known amount from body reserves, though it does not rule out the possibility, suggested above, that the sensory stimulation by food of peripheral sensory sites had become associated with glucose changes and become the proximal factors regulating intake, merely being updated in the long term to adjust for discrepancies.

However, Fleming (1969) did find that parabiotic rats (with a joint blood circulation) were influenced by the hunger state of the other, with one rat showing evidence of satiation two hours after the other had eaten, though it appeared that glucose was not the sole signal.

The potential influence of changes in the body reserves on hunger is even more obscure. Kennedy (1966) has identified lipo-receptors which could be instrumental in sensing the size of the reserves, so the necessary mechanism exists. The main evidence for the role of the reserves comes from the effect of body-weight changes on consumption. For example, Collier (1969) has studied the recovery of body-weight by rats following a period of food deprivation. Following deprivation, body-weight recovered at a rate proportional to the discrepancy between the current and the terminal values. This implies that there is some mechanism for detecting the mis-match between the two values, which depends on a mechanism for measuring the current reserves: a mechanism which depended solely on regulating blood glucose levels, with body reserves playing a passive role, would not result in this effect.

From the above, it can be seen that there are three basic time scales involved in the regulation of intake. These relate to the oro-pharyngeal/gastric level, blood composition and body reserves. The two aspects of the first level are considered together, since, while it is possible that the two could change at different rates, it would seem more likely that they would become associated. From the point of view of analysing the functional response, the longer-term regulation depending on the body reserves is unlikely to be of importance unless there are changes in food quality with different food densities, and this did not occur in the conditions I studied. In the next section, I will develop an operational model of hunger which deals with the hunger components operating on the two shorter time scales.

5.2.1.2 Formulation of a hunger model

The hunger model that we require needs to be capable of generating a realistic pattern of food intake, given a knowledge of the animal's past eating history. The value of the work discussed in the previous section has been to show that the model needs to include at least two time scales. Processes on the first time scale respond directly to food intake, while for those on the second time scale, fluctuations in intake are damped in the course of digestion and assimilation.

All the previous studies have implicitly included the idea that there is at least one physiological or neurophysiological variable whose value changes as food is eaten, with these changes being monitored as changes in hunger. We shall start the development of the model with the assumption, therefore, that there is one such variable, and that it reacts instantly to food intake (i.e. it operates on the oro-pharyngeal/gastric time scale): This gives the first brick in the model:

(a) a short-term hunger variable.

But we know that an animal is either in a state of eating or of not eating. The easiest way of including this is to place a threshold over which the variable moves: eating starts when hunger is above the threshold and stops when below it, thus:

(b) a start-eating/stop-eating threshold.

But it is also a fact that most animals tend to eat in bouts (meals) rather than to nibble at food (Wiepkema, 1968, 1971; de Ruiter et al, 1969), and in this model, this requires the separation of the one threshold into two:

(c) separate start-eating and stop-eating thresholds.

Le Magnen (1969) found that, while there is no correlation between bout size and the length of the preceding interval, there is a very definite positive correlation between the succeeding interval size and bout length. This was also found to apply to the feeding of poultry (Duncan et al, 1970), and was a common feature of the results obtained from records of feeding activity from my own work on voles. Table 5.2.1.2-1 shows the relationships between the weight of food eaten in a bout, and the length of the preceding and succeeding intervals, using data obtained from the automatic feeding machine (described in Appendix A3). These results indicate that it is a common feature of the feeding process, and can be readily included by assuming that the relationship between hunger and the stop-eating threshold is not accurately assessed, or, what is the same:

(d) start-eating threshold is fairly constant, stop-eating threshold more variable.

There is no way in which the model so far developed can account for long-term regulation of intake. It is therefore necessary to introduce another variable which acts on a longer time scale. It is useful (though not essential) to consider this variable as a compartment which receives food that has passed through the short-term compartment:

Table 5.2.1.2-1

The relationship between the weight of food eaten in a bout, and the preceding and succeeding interval lengths.

D.F	Correlation between weight of food eaten in bout and interval: A	B	C	D
140	.03	-.04	$.56^{+++}$	.17
194	.01	-.02	$.56^{+++}$	$.32^{+++}$
148	-.07	-.14	$.21^{+}$	-.01
32	-.01	.08	$.35^{+++}$	.12
58	$.33^{++}$	$.26^{+}$	$.55^{+++}$	$.35^{++}$
44	-.03	-.01	.13	-.01
55	$.34^{++}$	$.38^{++}$	.19	-.03
13	.03	.05	$.53^{+}$	.45
67	-.10	-.11	$.32^{++}$	.22
102	-.04	-.05	$.57^{+++}$	$.42^{+++}$
66	$.25^{+}$	-.06	$.78^{+++}$	-.01
45	.01	.18	$.61^{+++}$	.15
13	.38	.39	$.84^{+++}$	$.55^{+}$
45	.08	.13	$.74^{+++}$	$.47^{+++}$
171	.02	-.01	$.47^{+++}$	$.34^{+++}$
130	-.16	$-.22^{+}$	$.41^{+++}$	$.26^{++}$
210	-.08	-.11	$.57^{+++}$	$.44^{+++}$

Notes: 1- A: Interval from start of last bout to start of current bout.

B: Interval from end of last bout to start of current bout.

C: Interval from start of current bout to start of next bout.

D: Interval from end of current bout to start of next bout.

2- Significance levels

+ 5% ++ 1% +++ 0.1%

3- A bout was defined to include all intervals less than 30 mins.

4- Seed weights assumed: Groats 30 mg
Wheat 45 mg

(e) a second, long-term hunger variable.

We can be sure that this variable does not operate with a stop-eating threshold, since the lag would be too great to act within the time scale of the individual bout. Nor, if we accept the assumption (d) above, could it operate in conjunction with its own start-eating threshold, since this would then manifest itself as a variable short-term start-eating threshold, and we have already seen that this threshold is relatively constant. Therefore, the only way in which this second variable can exert its regulatory effect within the bounds of the model is through an effect on either of the short-term thresholds:

(f) second hunger variable influences value of start-eating and/or stop-eating thresholds.

But such an effect would not have a regulatory action if the rate of increase of the short-term hunger variable was linear; in this case, raising the threshold would not actually increase the through-put of the short-term compartment, and only such an increase would be able to restore a rise in the hunger value of the long-term variable to the correct level. Therefore, it necessarily follows that the value of the short-term compartment decays asymptotically towards some low value. This results in a greater through-put of this compartment the higher its average value (i.e. the lower the average short-term hunger level). This is a conclusion of some importance, and it is interesting to note that it agrees with the completely independent observations of those who have studied the rate of passage of food out of the stomach in invertebrates (see Holling, 1965) - these results tend to show that food passes out at a rate proportional to the current value of the compartment, producing an exponential decay (though Magnuson (1969) has reported that a constant amount of food passes out of the stomach of the skipjack tuna per unit time).

(g) rate of through-put of short-term compartment must be greater the greater its current value.

The effect of the long-term compartment on the start-eating and/stop-eating thresholds must be such that the average value of the short-term compartment is higher the lower the value of the long-term compartment. This is the only way that the through-put of the short-term compartment can be increased. The following Table lists the possible effects on the thresholds for a drop in the value of the long-term variable, together with the implications of each possibility for bout length and subsequent interval length.

Effect of lowering long-term variable:

	Bout length	Subsequent interval length
Raises stop only	Increases	Increases
Raises start only	Decreases	Decreases
Stop raised more than start	Increases	Increases, same, or decreases
Stop raised same as start	Same	Decreases
Stop raised less than start	Decreases	Decreases

Note that the above effects refer to conditions of ad lib. food; thus, if the animal was deprived of food in order to lower the value of the long-term variable, the first bout will not fit the above scheme, since the value of the short-term compartment will be starting from a value lower than the start-eating threshold.

It can be seen that this provides a ready frame-work which to interpret meal patterns following deprivation. Wiepkema (1971) found that the mean duration of bout length and interval length following 24 hours deprivation were 12.6 sec and 9.5 sec, while the corresponding figures following 2 hours deprivation were 7.7 sec and 14.4 sec. The only conditions under which this should occur are when the stop-eating threshold is raised more than the start-eating threshold, though only slightly more. However, it seems likely that these bouts are in fact mini-bouts occurring within one true bout, where a true bout is defined by the time required for the short-term variable to rise from the start-eating threshold to the stop-eating threshold: when a vole can eat some 500 mg of food in one bout, it seems unlikely that a mouse can satiate the short-term variable in some ten seconds.

My own work on recording food intake before and after deprivation, to be described later, suggest that for the vole both bout length and interval length are decreased following deprivation. This would then imply, in terms of the model as formulated so far, that the start-eating threshold is increased, with the stop-eating threshold being increased less or not at all.

The model as formulated adequately represents many of the known qualitative features of meal patterning. In order to produce a quantitative model, more information is required on two aspects of the system. The first concerns the factors governing the flow of food out of the short-term compartment, into the long-term compartment, and out of this compartment: note that we are not necessarily assuming that anything flowing out of the first flows immediately into the second. The next section will be devoted to this aspect.

The second aspect concerns the precise nature of the relationship which relates the two thresholds to the value of the long-term variable. All that can be safely said is that in both cases the threshold has upper and lower bounds. The upper bound of the stop-eating threshold will be set by the maximum capacity of the short-term compartment, while that of the start-eating threshold will be some value less than this. Conversely, the lower bound of the start-eating threshold will be the value zero (compartment empty), with the stop-eating threshold's lower bound being some value above this. It is not possible at this stage to say what the form of the relationship between these two limits is, nor the values of the long-term variable which correspond with the start and end of this intermediate range. It is however likely that under normal conditions these hypothetical bounds will not be met, so we can represent the relationship between each threshold and the long-term variable as being linear with negative slope: the actual value of the slope would then to be adjusted in any simulation of the system to produce the best fit to experimental results, in terms of bout patterning following deprivation.

5.2.2 Experimental study of components of hunger

The model of the hunger system developed in the previous section was based on two variables (or compartments), whose nature was not explicitly linked to precise physiological components. For example, the short-term variable was defined in terms of the time-scale on which it operated, such that it could respond instantly to ingested food. It could thus be associated with either oro-pharngeal or with gastric features, but the validity of the model did not depend on which was in fact the most realistic. In order to make the model quantitative, however, it is now necessary to assume that the hypothetical variables correspond to definite physiological components, so that the mechanisms governing the dynamics of the variables can be determined, along with the numerical values of the associated parameters.

I have based my assumptions on the actual course followed by the food in the course of digestion and assimilation. In the vole, four separate components can be recognised. The digestive tract of the vole is fairly simple, with the food passing from the stomach (component one), to a relatively undifferentiated gut (component two). The gut is not well equipped for digesting cellulose, having a much smaller caecum than the short-tailed vole (Microtus agrestis)(Vorontzov,1962), and can therefore be considered as a single compartment. From there, food passes into the blood stream (component three), which exchanges food in either direction with the body-reserves (component four). For the purposes of this analysis, component four, and its interaction with component three, will be ignored: this is equivalent to assuming that under the functional response conditions considered, the body-reserves do not change to any large extent, nor are they mobilised to make up for temporary deficits in the blood component. This last point is the most suspect, since we can imagine at least glycogen reserves being mobilised fairly rapidly.

The units of measurement will all be expressed in terms of air-dry weight of food. This removes the need to decide which particular aspect of the food is involved in hunger alleviation at the various stages, and simplifies the analysis of the experimental results.

The problem is now to determine the relationships governing the rate at which food passes out of the stomach into the gut, out of the gut into the blood, and out of the blood. In terms of the two hypothetical variables proposed before, the first is now represented by the stomach, or short-term component; the second by the blood, or long-term component, and the gut has been placed between the two as an intermediate component needed to introduce the correct transfer characteristics into the model.

5.2.2.1 The short-term component

The assumptions made so far have resulted in the postulate that ingested food reduces a vole's "hunger" by increasing the level of a compartment, which is assumed to be the stomach. Further, it is assumed that hunger increases with time as food passes out of this compartment, and it is thus important to be able to estimate the rate at which the food passes out.

This problem has been tackled with other animals, using two methods. The first has involved satiating the animal, depriving it for various periods of time thereafter, then measuring the amount of food required to satiate the animal again. The assumption behind this method is that an animal is satiated when its stomach is full. This method was used, for example, by Holling (1966) in his study of the hunger mechanism of the preying mantid. He found that the amount of food needed to satiate the mantid for the second time could be explained by assuming that food passed out of the stomach at a rate proportional to the amount remaining, i.e.

$$\frac{dX}{dt} = -a.X \qquad \text{where: } X = \text{current stomach contents, and}$$

$$a = \text{a constant.}$$

Holling points out that such a relationship has also been found in other species, using similar methods.

A more direct method has been to satiate the animal (usually by depriving for a lengthy period of time and then exposing to ad lib. food), to deprive for various periods of time, and then to kill the animal and actually measure the amount of food remaining in the stomach. This method has been commonly used in fish studies (see Magnuson, 1969). Magnuson used this method when studying the food consumption of the skipjack tuna, feeding on smelt, and found that the relationship between stomach contents and time since satiation was essentially linear, implying that a constant amount of food passed out per unit time until the stomach was empty, i.e.

$$\frac{dX}{dt} = -a \quad \ldots \quad X > 0.0$$

$$\frac{dX}{dt} = 0.0 \quad \ldots \quad X = 0.0$$

Other studies, quoted in this paper, apparently show a non-linear relationship, since the time to complete emptying of the stomach is more than twice the time to 50% emptying; for example, Windell (1967) calculated the time to 50% as 5 hours, and the time to 100% as 18 hours.

However, Magnuson also measured the amount of food eaten after various periods of deprivation from satiation, and found that these were greater than the estimated amount of food that had passed out of the stomach. In addition, the relationship was now curvilinear, so that taken in isolation it would have indicated the first type of relationship for passage of food out of the stomach. This could mean that the stomach contains less food after the end of the meal following the initial deprivation than after the next. This seems unlikely, especially since the total amount actually eaten does not exceed that eaten after the initial period of deprivation. It seems more likely that the ingestion of some food causes that still remaining in the stomach to be passed out much faster. Even then, these results are disturbing for those studies based on the first method alone, though as far as I am aware, this artefact has not been shown in mammals.

The approach used in the present study was similar to the first method. Fourteen bank voles were maintained on groats alone in large cages at ambient temperature (c. 20°C). Body-weight and consumption were monitored for two periods of three days at c.1600 hours, then all food was removed at midnight following the end of the second period. Food was restored at 0930 the next day, and left in the cages for 30 minutes. This procedure was needed since voles are very sensitive to movement, and it would have been impractical to watch each vole and remove the food once a bout of feeding appeared to have ended. Following this, voles were deprived for N hours, allowed to feed for 30 minutes, deprived for N hours, and so on until c.1730. N took the value of 1, 2, 3 and 4 for four groups of voles, with 5 voles in the first group and 3 in the others. The amount eaten in each bout by each vole was recorded, and consumption and body-weight were recorded for the next two days. This method was designed to give repeat measurements for each vole of the amount of food needed to satiate after periods of deprivation, it being assumed that the vole does in fact eat to fill its stomach after each deprivation period.

Three complications were foreseen. First, it was not known when the vole was actually eating during the 30 minutes, so an apparent gap of 1.5 hours between bouts could be in error by 30 minutes either way. Second, the voles might not be hungry enough to start a bout during a particular 30 minutes; this was allowed for by adjusting the relevant gap between bouts. Third, a vole could be disturbed in the middle of a bout, giving an underestimate of the amount that should have been eaten. This could be allowed for only by visual inspection of the data for discrepant values.

The results are presented in Tables 5.2.2.1-1 and 5.2.2.1-2 The first table shows the daily consumption of groats over the nine days of the experiment, with the mean daily values calculated from the three-day values for the first two periods, and including the main experimental day (arrowed). This table also shows the body-weight of the voles on five occasions during the nine days. The second table shows the schedule of food presentation for the four groups following the 9.5 hours deprivation, with each dash representing a half-hour of subsequent deprivation. The values show the weight of groats eaten in a half-hour period, measured in grams. It can be seen that the experimental period finished at different times around 1730 for the different groups, depending on the particular feeding-deprivation regime. Although these tables show the original data, the analysis of the results was done on corrected values: in the case of daily intake, values for the last three days were converted to a percentage of the mean value for the first six days; and the half-hour data was converted to a percentage of the first half-hour value following the deprivation. These conversions were designed to reduce variability due to differences in absolute values.

The results showed that the voles were less deprived than anticipated after the 9.5 hours deprivation, due to the fact that in almost all cases more food was eaten in the period from 1700 to 0000 just preceding this, than would be expected on a pro rata

Table 5.2.2.1-1

Consumption of food by voles between times indicated (gm)

25/1	1515														
		7.44	6.34	6.14	7.38	6.93	7.43	8.65	4.71	5.52	7.52	10.85	7.68	6.99	7.99
		* 2.48	2.11	2.05	2.46	2.31	2.48	2.88	1.57	1.84	2.51	3.62	2.56	2.33	2.66
28/1	1600														
		6.42	6.41	5.94	6.94	7.52	6.28	8.32	5.20	5.54	6.76	9.99	7.11	6.92	7.45
		* 2.14	2.14	1.98	2.31	2.51	2.09	2.77	1.73	1.85	2.25	3.33	2.37	2.31	2.48
31/1	1700														
→		1.84	1.97	1.94	2.29	2.22	1.65	2.69	1.79	1.86	2.26	2.33	1.43	2.23	2.18
1/2	c1730														
		2.57	2.30	2.24	2.77	2.46	2.31	2.42	1.88	2.14	2.50	2.70	1.90	2.50	2.78
2/2	1700														
		2.79	2.31	1.81	2.59	2.79	2.53	3.01	1.88	2.50	2.63	3.27	2.31	2.45	3.33
3/2	1630														

* Daily average

Body weight of voles at times indicated (gm)

25/1	1515	12.5	13.0	11.8	15.8	21.6	19.0	16.1	11.9	13.0	14.0	17.9	17.0	15.5	13.8
28/1	1600	13.3	13.0	11.6	17.0	20.8	18.7	16.5	11.7	12.7	14.8	19.2	16.6	16.1	14.1
31/1	1700	13.1	12.5	11.8	17.2	20.3	17.2	16.3	11.9	12.1	14.2	19.5	16.5	16.6	14.0
2/2	1700	12.9	12.7	11.9	16.8	19.6	16.6	15.8	12.4	12.6	14.1	18.9	15.4	16.9	14.3
3/2	1630	13.4	13.0	11.5	17.3	19.8	17.2	16.1	12.2	12.8	14.1	19.3	15.7	17.2	14.8

Table 5.2.2.1-2

Consumption by voles following deprivation

	Group 1					Group 2			Group 3			Group 4		
0930														
	.36	.41	.43	.87	.36	.34	.76	.36	.26	.66	.46	.17	.45	.58
1000														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1030														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1100														
	.0	.26	.24	.0	.18	-	-	-	-	-	-	-	-	-
1130														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1200														
	-	-	-	-	-	.34	.0	.22	-	-	-	-	-	-
1230														
	.25	.16	.0	.0	.22	-	-	-	-	-	-	-	-	-
1300														
	-	-	-	-	-	-	-	-	.39	.0	.30	-	-	-
1330														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1400														
	.20	.23	.18	.23	.18	-	-	-	-	-	-	.18	.10	.53
1430														
	-	-	-	-	-	.26	.33	.23	-	-	-	-	-	-
1500														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1530														
	.19	.0	.24	.15	.0	-	-	-	-	-	-	-	-	-
1600														
	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1630														
	-	-	-	-	-	-	-	-	.28	.47	.33	-	-	-
1700														
	.0	.09	.02	.01	.42	.03	.23	.20				-	-	-
												-	-	-
												.05	.42	.02

basis. In Fig. 5.2.2.1-1, the cumulative intake, as a percentage of the pre-deprivation daily intake, is plotted from 1700 hours on the day preceding deprivation. It can be seen that an average of 42% of the standard daily intake had been eaten by this stage, whereas only 29% would have been expected. The reason for this is not known, as no diurnal cycle has been found in any continuous recordings of consumption: it could be that the normal daily handling procedure, lasting about an hour, caused a feeding bout to be postponed to fall within this period, thus inflating the pre-midnight consumption. Despite this, it can be seen that most voles remain in deficit after the first bout, and indeed up to the end of the experimental period. It is only by the end of the next day, after 24 hours of ad lib. food, that most voles have made up the deficit caused by the period of deprivation.

The consequence of this result is quite significant. It means that, following a period of deprivation, the vole is not able to make up completely the resulting deficit in the first bout. This in turn means that the measure of hunger does not reside completely in the short-term component; if this had been the case, then the vole should have eaten the maximum possible in the first bout, but thereafter eaten at the usual rate, so that the deficit would not be eliminated.

The size of the first bout was then calculated as a percentage of the normal daily intake, for those voles in which the first bout was the largest (twelve voles). It can be seen from Fig. 5.2.2.1-2a that all except one of the voles had an initial bout lying between 13% and 28% of daily intake. The spread of these values is greater than that expected on purely morphological

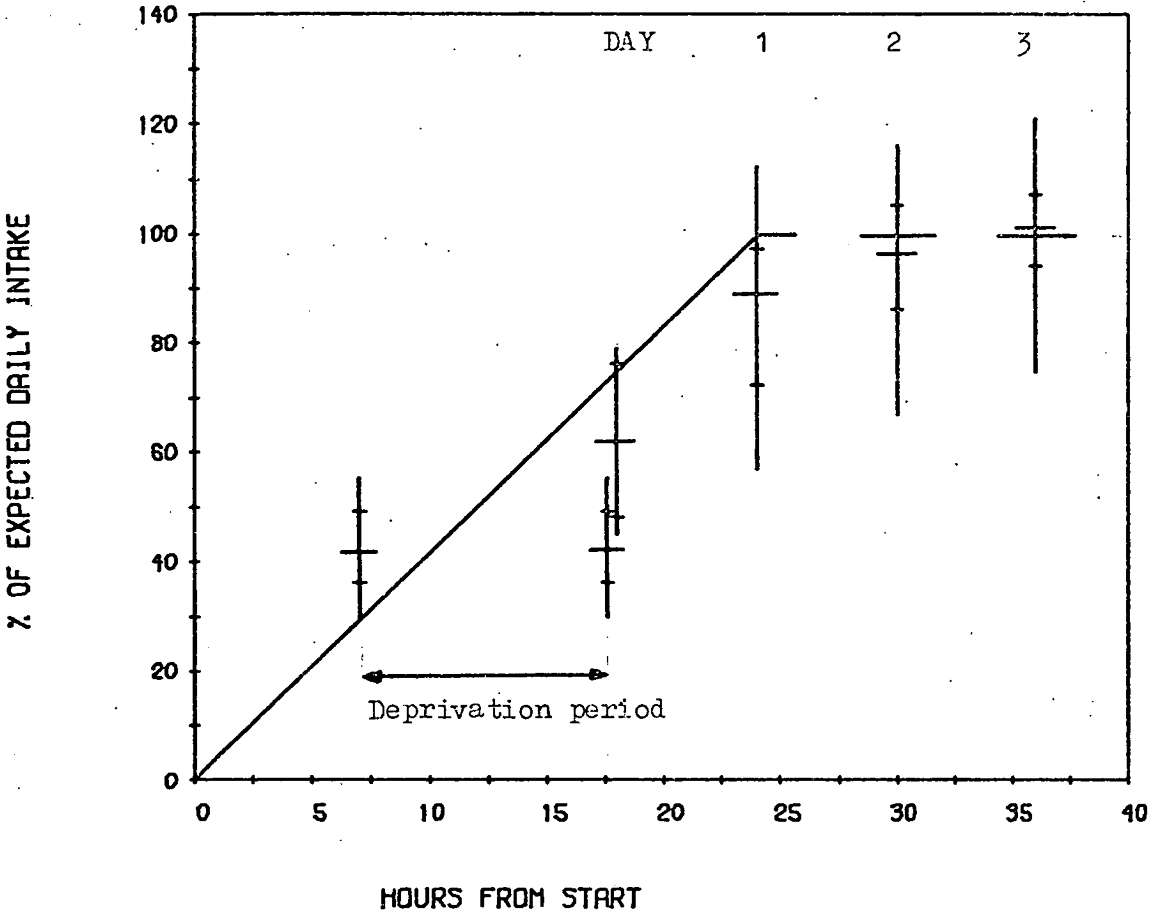


Fig. 5.2.2.1-1

Food intake following deprivation. Vertical line indicates range of data points with median and 95% confidence limits for the median.

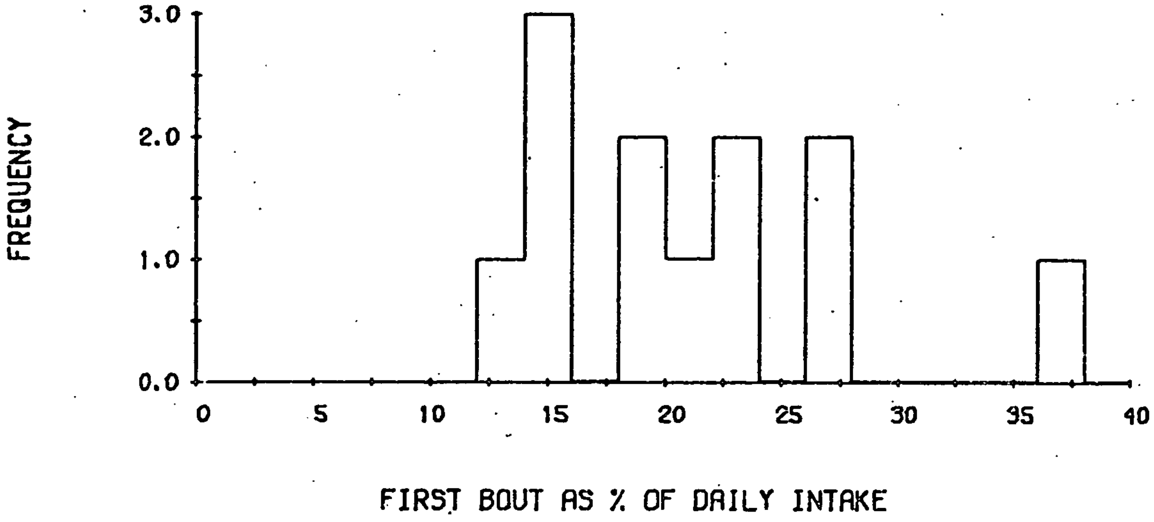


Fig. 5.2.2.1-2a

Frequency distribution of first bout size as percentage of daily intake.

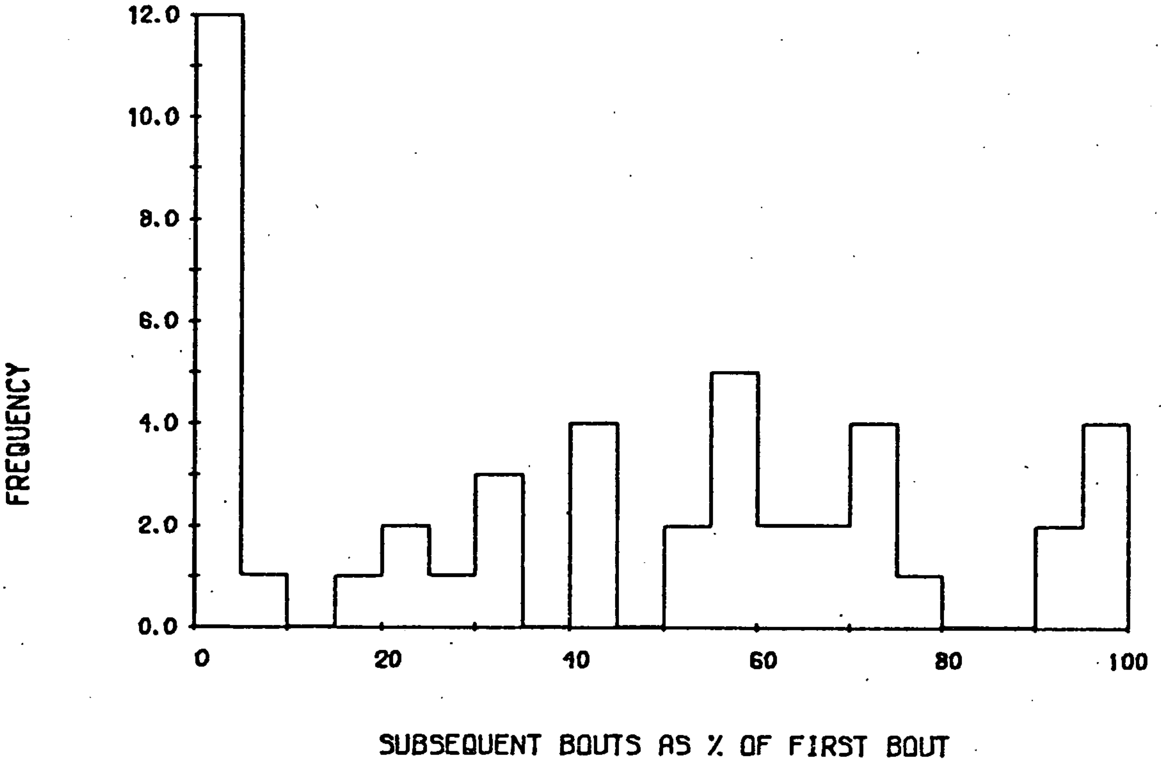


Fig. 5.2.2.1-2b

Frequency distribution of subsequent bout as percentage of first bout.

grounds, and implies that the factor ending the bout is psychological rather than a physical or physiological. This conclusion is strengthened by the following evidence. Feeding records show that voles normally have seven bouts per day under ad lib. conditions, and that this is a fairly constant feature. In this case, each bout should contain 14% of the daily intake on average. The fact that some voles eat only this amount after 9.5 hours deprivation, and yet still eventually eliminate the deficit, implies that the stomach does not contain as much at the end of the first bout as it will do later. Magnuson has shown a similar effect for skipjack tuna, since the fish eat more after the first bout following deprivation than is needed to make up for that lost from the stomach. Similar effects, after prolonged starvation, are known for rats, and humans do not eat a large meal when breaking a fast. Thus, some voles may be less tolerant than others to the 9.5 hours deprivation, and this may be reflected by a smaller first bout. Physical limitations appear to be unimportant for the larger initial bouts as well: the subsequent bouts for those voles which showed an initial bout larger than 25% of daily intake were analysed, and in all cases fell below those shown by other voles on a relative scale, whereas if these voles simply had larger stomachs the subsequent bouts should have borne the same relation to the initial bout as in the other voles.

Fig. 5.2.2.1-2b shows the frequency distribution of all bouts other than the first one, expressed as a percentage of the initial bout. It can be seen that the distribution is bi-modal, with most values being either less than 5% or greater than 20% of the initial bout. From this it can be deduced that feeding only starts in a particular half-hour period if the deficit in the stomach factor is greater than approximately 20% of its maximum value. In terms of the model proposed in the previous section, the maximum value for the starting-eating threshold value is 80% of the maximum value of the stop-eating threshold.

To determine the way in which the value of the short-term compartment decays over time, and to estimate a value for the appropriate rate constant, the value for each bout after the initial one was plotted against the time of deprivation since the previous bout (Fig. 5.2.2.1-3). If no food, or very little, was eaten in a half-hour period, then the deprivation period calculated for the next bout was the sum of the two scheduled periods. The data points for those voles which had shown particularly small or large initial bouts are excluded, since the associated values tended to be more extreme.

Despite the variability of the data, and several unexplainably low values which could be interrupted bouts, it is apparent that a linear relationship does not fit the data. The fitted curve was calculated on the assumption that the stomach empties at a rate proportional to its current value, i.e.

$$\frac{dX}{dt} = -a.X$$

as before, where a has the value of 0.39, which corresponds to a finite rate of 68% per hour. In other words, the value at any time is 68% of the value an hour before. The variability of the data prevents us from having a great deal of confidence in this particular relationship, but it seems to fit the data fairly well and has been adopted here in view of its applicability to other

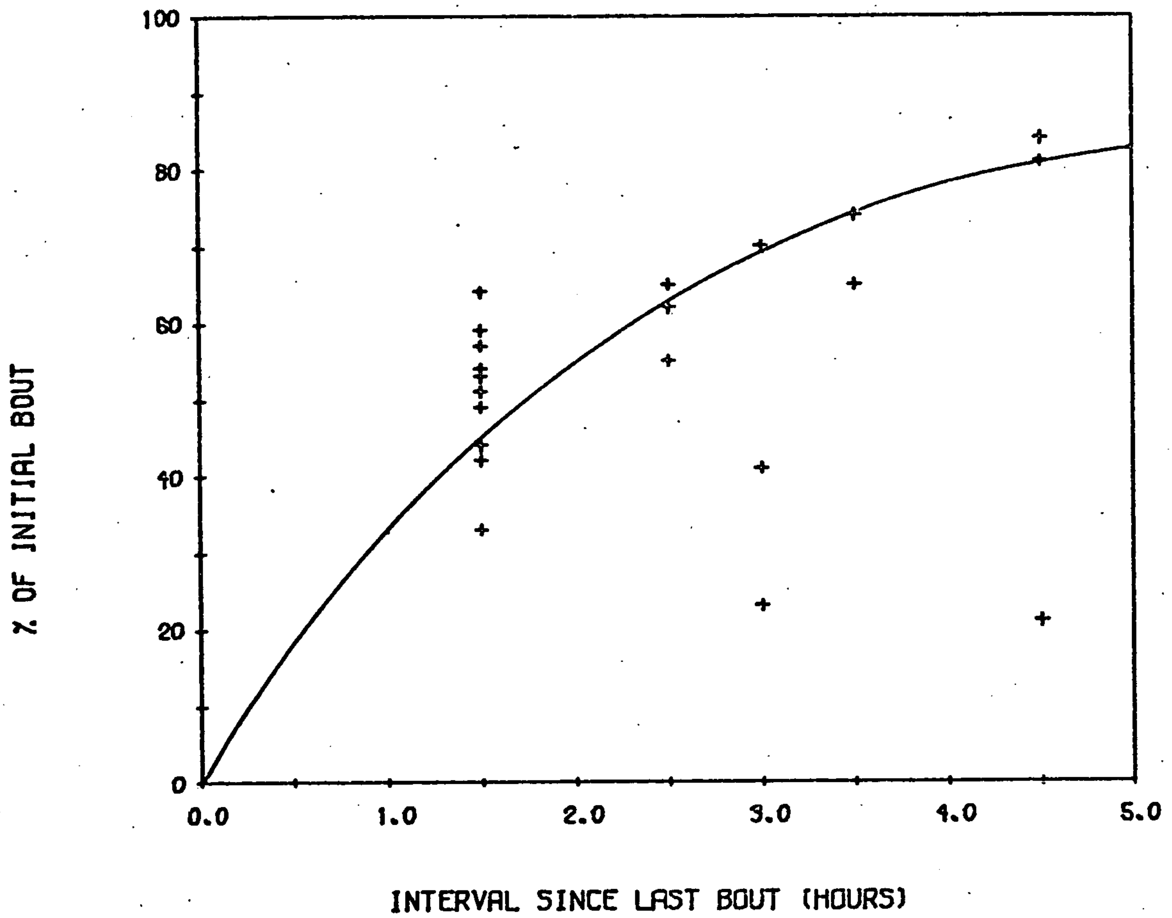


Fig. 5.2.2.1-3

Relationship between size of bout and interval since last bout.

species. Only this relationship, or a simple linear alternative fits a simple physical model of the way the stomach empties.

In conclusion, this experiment has yielded three results of relevance to the model of hunger as formulated so far. First, I can specify an approximate upper limit to the stop-eating threshold, at approximately 20-23% of normal daily intake, as determined by the size of the initial bout. The fact that a few voles showed initial bouts above this value does not invalidate this, but could simply mean that the maximum is not set by purely physical factors. Second, I can specify an upper limit for the start-eating threshold, at less than 80% of the stop-eating threshold. Since we have seen that the start-eating threshold should rise more rapidly than the stop-eating one as the value of the long-term compartment decreases, this implies that the difference between the two thresholds would normally be greater than 20%. Third, the relationship governing the rate of emptying of the stomach can be determined, and an appropriate value calculated for the rate constant.

5.2.2.2 The intermediate and long-term hunger components

It was possible to analyse the short-term hunger component by blurring the distinction between the behavioural and physical properties of this component. Behavioural information - on the amount of food eaten following short periods of deprivation following satiation - was used to make deductions about the physical process of food passage out of the stomach.

It is not possible to use this approach for the intermediate and long-term components (assumed to correspond with the gut and blood). There is information on the rate of passage of wheat through the gut of the bank vole (Kostelecka-Myrcha and Myrcha 1964), based on the use of stained food which could be detected in the faeces. These results showed that the amount of stained food passing out per unit time dropped off exponentially, with approximately 85% having passed out after 24 hours.

However, it is not possible to use this information to determine the characteristics of food assimilation, for two reasons. First, dilution of the stained food with unstained food in the rate-of-passage experiments means that little can be deduced about the transfer characteristics of all food on the gut, as a function of gut contents. Second, there is no reason to assume that the relationship governing the rate of loss of gut contents to faeces parallels the rate of loss through assimilation.

Nevertheless, these results put an upper limit to the time required for assimilation. In addition, it seems reasonable to assume that, as with the short-term component, the rate of passage of food out of the gut is proportional to gut contents. The alternative simple assumption - that a constant amount of food is assimilated per unit time - would be incapable of generating changes in the long-term component required by the hunger model (section 5.2.1.2).

It can be assumed that loss from the long-term component is a constant, if body-weight is assumed not to change, and if fluctuations in body reserves are ignored. The rate of loss will then be equal to the mean rate of assimilation, or the mean rate of food intake times the coefficient of digestability.

This analysis of the possible components of the hunger system must be left at this stage, in view of uncertainty over rate coefficient values, and, more fundamentally, over the degree of correspondence between the physical components of the vole's body and the "true" system components.

5.3 Specific hunger

5.3.1 Introduction

The intervening component of hunger was the most obvious way in which the results of an animal's search could feed back on its subsequent behaviour. All foods were considered to affect the component through some common factor, which is normally considered to be carbohydrate. Thus, the effect of each food on the hunger system would then be a function of its carbohydrate content (or something correlated with it, such as bulk in the stomach). But the body has requirements for other nutrients - protein, fat, minerals, vitamins - which may be deficient in certain types of food. A deficiency of a particular nutrient, as opposed to a deficiency in the total amount of food, is termed a specific hunger for the nutrient in short supply.

In the functional response situation, we are clearly concerned with situations in which at least one food type is in short supply. If this food contains an essential nutrient, this could well affect the animal's subsequent response, since obtaining this food type would then become a matter of some importance, and the effort put into finding this food would be greater than predicted in the absence of specific hunger. In addition, specific hunger could operate on the same time scale as hunger, so that, if a particular key food type is missing from the diet for several hours, behavioural changes increasing the chances of the food type being found might occur.

Conversely, when a particular food type is very abundant, an unbalanced diet may result if the food is eaten in proportion to its abundance. This may result in less being eaten. Tinbergen (1960) has found that the risk index of a particular prey species of the great tit is reduced at very high densities.

It is important to note the distinction between the particular nutrients in which an animal may be deficient, and the particular foods from those available that it may have to eat in order to restore the balance. Each food will contain all the nutrients required by the animal, but most likely in sub-optimum proportions. Westoby (1974) has shown that the optimum ratio of various foods to take in order to obtain the correct balance of nutrients is a straightforward problem in linear programming, when all foods are abundant. In many cases, some foods will not be abundant, and it is then necessary to compromise, taking into account: the optimum ratio of foods; the effort required to find each food type; and the effort required to remove excess nutrients from the body when proportions are sub-optimal.

The above discussion has been framed in terms of the metabolic effects of food. The concept of specific hunger can be generalised to include any case in which the probability of an animal eating a specific food type is influenced by its past diet, without implying anything about the level at which it acts. This makes it possible to include peripheral sensory as well as metabolic effects.

In the following section, I will consider the evidence indicating that animals do in fact respond to specific hungers, and the level on which they operate. Following that, I will present data obtained from the automatic feeding machine, showing the fine detail of groat and wheat selection following restriction to one food type.

5.3.2 The nature of specific hunger

Animals often maintain a mixed diet when feeding on several foods, even when the foods are all in abundant supply. Very few voles showed a 100% preference for groats (section 4.5.2). Young (1948) has commented on the wide-spread occurence of the mixed diet, and Tingergen (1960) found that great tits ate less of a particular prey species at high prey densities than would be predicted on the basis of a random search hypothesis; his interpretation of this as a change in the risk index of the prey species at high densities is compatible with the view that the birds were avoiding a monotonous diet; this is of special interest when it is remembered that the prey observed were taken for nestlings and not for the adults themselves.

Individuals also tend to be very stable in the composition of the mixed diet (Young, 1948). This was also very apparent in the bank vole (section 4.5.3). This would be expected if the mixed diet was the result of an active attempt to take foods in certain proportions, rather than a random choice. This conclusion is supported by the fact that, in some voles, the percentage of the diet made up by groats fluctuates gradually over time. The fact that different voles show different diet composition under the same conditions (see Young op. cit), while casting doubt on the idea that the only function of the mixed diet is to provide the main nutrients in the correct ratio, also confirms the relative stability of diet within the individual.

The preceding findings do not prove that a mixed diet is nutritionally more adequate, since the individual foods contain a large range of nutrients, and voles can exist quite satisfactorily on groats or wheat alone. More satisfactory evidence comes from the findings that animals feeding on nutritionally simple foods maintain a mixed diet which is also balanced. Davis (1928) showed that newly-weaned human babies could regulate the composition of their diet for long periods of time, though in the short term their diet tended to consist of runs of one food type followed by runs of another, implying that diet selection was responding to long term metabolic fluctuations. The picture in human adults is not so clear, as acquired habits appear to make self-selection more difficult (Remington, 1936). Richter (1942a) has shown that rats can maintain a balanced diet by selecting from dishes containing salt, sugar, fat and other components. He confirmed (1942b) the findings of Dove (1939) that animals could actually grow faster on such a diet than on standard laboratory preparations. Dove found that not all chicks, rats or cattle could show self-selection, but that a diet made up from the ratios of those that could, and fed to the others, resulted in considerable improvements in their productive performance. The ability to self-select the diet appears to be under genetic control, and is also affected by age (Pilgrim and Patton, 1947).

These results strongly imply that an animal can actively balance its intake in order to satisfy its nutritional requirements. Further evidence for this comes from experiments in which the diet is made to be monotonous, followed by a return to a free choice. In section 4.5.5, I have described experiments with the bank vole in which voles were restricted to groats only or wheat only for a period of time. In one experiment, restriction of voles to wheat only for one, two or three days resulted in a significantly higher proportion of groats being eaten on the first day of return to free choice than on the second. Voles restricted either to groats or to wheat for two months after captivity showed a very marked preference for the food of which they had been deprived. Similarly, Young (1944) has shown that rats, normally preferring sugar to casein, reverse the preference following restriction to sugar only.

More precise indications come from deliberate modification of the internal environment. Lewis (1960) found that removing the adrenal gland, resulting in a decrease of sodium chloride in the blood through increased excretion, caused rats to increase the amount of salt in their diet. Removal of the thyroid (Richter, 1939) both causes blood calcium to decrease and blood phosphorus to increase; rats respond by increasing the calcium and decreasing the phosphorus in their diet. This indicates the specificity of the effect, and that it can operate in both directions. A specific hunger may affect the intake of more than the specific substance: thus, removal of the pancreas, resulting in an increase in blood sugar, causes not only a decrease in sugar intake but an increase in the intake of fat

(Richter and Schmidt, 1941). Similarly, thiamin-deficient rats decrease sugar intake and increase fat intake, since this vitamin affects the metabolism of the substances (Richter and Hawkes, 1941).

Correction of internal deficiencies can only take place if the required substance can be accurately selected. Thus, while deficiencies of most of the vitamins in the B complex can result in rats selecting the food containing the missing one, rats cannot thus correct a panthothenic acid deficiency (Scott and Quint, 1946). However, if the food containing this vitamin is flavoured with an irrelevant substance (anise), then it can be accurately selected (Scott and Verney, 1947).

The above findings are all compatible with the hypothesis that specific hungers always have a direct association with specific metabolic deficiencies. Further evidence for this comes from the study of pregnant females and nursing mothers: the changing metabolic requirements of the foetus and the baby are reflected in the changing diet of the mother (see Morgan, 1965). However, it is clear that metabolic requirements are not the sole determinants of diet. The two main complications arise from habit formation and peripheral sensory factors.

Young (1949) found that some rats deprived of casein and allowed access to ample sugar continued to prefer sugar when allowed access to both for a certain period of time, before switching the preference to casein. Young put this down to habit, so that the rats tended to follow a set feeding pattern despite changing metabolic needs. If the animal was put into a different feeding situation, say with the two dishes separated rather than next to each other, then a greater preference for casein was shown; the rat could even be alternated between the two situations, with the relative preferences changing to and fro. The presence of such habits would be even more likely to distort the true picture in a functional response situation, especially if different foods occur in different areas and vary seasonally, and their operation would be very difficult to represent in a formal way.

Evidence for the role of peripheral sensory factors in relation to specific hungers takes two forms. First, factors other than the nutritional worth of foods are important in their selection. Thus, foods containing saccharin may be selected even though the saccharin is nutritionally of no value (Young, 1949; Plice, 1952). Also, the physical nature of the food may be important: for example, the texture and the temperature of food may influence its apparent palatability without changing its nutritional value. The relative preference of voles for groats and wheat is markedly affected by presenting the two foods in powdered form, although nutritional differences from the whole grains should be minimal, even if grinding causes enzyme release.

Second, the metabolic interpretation of specific hunger does not explain why the diet should be mixed in the short term, before metabolic responses could occur, or why a mixed diet should be maintained at all when foods differ only in palatability: it would be expected in this latter case that if two foods are nutritionally equivalent and one is more palatable than the other, then the one would be taken 100% of the time. That this is not so has been shown by Morrison (1974). Rats, given a choice between .005% quinine hydrochloride and water for 2 hr per day for 26 days, take on average 20% of total intake from the quinine solution: this was not due to failure to discriminate by some rats, and no trend over time was apparent.

Once again, this can be investigated by restricting the animal to one food type then offering a choice. Since any effect is assumed to operate peripherally, the time period used for the initial restricted feeding and subsequent choice has been fairly short. Morrison (1974) restricted rats to water, saccharin solution or quinine solution for half an hour, then gave a choice of the same solution and one other for the next half an hour. In all cases, the subsequent choice was away from the initial solution. Since these results could be due in part to the difference in palatability of the different solutions, with consequent effect on the amount consumed during the initial period, the same experiment was repeated using two palatable and equally nutritious liquid foods of different flavours, with the same results. This implies that restriction to one food lowers its relative palatability. Introduction of a delay of half an hour before the two-choice test removed the initial effect, suggesting that this effect had decayed over this short period. Holman (1973) has obtained similar results for rats feeding on HCl- and quinine-flavoured sucrose solutions, though with a decay time of approximately 3 hours. He has pointed out that similarity between this situation and spontaneous alternation in a T-maze, with a similar decay time. It is possible that the decay time may depend on the particular sense involved, whether sight, touch, taste, hearing or smell. Consumption of a neutral solution during the delay period did not greatly affect the result, implying that the results were not simply due to an after-taste in the mouth.

These results indicate that a peripheral sensory effect can be important in governing the item-to-item selection of different foods. Fortunately, as Young (1949) has pointed out, there is often a good correspondence between these superficial preferences and what is nutritionally good for the animal. The two mechanisms need not be independent, and it is reasonable to assume that slight errors in the operation of the peripheral system could be corrected through the resulting longer-term metabolic changes. Comparison of this model with others for fine-scale choice mechanisms will be considered in the next section.

The purpose of the intervening components is both to generate broad, robust predictions in relation to the functional response system, and also, ideally, to produce a precise representation of the component so that its effect on other components can be investigated, as Holling (1966) did with the hunger component. Since I will not produce a model of the specific hunger system, it is not possible to consider the effect of changing specific hunger for groats or wheat on the other components. However, it does seem likely that such effects do exist. Thus, Lewis (1960) that a specific hunger (in his case, for sodium chloride) can have an effect on several aspects of an animal's behaviour:

a) learning (rate of bar-pressing in a Skinner box, or rate of learning to make the correct choice in a T-maze),

b) response strength (of, for example, bar-pressing),

c) discrimination ability.

These features could clearly be of relevance in the functional response situation.

5.3.3 Analysis of automatic feeder records

It was shown in section 4.5.5 that the apparent preference of one food over another is reduced if the vole had been previously limited to this food for a period of time. These results indicated the necessity of including a specific hunger component in a functional response model, but they do not show how this component should be included. In addition, just as the intervening component of hunger needed to be modelled in such a way that it could generate the consumption for specific food items (section 5.2), so a model is required to generate consumption of items of the specific food types.

Holling (1965) assumed that each food type has an attack threshold on the hunger scale, above which it would be eaten if encountered and below which it would be left. For palatable foods, experience with the food lowers its attack threshold (i.e. the animal accepts it when not so hungry), and lack of experience results in the attack threshold rising to some general level. From the point of view of the specific hunger component, this model has several deficiencies:

a) the only effect of contact with a specific food item is to increase the chances of that type being eaten, whereas it has already been shown that limitation to one food type usually decreases the proportion eaten immediately after Holman, 1973; Morrison, 1974).

b) no mechanism is postulated for enabling the animal to select one type or the other when both are abundant, and hunger level is above both attack thresholds.

c) it seems unlikely that the only reason for an animal maintaining a mixed diet is that its hunger at the start of a feeding bout is above the attack threshold for anything but the most preferred food type.

d) no allowance is made for the nutrient properties of the food to influence subsequent selection.

e) the model predicts that the less preferred food should only be eaten at the start of a bout, whereas we will see that no such pattern is apparent.

Dawkins (1969) proposed a similar model to account for the sequence in which chicks peck at two coloured panels. He proposed that a variable moves randomly up and down across two thresholds: when it is above both of them, each colour has an equal probability of being pecked at, but only one will be pecked at if the variable is below the threshold of the other. This model predicts longer runs of the preferred colour will be interspersed by random run lengths of the other, and appears to correctly predict the transitive property of preferences. However, it is difficult to see what the random variable could represent in a feeding situation, and again this model makes no allowance for future selection being influenced by past eating pattern.

The records of the automatic feeder (described in Appendix A3) were analysed to see if the mechanism of groat and wheat selection could be determined. In this system, a groat grain and a wheat grain were presented approximately 3 cm apart, the animal's action in taking one or the other was recorded, and the grain taken was replaced within approximately 10 secs by another of the same type. The possibility of the vole showing a position preference was discounted by switching the sides and noting that the selection pattern was not affected. The possibility that the vole was showing spontaneous alternation between two more-or-less equivalent stimuli (Hinde, 1966, p.206) was investigated by arranging for both positions to contain the same type of grain; under these conditions, the pattern was greatly altered, with much longer runs from each side being shown.

Normal within-bout patterns

Voles varied in the form and stability of the patterning of selection within bouts. Fig. 5.3.3-1 shows 25 consecutive bouts for two voles. It can be seen that one vole shows a very consistent bout pattern, whereas the other is much more variable. It should be noted that the less preferred food does not consistently come at the beginning of a bout. The consistency of bout pattern for the first vole suggests that it could be another example of the habit formation described by Young

Vole 1	Vole 2
G G G W	W G G W
G G W W	W W G G G G W
G G G G G G W	W W G G G G
G G G G G G W	W G G G G W
G G G G G G W	G G G W G W
G G G G	G G
G G G G G G G W	G G G
G G G G G G G G W	G G G G
G W G G G G G W	W W G
G G G G W	G G W W
G W G G G W	W G G G
G G G G G W	W G G G G G
G G G G W	G
G G G W	W G G G G
G G G G G G G W	G
W G G G G	G W G W
G G G W W G G G	W W G G G G
G G G G G W	W G G G G G
G G W G G G G G G W	W G G G G G
G G G G G G G G W	W G G W G G W
G G G G W	G G G G G
G G G W W	W G G G
W G G G G G W	G W W G G W
G G G G W	W G W G G G
G G G G G G G W	W G

Fig. 5.3.3-1

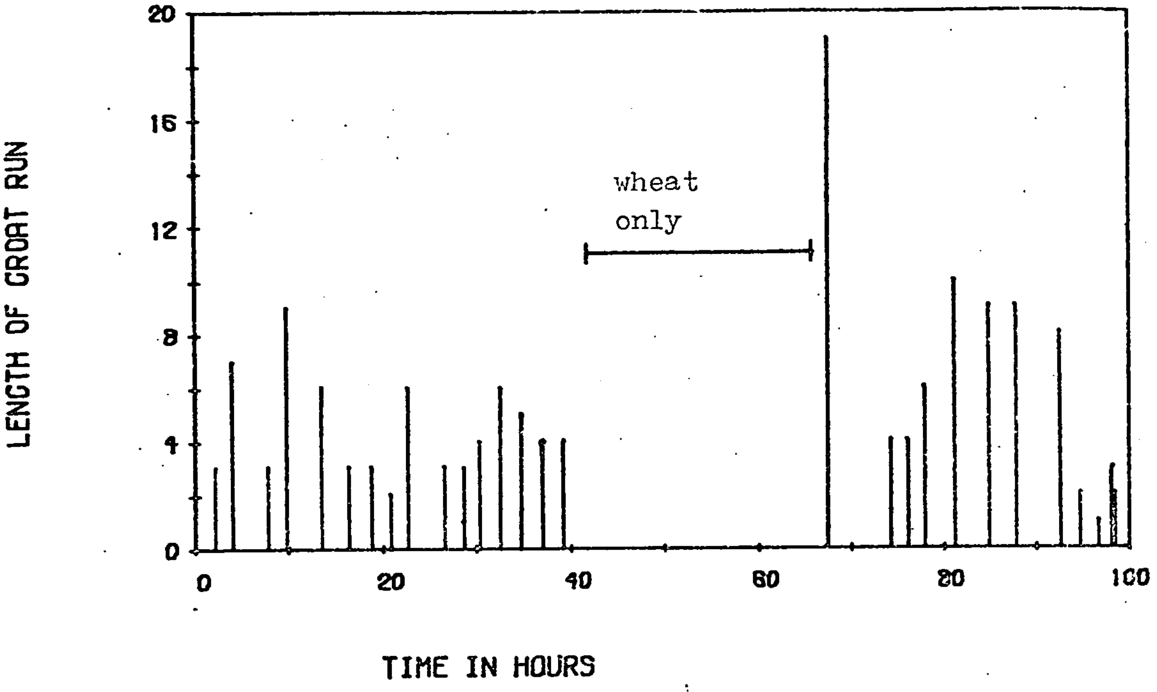
Composition of 25 bouts for two voles.

G = selection of a groat grain
W = selection of a wheat grain

(1949). In this present case, however, the habit could be the result of the vole gradually learning what ratio of the two foods to take in order to obtain the optimum nutrient balance. On the other hand, the regularity shown by this vole is equally compatable with an explanation based on the type of incremental and decremental effects proposed by Morrison (1974).

Effect of limitation to one food type

Fig. 5.3.3-2 shows the results obtained in one case when a vole was limited to wheat only. For the forty hours before limitation to wheat, it was found that one wheat grain was eaten for every 2.87 groat grains. A selection index can then be constructed by adding 1.0 every time a groat was eaten and subtracting 2.87 every time a wheat grain was eaten. Fig. 5.3.3-2a shows the way this index fluctuated before and after limitation to wheat. It is that preference switches sharply to groats following the limitation to wheat, with a tendency to level off after approximately 30 hours. Fig. 5.3.3-2b shows the length of runs of groats in between selections of wheat, and it is obvious that the first run following the return to a two-food choice is much longer than those before or after.



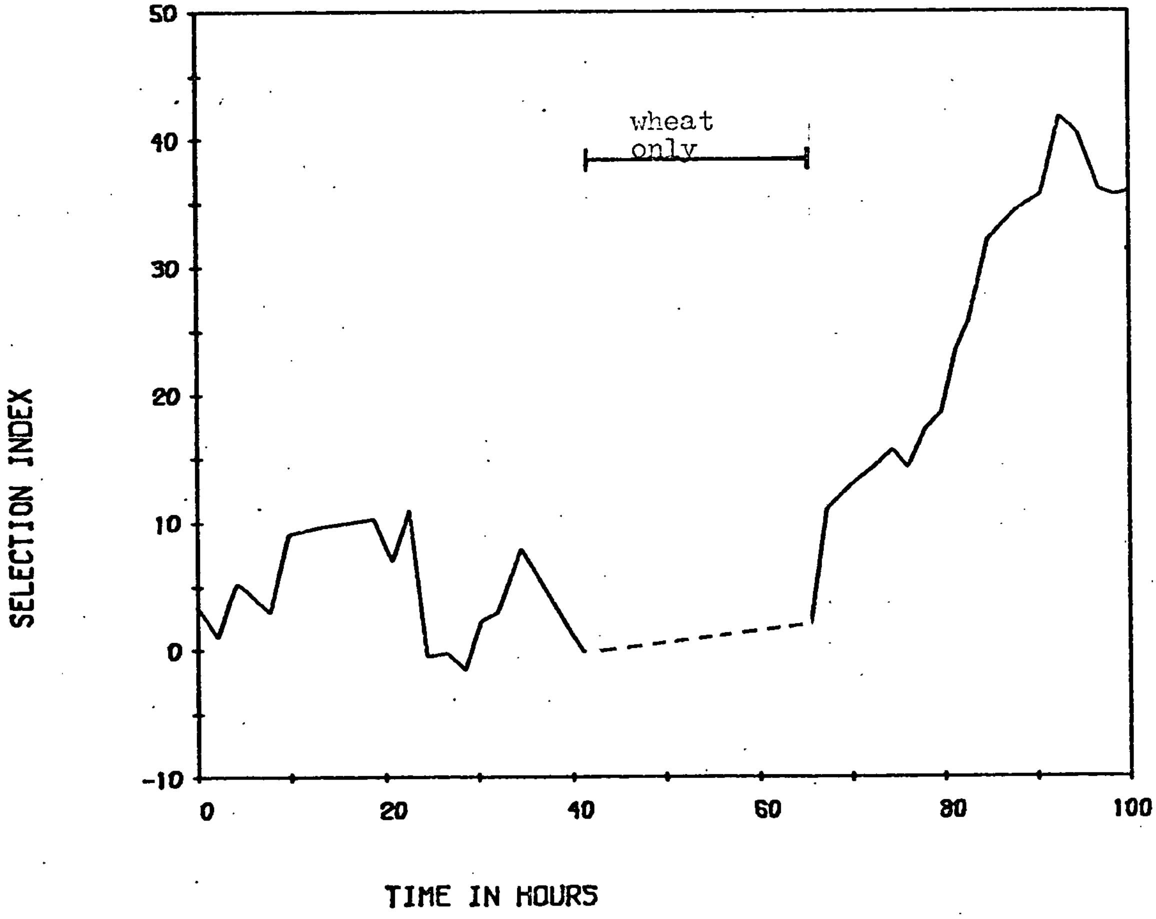


Fig. 5.3.3-2a (bottom)

Fluctuation in selection index before and after wheat-only period.

Fig. 5.3.3-2b (top)

Run length for groats before and after wheat-only period.

Run length frequency distribution

The run length for groats or wheat is the number of grains of one type eaten in a sequence uninterrupted by a grain of another type. No distinction is made between inter-bout and intra-bout intervals for the purpose of this analysis. The run length frequency distributions for groats and for wheat are shown in Fig. 5.3.3-3a, b for two voles. The dashed curve represents the theoretical distribution based on the assumption that each selection event has a fixed probability of involving a groat grain or a wheat grain. Thus, if a given vole took groats and wheat in the ratio of 70:30, then the probability that a groat will be taken in any one selection event is taken to be 0.7, and the probability that wheat will be taken is 0.3. Then, the probability that a groat run will be only one grain long is equal to the probability that the next grain taken is wheat, i.e. 0.3. Similarly, the probability that the run will be two grains long is equal to the probability that the next grain will be groats multiplied by the probability that the following grain will be wheat, i.e. 0.7 x 0.3. In general, in a two-choice situation, the probability of obtaining a run length j items long for grain type 1 ($R_{1,j}$) is given by:

$$R_{1,j} = P_1^{(j-1)} \times P_2$$

where P_1, P_2 are the fixed probabilities that the next item taken will be of type 1 or type 2.

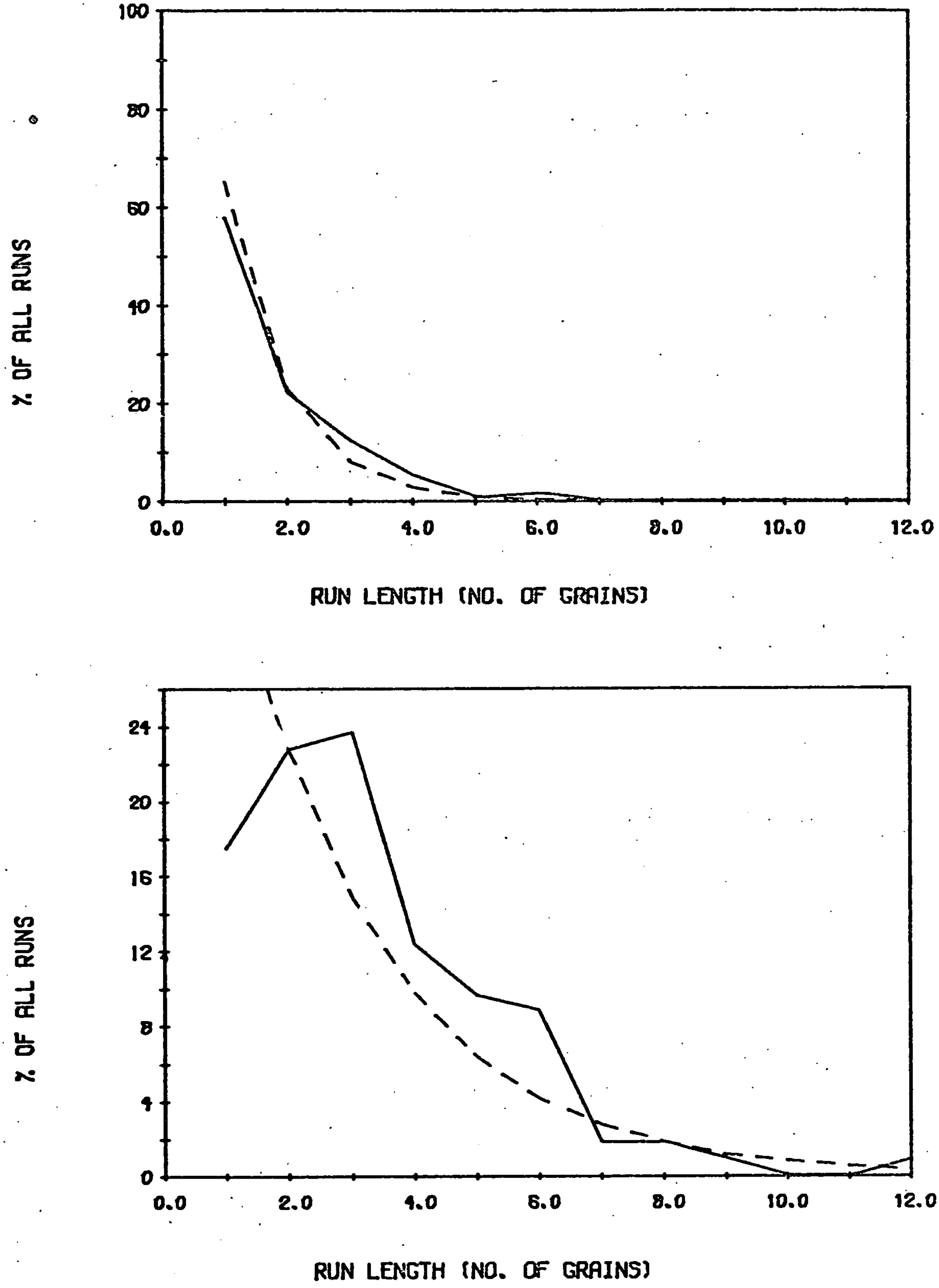


Fig. 5.3.3a

Run length frequency distribution for wheat (top) and groats (bottom), for one vole.

——— : Observed
– – – – : Expected

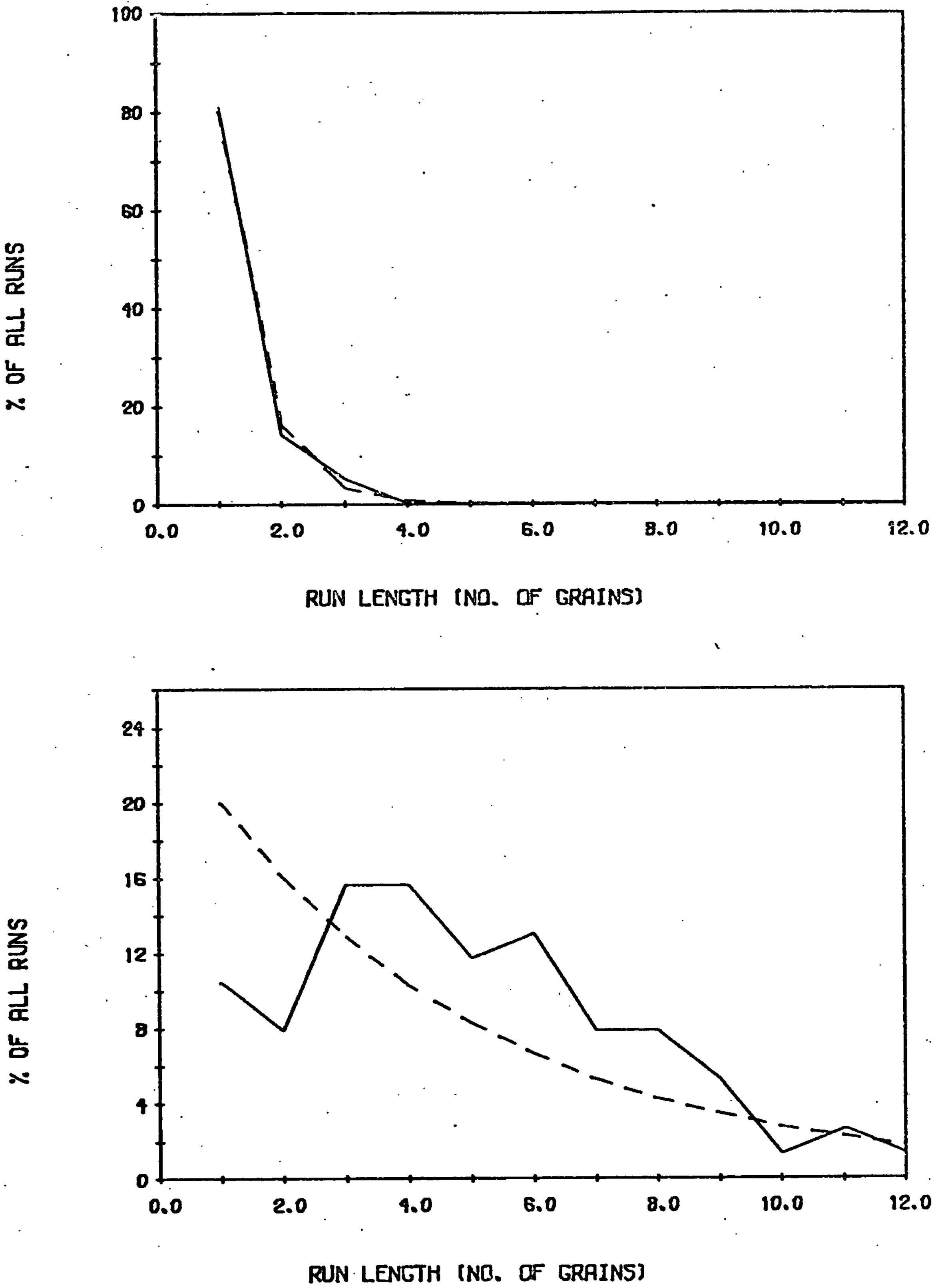


Fig. 5.3.3-3b

As for preceding figure, for another vole.

It is clear from the comparison of the actual and theoretical frequency distributions that groats tend to occur in runs longer than would be expected, whereas wheat grains tend to follow the expected line fairly closely. This means that the selection of a groat tends to be followed more frequently than expected by the selection of another groat, while the same is not true for wheat. These findings are broadly in agreement with the predictions of the models proposed by Holling (1965) and Dawkins (1969), if it is assumed that in Holling's model each food item has the same probability of being taken if the hunger level is above both thresholds.

However, similar results would also be expected if the consumption of a grain of one type tended to lower the relative palatability of that grain type (Morrison, 1974). If this effect was larger for wheat than for groats, then the consumption of one wheat grain should always make groats relatively more palatable, whereas several groats would have to be eaten in order for the wheat to be the more palatable, under ad lib. conditions for both foods.

5.3.4 The representation of the specific hunger component

The results obtained from the monitoring experiments (section 4.5.5) and from the automatic feeder (section 5.3.3) indicate that specific hunger, like the component of hunger itself, needs to be considered on both the long-term and the short-term levels.

In the long term, limitation to one food for a period of days or weeks increases the amount taken of the alternative food. This effect is large enough to be detected on a day-to-day basis. The automatic feeder results also indicate that limitations to one food type can influence more than just the first bout following the return to a choice situation. This implies that the limitation caused long-term changes in responsiveness to the two food types, and that the voles does not return to its previous pattern as soon as one grain of the type to which it had previously been limited is eaten. It is not possible to say on the basis of the available evidence whether this long-term response reflects the vole's metabolic requirements, or whether it operates on the level of relative palatabilities. But from the operational point of view there is no need to distinguish between these two possibilities.

The short term effect is revealed by the first bout following limitation to one food type. Typically, there is a run of grains of the type witheld before one grain of the other type is taken. Presumably, the relative palatability of the available type had been lowered to such an extent by its monotonous consumption that many grains of the previously withheld type needed to be eaten before the latter's relative palatability also dropped to a low level.

This way of representing the specific hunger component is a familiar one in economic situations (e.g. Lipsey, 1966). The theory of marginal utility assumes that the more units of a particular commodity that are purchased, the less the consumer is willing to pay for each additional item, that is, the marginal utility (or worth) to the consumer of each additional item decreases. If the marginal utility of one commodity then falls below the marginal utility of another commodity, then the consumer will spend his money on the latter, since it will give more satisfaction for a given amount of money spent. This is analagous to the vole's selection of two food types when the specific hunger component is assumed to operate through changes in the relative palatabilities of two foods; it is not such a good representation of changes in specific hunger resulting from nutritional imbalance, and in this situation the linear programming approach (Westoby, 1974) is a more reasonable model, though this makes no predictions about the patterning of food intake needed to ensure the optimum balance of nutrients. It should further be noted in relation to the marginal utility model that no mechanism is provided for causing the marginal utility of a particular commodity to increase over time, either due to the mere passage of time or through "consumption" of an alternative commodity.

Indeed, although the broad features of the specific hunger component are now apparent, and we can make qualitative statements about the direction of its effect, the precise modelling of this component cannot be undertaken in the same manner of logical progression that was used for the hunger component. Thus, it is not possible to say from the available evidence whether each food type should have its own short-term and long-term palatability variables, or whether a single short-term and a long-term variable would be sufficient to represent their relative palatabilities; whether the specific hunger variables increase through the mere absence of contact with the associated food type of through contact with the other food type; and whether the effect of contact with the associated food type varies as a function of, for example, the specific hungers of this and the other food type, hunger level and familiarity with the food. It can be seen that in a multi-food situation, the problems of representing the specific hunger component become even more considerable.

5.4 Learning

Learning refers to "changes which cannot be understood in terms of maturational growth processes in the nervous system, fatigue, or sensory adaptation" (Hinde, 1966). Learning is not memory, but rather the process by which memory becomes established. It operates on the neuro-physiological level, taking sensory information as input and manifesting itself as changes in behaviour under constant conditions. Learning can, however, take place without immediate changes in behaviour, as in latent learning (Thorpe, 1963); rats are better at running a maze if they are first allowed to run around it with no reward.

Unlike the intervening components of hunger (5.2) and specific hunger (5.3), the need to invoke the intervening component of learning comes from the functional response results themselves. For this reason, the conclusions drawn from the analysis of this component can not be checked independently, but must be viewed as little more than an empirical description of the results obtained. The reasons for including a learning component will be discussed in section 5.4.1; they are based on the fact that there are differences in a vole's response under comparable conditions, differences which cannot be ascribed to hunger or specific hunger.

While some aspects of the functional response virtually require that a learning component be introduced, there is another aspect - the depression of the response at low food densities - for which learning has been proposed as a possible explanation (e.g. Tingergen, 1960; Holling, 1965). Unlike the first reason for including a learning component, based on differences in behaviour over time, learning is used in this context to explain the equilibrium response itself, that is, the animal's response after it has adjusted to constant conditions. This approach, and the problems it raises, are discussed in section 5.4.2.

5.4.1 Evidence of learning from the functional response experiments

There are three aspects of the functional response experiments which suggest that a learning process is involved. These are discussed more fully in section 3.34, and will only be summarised here and considered in relation to learning.

Initial adjustment to functional response conditions (3.3.4.1)

When first introduced into the brushes system for measuring the functional response to changing groat density, conditions were kept constant for approximately six days. The animal's response over this period was not constant, as measured either by the index of number of groat grains taken, or by distance travelled per day. The value of both indices was generally lower initially, usually reaching a fairly constant (plateau) value by the third day. The total amount of food eaten per day did not show this initial depression, ruling out the possibility that these results reflected an over-all lowering in feeding motivation due to the stress of being introduced into an unfamiliar setting.

Holling (1965) found a similar effect for deer mice searching for buried sawfly cocoons, with the constant response again being reached by the third day. If the buried food was unpalatable, there was an initial response which then declined rather than increased.

It thus seems that in this type of situation small mammals show an initial response to the new conditions which then decreases if the response is not rewarded, or increases if it is rewarded. We can thus say that the animal has learnt to associate the feeding area with a source of food, and that this association has been completed in approximately three days.

These results closely follow those found by animal psychologists, in particular, those relating to operant conditioning (Skinner, 1938). In conditioning, a relationship is developed between a stimulus and a response. In the following discussion, reference is made to Table 5.4.1-1. In classical conditioning (also called Pavlovian, type S, or classical conditioning type I), the temporal association between two stimuli, only one of which initially elicits a particular response, results in the other, irrelevant stimulus also eliciting the response. This type of conditioning does not concern us here.

In operant conditioning, on the other hand, (also called instrumental conditioning, instrumental learning, type R conditioning, or classical conditioning type II), the animal's response is not originally an unconditioned response to an unconditioned stimulus. Rather, a response, such as pressing a lever, occurs more frequently if it is followed by a reinforcement, such as food. Trial-and-error learning, usually applied to such things as learning to run a maze, may be considered as a sub-set of operant conditioning (Morgan, 1965). In both bar-pressing and maze-running, we can identify an unconditioned stimulus (e.g. food), a conditioned stimulus+ (the bar, the maze branches), an unconditioned response (eating), and a conditioned response (bar-pressing, selecting the correct path).

The animal in the functional response context clearly fits

+ Some authors (e.g. Morgan, 1965) state that there is no conditioned stimulus in operant conditioning. There seems little reason why what Skinner (1938) calls the discriminative stimulus should not be called this for consistency.

Table 5.4.1-1

Summary of the two types of conditioning discussed in the text.

Classical conditioning.

	US (sight of food)	elicits	UR (salivating)
AND	CS (sound of bell)	coincides with	US (sight of food)
THEN	CS (sound of bell)	elicits	CR (salivating)

Note: CR is the same behavioural act as UR.

Operant conditioning.

	US (sight of food)	elicits	UR (eating)
AND	CS (sight of bar)	elicits	CR (bar-pressing)
AND	CR (bar-pressing)	results in	US (sight of food)
THEN	CS (sight of bar)	facilitates	CR (bar-pressing)

Note: CR is a different behavioural act from UR.

Abbreviations.

US	unconditioned stimulus; a stimulus which the animal responds to with an unconditioned response before training.
UR	unconditioned response; a response, elicited by an unconditioned stimulus, which the animal showed before training.
CS	conditioned stimulus; a stimulus which the animal responds to with a conditioned response as a result of training; this also refers to the same stimulus before training; i.e. a to-be-conditioned stimulus.
CR	conditioned response; a response elicited by a conditioned stimulus, more so after training; also refers to the same behaviour pattern before training, i.e. a to-be-conditioned response.

into this scheme. The unconditioned stimulus and response remain the same (food and eating), with the conditioned stimulus now becoming the feeding area, and the conditioned response becoming the action of entering the feeding area. We can thus make use of the results of operant conditioning experiments to illustrate relevant parts of the functional response experiments.

In all operant conditioning experiments, there is an initial delay before the response reaches its equilibrium level. When the animal is required to learn a simple operation, this initial period may be short, and the association between the unconditioned and the conditioned stimulus may be made very quickly. Thus, Skinner (1938) found that rats responded at a maximum rate within 2 to 120 mins, after only 1 to 3 reinforced responses. When the response required is more complicated, the initial learning time is longer. Examples of complications include rewarding only one in say five correct responses (fixed ratio reinforcement), requiring a more specific response, requiring several correct responses in a row (such as maze running), or requiring the selection of one of two similar stimuli (discriminative learning). The functional response situation mainly involves the first complication, since travelling a unit distance over the feeding area will not always result in the discovery of an item of food. My results thus agree with those obtained from operant conditioning; in addition, the fact that the vole had an alternative source of food will delay the learning, since the relevant motivating force of hunger would not become as strong.

Response to zero groat density (3.4.4.3)

On dropping groat density to zero from fairly high groat densities, most voles showed an increase in daily distance travelled on the first day of the zero density, followed by a decrease to a low level on subsequent days. This changing behaviour under constant conditions cannot be ascribed to the intervening components of hunger or specific hunger. In either case, the tendency if any should be for the motivation to search for groats to increase rather than decrease over the period of zero groats. Hunger would increase if the vole did not make up its total requirements on wheat alone, and the specific hunger for groats should increase the longer the period of groat deprivation.

Holling (1965) reports a similar type of experiment with the shrew, which had become accustomed to digging for buried sawfly cocoons. On removing the cocoons, the number of holes dug per day declined over the next few days. It would at first appear that this experiment was analagous to those described above, and the results similar to mine except for the lack of an initial increase in searching, and the longer time required for searching to drop to a low level. However, there is a fundamental difference between the two situations. In my experiments, the index used for vole activity was distanced travelled per day, which was a conditioned response to the conditioned stimulus of the brushes; this stimulus remained even when the groats were removed. In Holling's experiments, however, shrews normally only dig holes above buried cocoons; these would then appear to be the conditioned stimulus, and removal of the reinforcement results in removal of the conditioned stimulus. It would thus seem that the random hole-digging of the shrew when the cocoons were removed is more an example of frustration (Hinde, 1966, p.289). An alternative explanation of Holling's situation, that the cocoon and the digging for it were unconditioned stimulus and response, with the area and travelling over it the conditioned stimulus and response, would also invalidate Holling's interpretation of the results; in this case, the relevant variable to measure should be distance travelled and not number of holes dug.

Holling called his results "forgetting". But in 1938 Skinner had drawn the distinction between forgetting and the extinction of an operant response: forgetting is the decrease in a response due to the passive passage of time, while the extinction of a response requires elicitation without reinforcement. The difference was neatly shown by training rats in a Skinner box and then re-introducing the rats after one day or 45 days with no reinforcement: both showed almost the same extinction curves (rate of responding gradually declining), and the similarity of the two showed the absence of a forgetting effect.

Skinner found that rats responded in a consistent way when reinforcement was removed after 100 reinforced responses. The initial response rate was very higher (approximately 700/hr as against 200/hr for the reinforced responses), but that this rate declined within the hour to virtually zero. Similar results have been obtained with chaffinches (Kling and Stevenson-Hinde, 1972). These results are qualitatively similar to those obtained for the vole following removal of groats, and differ only in that the vole's response was extinguished more slowly and tended to an asymptotic value considerably above zero. Further, it was not possible to plot the extinction curve for the vole, since results were only obtained once per day.

In both of the studies on operant conditioning referred to above, it was found that spontaneous recovery of the response occurred following an intervening period out of the experimental apparatus. This could not be investigated with the vole, due to the relative coarse time unit used and the possible effect of emotional disturbance, but has interesting implications for animals under natural conditions. In a patchy environment, an animal which had become conditioned to finding a preferred food species in a certain area would show extinction of the response when the species decreased in numbers. But on re-visiting the area at some later time, its initial response would be at a rate greater than when it had left, thus enabling the animal to rapidly assess the new food status of the area. This would complement the tendency, shown by voles, to maintain the response at a low level even after several days of zero groat density, which could function to inform the animal when the food situation changed. This is analagous to the need for a predator intermittently to sample the model-mimic complex in Batesian mimicry in order to assess when the mimic is becoming frequent enough to warrant exploitation.

Differences between periods of rising and of falling groat density. (3.4.4.7)

Some voles showed differences in their functional response to groat density depending on whether the groat density was gradually increasing or gradually decreasing. For these voles, the response at any density tended to be larger if the previous density had been higher than if it had been lower than the current ones. This applied whether the index of number of groats eaten or distance travelled was used. Again, neither the intervening component of hunger nor of specific hunger for groats can reasonably explain this result, for the reasons listed previously in relation to the drop to zero groat density. Since voles showed this effect whether their schedule was in the sequence rising/falling or falling/ rising groat density, we must assume that the difference in response is a conditioning effect carried over from the preceding density level, and that the same level of response would be reached in either case if the vole was kept for many days at the same density. As it was, no consistent difference between the first and the second day at the relevant densities could be found for either increasing or for decreasing groat density. It must be assumed then that the vole would only gradually recover from the effects of the previous density and tend towards the stable response level.

To my knowledge, experimental studies of the functional response have not included the possible effect of the preceding density. In Holling's (1965) study of the deer mouse for example, the random density schedule only used one day at a time for any one density level, and therefore any carry-over effect would be difficult to identify, even if he had given the exact density sequence and the corresponding results. In Ivlev's (1961) study of the feeding relationships of carp, density of a particular food is only varied by the fish's consumption of this and the other food types; the fact that in all cases the density decreases, and no two consecutive days have the same density regime, again make it difficult to identify carry-over effects.

In studies of the functional response under field conditions, the changing density is often brought about by seasonal population changes in the food item. This method has been used for birds (Tinbergen, 1960; Royama, 1970), and also for sheep (Hunter, 1954). Although in this latter case the time scale of the changes would tend to rule out the possibility of carry-over effects from previous density levels, such an effect seems more likely in the bird studies, since the numbers of the prey items may increase very rapidly. This means that if we consider only the rising density segment for a specific prey species, a negatively-accelerated feature of the response curve could result solely from the temporal sequence of density changes rather than from a genuine equilibrium response. For the wood pigeons studied by Murton et al (1963) on the other hand, the different density values were obtained from different fields over the same time; since one bird could visit several fields in one day, the possibility of a carry-over effect would be greater, but this should not introduce any serious bias.

Skinner (1938) found that rats re-adjusted their rate of responding within an hour when the regime was changed from one reinforcement every nine minutes to one every three minutes. This rapid adjustment suggests that this represents the equilibrium rate which would be approached if the earlier regime had a shorter reinforcement period rather than a longer one. Possibly the difference between this result and those obtained from the voles could be due to the simplicity of his apparatus, and the relatively complexity of the problem that the vole has to face: at the sort of densities at which this effect is most marked, the vole may only be finding say thirty grains per day, therefore it will have little information with which to up-date his assessment of the current food density based on the previous two days experience. The vole results are, however, consistent with those predicted by most conditioning experiments with longer time constants.

5.4.2 Representing the learning process

Holling (1965) recognised four key features of the learning process relevant to a model of the functional response:

a) a generalised responsiveness to unfamiliar stimuli,

b) the rate of attack must be capable of increasing or decreasing, depending on the palatability of the prey,

c) learning is specific to each food type,
d) learnt associations decay if not reinforced.

To account for these features, Holling proposed a model in which:

a) the attack threshold for all unfamiliar foods took the same, non-zero value,
b) contact with each item of palatable food lowered the attack threshold,
c) the effect of each contact depended on the current hunger level, the current value of the specific attack threshold, and the degree of palatability of the food type,
d) the value of the specific attack threshold decays with time, in the absence of contact with the food type.

Holling's model is represented in state variable form in Fig. 5.4.2-1a, with the intervening component of learning now represented by a compartment. This compartment ("memory") is specific to one food type, so there should be as many memory compartments as food whose density can change. Memory is seen to increase with each contact, the effect of the contact being a function of current hunger and memory levels. Memory decreases through "forgetting", which as we have seen in section 5.4.1 depends solely on the passage of time and the current memory level. Memory affects the

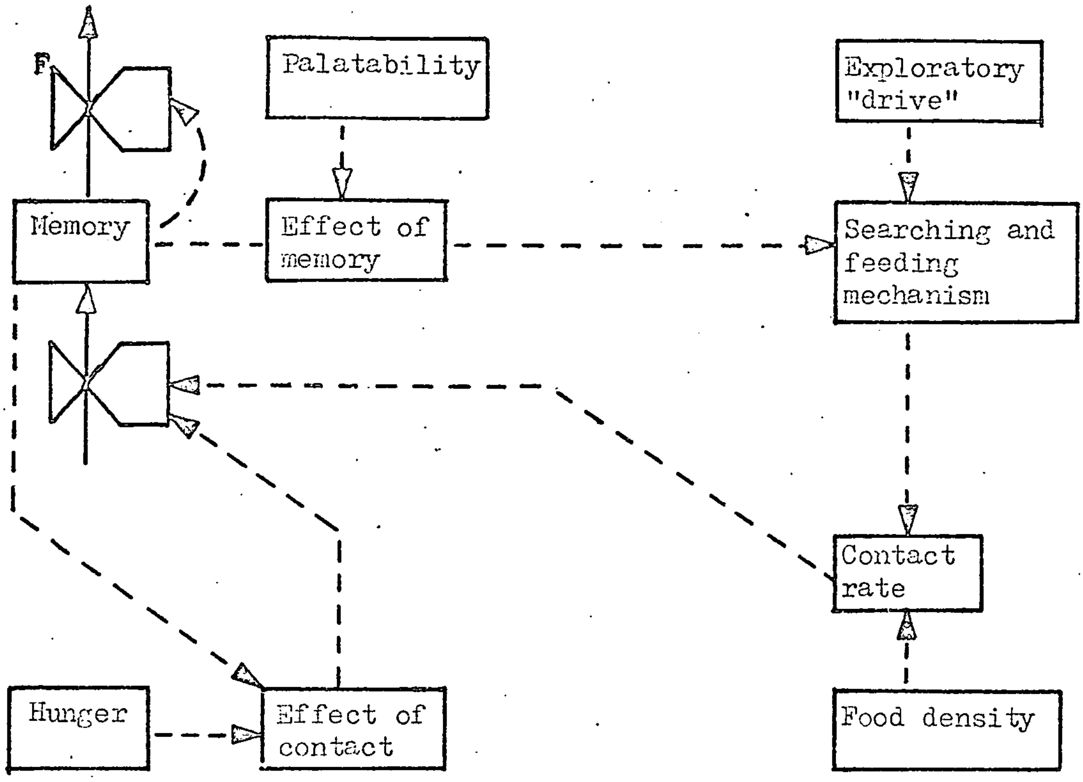
Fig. 5.4.2-1a

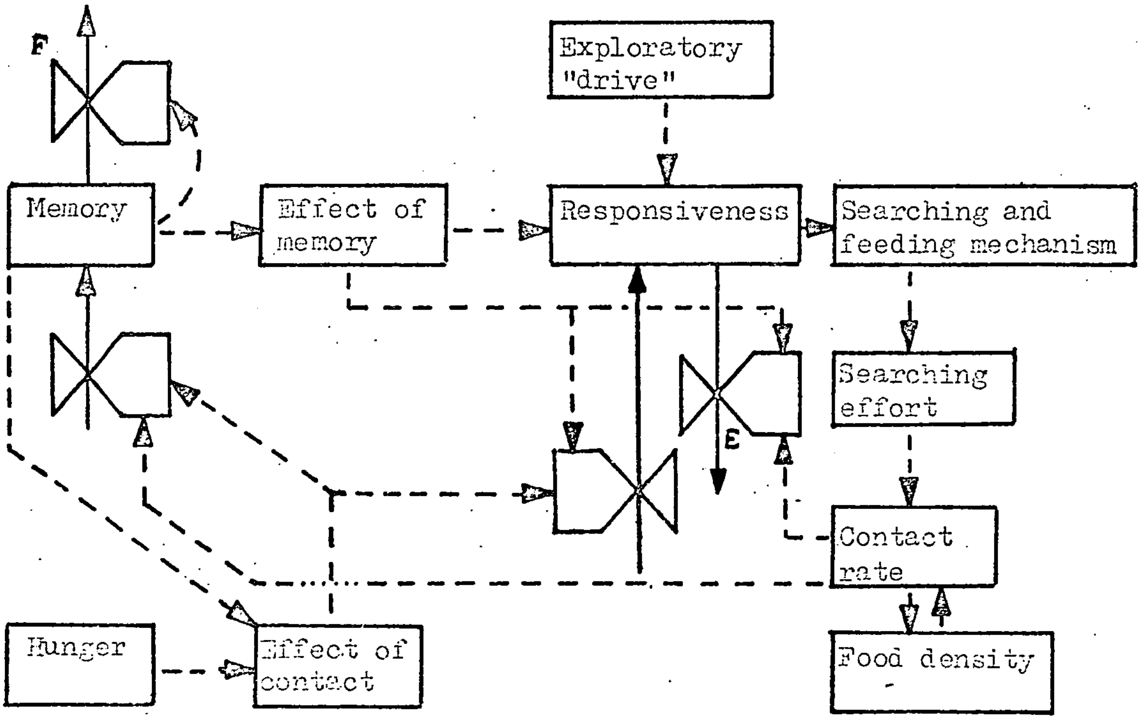
Representation of Holling's model of the learning process.

Key: F - Forgetting
E - Extinction

Fig. 5.4.2-1b

Modification of the learning model to permit extinction of a learnt response.


F
Palatability
Exploratory "drive"
Memory
Effect of memory
Searching and feeding mechanism
Contact rate
Hunger
Effect of contact
Food density


F
Exploratory "drive"
Memory
Effect of memory
Responsiveness
Searching and feeding mechanism
Searching effort
E
Contact rate
Hunger
Effect of contact
Food density

appropriate thresholds in the feeding system, with an effect depending on the palatability of the food. The feeding system is also affected by the initial responsiveness, for when the effect of memory is zero.

This model does not, however, distinguish between losing the memory for a specific food, and learning that the food is no longer present, i.e. between forgetting and extinction of a response (Skinner, 1938). The bank vole showed this distinction quite clearly. Reduction of groat density to zero caused extinction within two days of the searching response (section 3.3.4.3); this was shown to be different from forgetting in that a subsequent increase in groat density level resulted in an immediate increase in searching, much faster than the initial adjustment to the brushes system.

Fig. 5.4.2-1b shows one way in which the model can be expanded to account for extinction of a learnt response. Thresholds in the feeding system are now affected by the level of a compartment termed "responsiveness". The term is used to indicate the tendency to respond to a particular conditioned stimulus - such as the brushes in the brushes system or the food-delivery bar in operant-conditioning experiments - rather than responsiveness to the food itself. For a palatable food, responsiveness is decreased by searching, and increased by contact with food items. Both these effects are influenced by the memory of where the food may be found and the food's palatability. As in Holling's model, memory is increased by contact with the food and decreased through forgetting, though this model does not require that forgetting should take place at a high rate. Both the increase to memory and to responsiveness are influenced by the effect of each contact; this effect is itself influenced by feed-back from the two compartments, and by hunger and specific hunger levels.

This model, although only expressed in a qualitative form, accounts for the three features of the functional response experiment which vary with time and require an explanation in terms of a learning process. First, in the absence of a memory for the association between the brushes and groats, and in the absence of a responsiveness to the brushes as a source of groats, the vole shows an initial response to the brushes. In the context of the brushes system, this is perhaps better expressed as part of an exploratory drive, and use of the brushes for cover rather than Holling's "generalised responsiveness". When groats are discovered, the high contact rate increases the memory component and the responsiveness component, resulting in increased searching over the first few days.

Second, the rise in the distance travelled per day when groat density is dropped to zero is predicted by the model, since searching would continue until the amount of searching had drained the responsiveness to some low value. On subsequent days, memory that the area could contain groat grains would remain high, but responsiveness would remain at a low value due to the high ratio of searching to contact rate.

Third, the difference between the periods of rising and of falling groat density is predicted in a similar manner. During the period of rising groat density, the responsiveness will be always lower than the stable level for any density, and during the period of falling groat density, it will be higher.

Finally, this model retains the feature which originally caused Holling to include a learning component, namely the positively-accelerated feature of the functional response curve. This will occur at low groat densities if the large searching effort can cause the responsiveness to drop to a low value in between contacts.

5.5 Speed of movement

5.5.1 Background

The rate of movement of the feeding animal relative to its food is a key feature in determining the rate of successful search of the animal, and will this affect the shape of the functional response curve (Holling, 1965). In general terms, this component needs to be resolved into two components: the speed of the searching animal and the speed of its prey. This separation needs to be made if either is not a constant. For example, the speed of a searching animal may depend on its hunger (Reynolds and Pavlik, 1960) while the speed of the food may depend on its own population density, as Holling (1965) found for house-flies in the preying-mantid system, or on external environmental factors, as the passive movement of plankton will depend on the speed of water currents.

In specific cases, the speed of one of the items may be zero. Thus, barnacles are sessile and depend on filtering plankton out of a moving stream of water. Land-based herbivores, on the other hand, feed on a stationary food supply. Either case simplifies the analysis, since the relative speed of food and feeder is equivalent to the speed of the moving type. This is a major convenience in the case of multiple-food situations for herbivores, since we do not have to concern ourselves with different relative speeds for the different types of food.

5.5.2 Study of speed of movement

5.5.2.1 Introduction

I consider it essential to measure the speed of movement of the vole in the same situation as was used for conducting the functional experiments, since it is obvious that the component will be affected by the brushes used in those experiments. Compared with a situation where the vole could move without impediment, the brushes would not only reduce the vole's speed, all other things being equal, but could also affect the way that speed changes as a function of, for example, hunger; we might expect that speed is less easily affected if the vole is travelling through a difficult medium.

Fortunately, it was quite a simple matter to set up a situation where the vole could be observed from underneath travelling through the brushes. Since the brush bristles were black, both the vole's creamy underbelly and the pale groat seeds showed up very clearly against this background. In addition, an advantage of viewing the animal from underneath was that it appeared to be much less easily disturbed by light or movement: a vole viewed from above in open ground would probably have been reluctant to move into the open in the light, and would certainly have been easily disturbed by any movements made while I observed it. As it was, the vole often ate seeds where they were found, and, when it had finishes searching, would sometimes bed down under the brushes. Even moving the hand a couple of centimetres away on the underside of the glass would elicit no reaction, and indeed it could be quite difficult to persuade the vole to return to its nest-box at the end of the run. These observations also suggest that the vole was not worried at being on glass at some height: other work has shown that several animal species are reluctant to walk on a glass plate over a "cliff" (Walk, 1965). Possibly in this case the visual impression of height was not sufficient, the vole's eyes were not good enough, the vole might just not respond in this way, or it rapidly de-learnt this response.

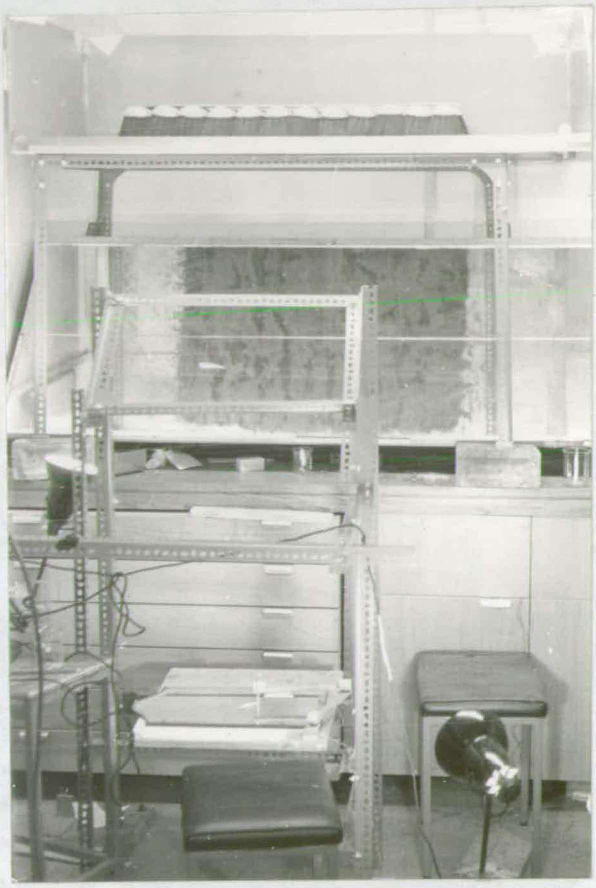
In order to investigate the relationship between speed and hunger, the vole was normally deprived of food before a particular session. The vole's short-term hunger should then decrease as the session progressed and it found more food.

Fig. 5.5.2.2-1

General view of arrangement for measuring the speed of the bank vole under the brushes.

From top to bottom:

Block of brushes (standing on glass plate)
View of underside of brushes on a mirror.
Pointing resting on small mirror.
Operator's seat.



As a control, one session was run in which there was no food, so that the short-term hunger would not decrease. The period of deprivation was variable and in one case there was no initial deprivation; it was thus hoped that changes of speed with long-term hunger could be detected, even if a precise relationship could not be defined.

Three voles, all males, were tested in this experiment. Each one was allowed to acclimatise to the set-up for several days at least before the first run, and during this time groats were only available under the brushes, so that the vole learnt where to find its food.

5.5.2.2 Method

A photo of the experimental arrangement is shown in Fig. 5.5.2.2-1. The experimental area consisted of a glass plate measuring 80 cm by 140 cm set in a wooden frame. The four sides were bordered by hardboard sheet 40 cm high, fastened in such a way that there was no exposed edge for the vole to start chewing on. The sheet of hardboard facing the room was removable, to enable the vole to be tended to and the experiment to be set up for the next run.

Two blocks of 12 brush heads were placed in the experimental area. The groats were always scattered under the brushes, except when the vole was being deprived from the previous night and a few groats were put out to prolong the start of deprivation; in this case they were placed in a petri-dish by the nest-box. The small wooden nest-box had a door-flap which made it easier to catch the vole at the start of a deprivation period or when the area was being set up for another run. A water bottle was always available, and except during an experiment wheat was available as an alternative source of food outside the brushes. The vole was normally deprived by placing in a cage which did not contain any bedding material, to remove the possibility of this being consumed by the hungry animal.

The experimental area was supported 200 cm above floor level by Dexion framing on a bench against one wall of the room.

Three methods were tried for recording the vole's movements. In the first, time lapse pictures were taken using a Super-8 cine camera but it was unable to resolve the groat seeds in the area, and it was very time consuming to recover the data using frame-by-frame analysis.

The second method used a "camera obscura" to project an image of the experimental area on to a plan of the area. A lens 15 cm in diameter was used (taken from an epiadiascope), set in the top of a tent made of dark material, and placed over the plan: I worked through a slit in the tent, recording the position of the vole at second intervals on the plan. Quite apart from the discomfort in operating the system, and the bright lights that were needed to give a reasonable image, it proved impossible to decipher the finished record, due to the vole doubling back on its own tracks, or staying in on position for a period of time.

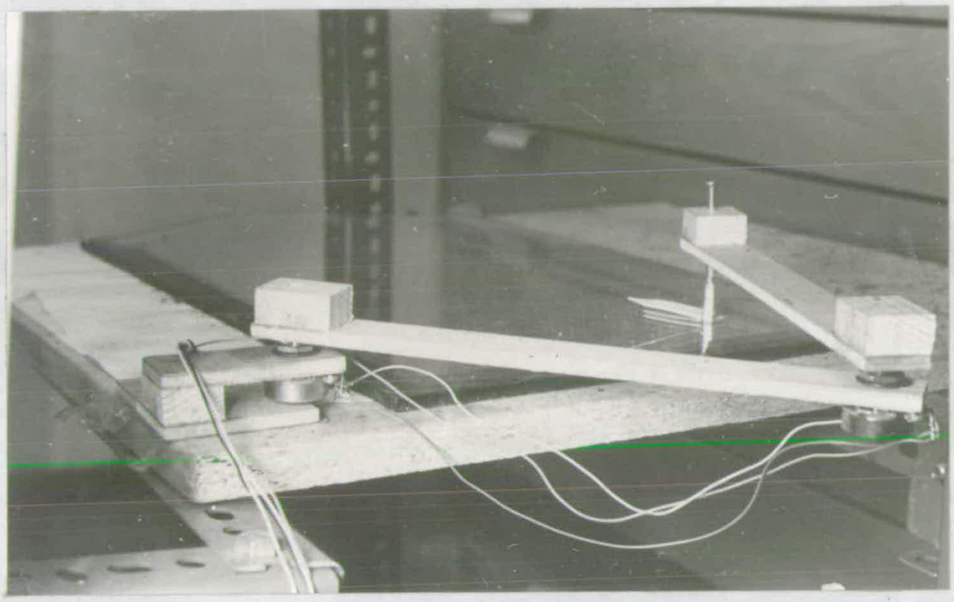
The method finally chosen used a modification of an X-Y plotter whose pointer was manually moved around to follow the image of the vole reflected in a mirror (Fig. 5.5.2.2-2).

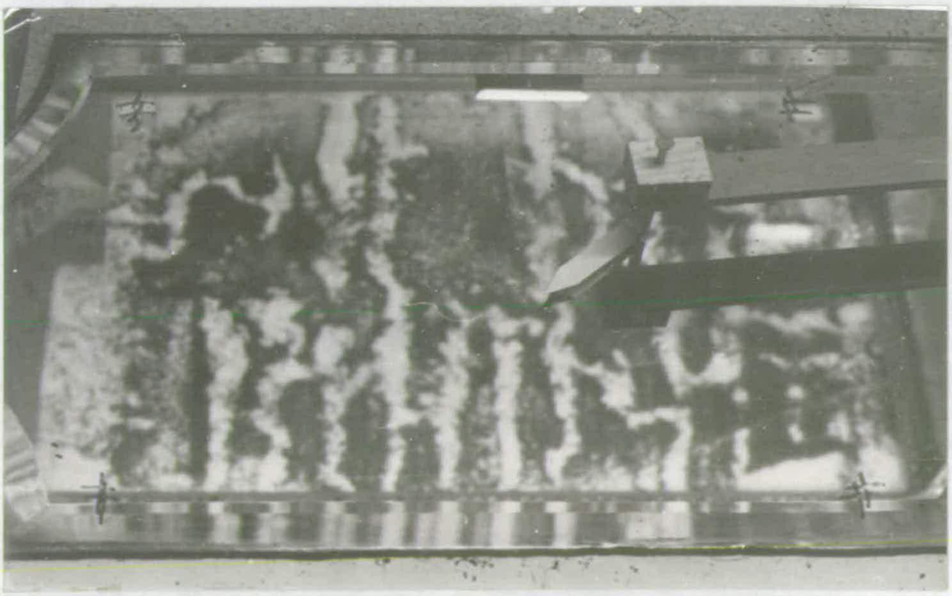
Fig. 5.5.2.2-2

Details of pointer resting on mirror. The two potentiometers can be seen at the two junctions.

Fig. 5.5.2.2-3

Operator's view when recording vole movements. The underside of the brushes (with many vole tracks) can be seen reflected in the mirror.





The output was to a data logger which sampled the plotter twice a second. In contrast to the usual type of X-Y plotter, whose output is two voltages proportional to the X and Y co-ordinates respectively, the apparatus consisted of two arms, one of which swivelled around a point on the base plate, the other of which swivelled around the end of the first one. The pointer was attached to the end of the second arm. At each junction, one arm was attached to the spindle of a 100 ohm potentiometer (volume control), while its base was attached to the other arm, or fixed to the base-board. Thus, as the pointer was moved, the angle at each junction changed, resulting in a change in the resistance of the potentiometer. A 1.5 volt battery was connected across the ends of the two potentiometers, and the output thus consisted of two voltage readings, related to the angle of the junction. It can be shown that any combination of angles for the two junctions specifies a unique point within the locus of points described by the pointer, so that this system is suitable for recording the vole's position. It is in fact a much simpler system to construct that the normal type of X-Y plotter, but it suffers from the disadvantage that the data is not readily interpretable in terms of the co-ordinates of the vole. But once the geometry of the apparatus has been initially determined, it is a simple matter to program the computer to convert the two voltages into the two angles, and thence into the co-ordinates. Since the output from the data logger was on paper tape, and in view of the large amount of data obtained (greater than 20,000 pairs of values) it was logical in any case to handle the data on the computer, so this conversion presented little extra burden.

At the start of a recording session, the pointer was moved to the four corners of the area. This data was later fed into a preliminary computer program which optimised the values for four parameters of the system dealing with the conversion from volts to degrees for the angles. This removed the need to have a constant voltage source over the duration of the experiments on speed of movement, a period of several months.

The pointer moved over a horizontal mirror fixed 40 cms. above the floor. The image of the four corners of the experimental area were marked on the mirror, and, at the start of a run my head rested in a fixed position on a support so that the four marks coincided with the four corners. Any movement of the head would result in error in recording the vole's position, and one eye needed to be kept closed during actual recording to eliminate switching between eyes. Although this was not very comfortable, the system worked very well, and errors were kept small, especially during a run, when the head would be in one position. Fig. 5.5.2.2-3 shows a view of the experimental area through the mirror as seen by the operator.

The temperature in the room was at ambient, approximately 20°C, but since it was an internal room, short-term fluctuations in the room were minimal. The lighting regime was the same as used in the functional response experiments, that is, 8 hours from 0900 to 1700.

Under normal maintenance conditions, the vole was provided with a supply of wheat near its nest-box, and an ample supply of groats under the brushes. Prior to an experiment, the daily consumption of the vole was recorded to assist in the calculation of hunger levels following deprivation. Peat was also scattered under the brushes, to provide an indication of the vole's normal use of the area.

Prior to a recording session, the vole was deprived of food, but not water, by placing in a wire-bottomed cage with an exit at its base. Remaining food was removed from the experimental area, and a known number of groat grains were placed under the brushes; the powdered peat was not replaced for the run. To start a run, the cage was simply lifted up so that the vole could leave through the bottom, and the recording pointer was manned. As soon as the vole appeared under the brushes, the pointer was moved to the position of its nose, and the paper punch on the data logger was switched on: the voltage analyser part was kept on so that there was no delay while it warmed up. The paper punch, kept in an adjacent room because of the noise it made, could barely be heard, and there was no visible reaction from the vole.

The recording continued until the vole left the brushes, or settled down in one spot. Apart from early sessions, the estimated duration of the sortie, the number of seeds eaten, and the interval between sorties was recorded. The process was repeated whenever the vole moved under the brushes, until the vole was inactive for at least 10 minutes, at which the period of observation was discontinued.

5.5.2.3 Analysis of Data

The basic aim of the experiment was to determine the average speed of the vole travelling through the brushes; a secondary aim was to test for a relationship between this speed and the short- and long-term hunger states of the vole. The first stage in the analysis of the data was to obtain a descriptive presentation of the main features of the run, as a basis for deciding which segments of the data to use in subsequent analysis.

In the following sections, a "run" refers to a single sortie by the vole, that is, an uninterrupted recording bout. A "series" is a group of runs terminated by a period of inactivity of at least 10 minutes.

For each run, the data was first presented in the following three ways:

a) A plan of the area, showing the position of all groat grains, and the position of the vole at one-second intervals (Fig. 5.5.2.3-1). The position was marked by a letter of the alphabet every ten seconds, and by the digits 1 - 9 for every second in between. This convention made it easier to analyse the record with respect to time, so that, for example, the time at which a seed was taken could be deduced.

b) A plot against time of the vole's speed at half-second intervals (Fig. 5.5.2.3-2). This was necessary for detecting periods of inactivity in the record, and for obtaining a visual impression of the pattern of the vole's activity with

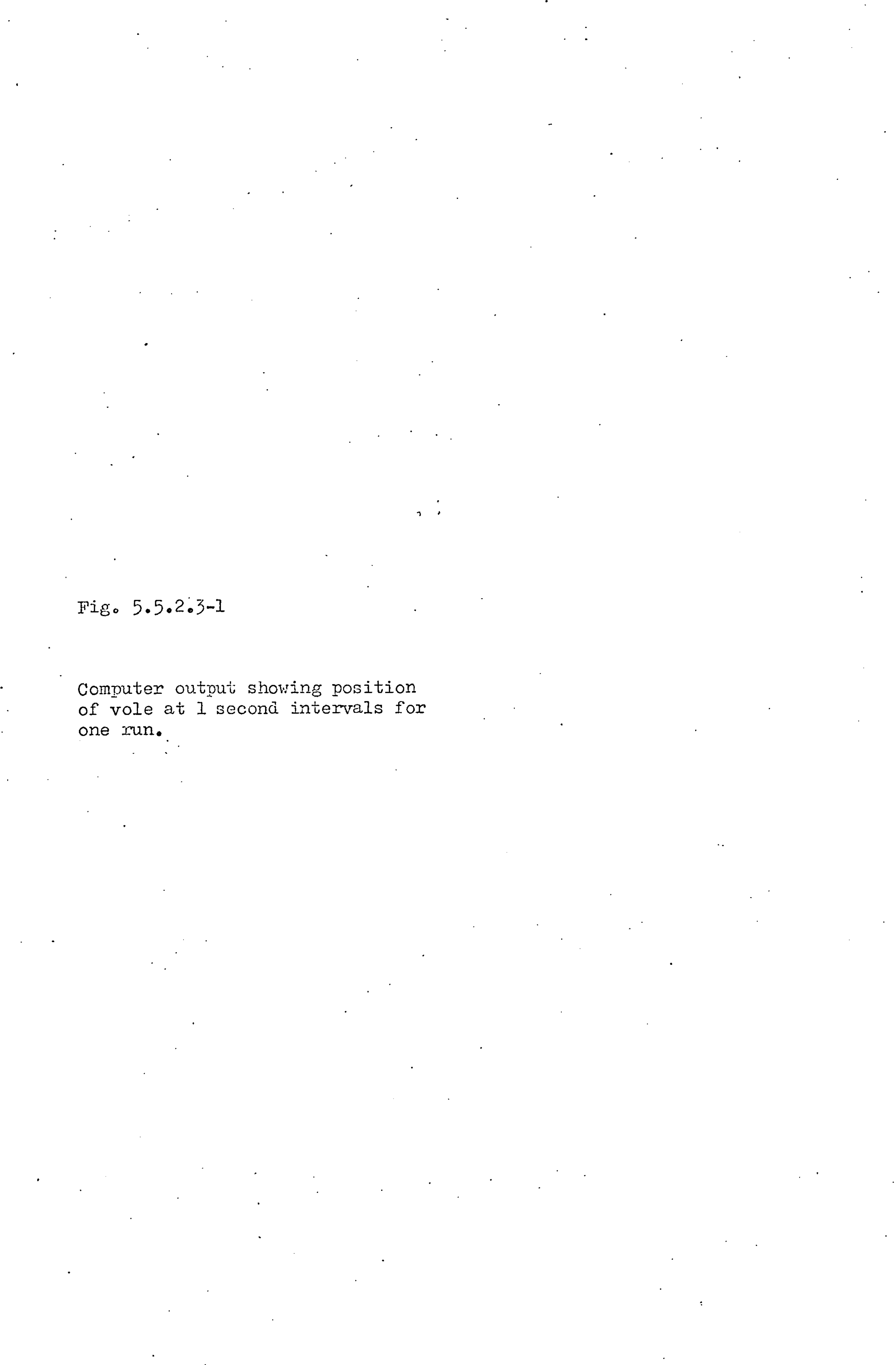


Fig. 5.5.2.3-1

Computer output showing position of vole at 1 second intervals for one run.

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          RUN     16

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.                                           6                                             .
.                                           5                                             .
.                    @                                    8                   6           .
.              .              .@            14        Q 9   .     @      2 .              .
..            ...            ...            .S.      1    7...   9     J 3...  7         ..
.              .              .       @   32 9            6 . 4KN   54315 H.              .
.                                                  2       25 818278     79               .
.                                            76    4     P1     436      6     83         .
.                              @                   569    9        9    68                .
.                                             5 4 R 87    8      10.  32  6    9 2        .
.                                                3        76     2       7    B  1  A     .
.                                                            5  3     451     1           .
.              .              .              .              .  4         8 . 2            .
..            ...            ...           ....            ...            @.43           ..
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Fig. 5.5.2.3-2

Computer plot of vole speed versus time.

```
                 ***  BEHAVIOUR  UNDER  BRUSHES  ***

                         - VELOCITY-TIME PLOT.


                 5J  3/6/73  1530 - 1830

                 SERIES   10
                 RUN      16


TIME            SPEED - CMS/SEC.

    0    1    2    3    4    5    6    7    8    9    10   11   12   13
  A !----------------------------I.         .         .         .
    !---------------I   .         .         .         .         .
  1 !--       I         .         .         .         .         .
    !---------I--       .         .         .         .         .
  2 !-----------------I .         .         .         .         .
    !-----------------------I     .         .         .         .
  3 !----------------------I-------         .         .         .
    !----------------   .I        .         .         .         .
  4 !---------------I   .         .         .         .         .
    !----------I----    .         .         .         .         .
  5 !--   I   .         .         .         .         .         .
    !-I       .         .         .         .         .         .
  6 !--      I.         .         .         .         .         .
    !------------------I----      .         .         .         .
  7 !--------------------------I-----       .         .         .
    !--------------------------I  .         .         .         .
  8 !---------------------I-      .         .         .         .
    !---------------I   .         .         .         .         .
  9 !----------I        .         .         .         .         .
    !------I- .         .         .         .         .         .
  B !--    I  .         .         .         .         .         .
    !-------I---        .         .         .         .         .
  1 !--------I---       .         .         .         .         .
    !----   I .         .         .         .         .         .
  2 !------I  .         .         .         .         .         .
    !------I----        .         .         .         .         .
  3 !---   I  .         .         .         .         .         .
    !----I-   .         .         .         .         .         .
  4 !-----   I.         .         .         .         .         .
    !-------I---------  .         .         .         .         .
  5 !---   I  .         .         .         .         .         .
    !-I       .         .         .         .         .         .
  6 !  I      .         .         .         .         .         .
    !-------I .         .         .         .         .         .
  7 !--------I--------  .         .         .         .         .
    !--     I .         .         .         .         .         .
  8 !---I--   .         .         .         .         .         .
    !---I     .         .         .         .         .         .
  9 !-I-      .         .         .         .         .         .
    ! I       .         .         .         .         .         .
  C !--       .         .         .         .         .         .
    !I        .         .         .         .         .         .
  1 !-        .         .         .         .         .         .
    !         .         .         .         .         .         .
  2 !    I    .         .         .         .         .         .
    !-----------I---    .         .         .         .         .
  3 !------------I--------        .         .         .         .
```

Fig. 5.5.2.3-3

Computer plot of vole speed frequency distribution for one run.

```
        ***  BEHAVIOUR  UNDER  BRUSHES  ***

                  VELOCITY FREQUENCY DISTRIBUTION

        5J  3/6/73  1530 - 1830

        SERIES  10
        RUN     16


40 !0 0
   !0 0
38 !0 0
   !0 0
36 !0 0
   !0 0
34 !0 0
   !0 0
32 !0 0
   !0 0
30 !0 0
   !0 0
28 !0 0
   !0 0
26 !0 0
   !0 0
24 !0 0
   !0 0
22 !0 0
   !0 0
20 !0 0
   !0 0
18 !0 0
   !0 0    0
16 !0 0    0
   !0 0    0
14 !0 0    0
   !0 0   00
12 !0 000 00 00 0
   !0 00000000000
10 !0 00000000000
   !0 000000000000 0
 8 !0 000000000000 0  0
   !00000000000000 00 0
 6 !00000000000000 00 0 00
   !0000000000000000000000
 4 !0000000000000000000000 00
   !0000000000000000000000 00     0
 2 !0000000000000000000000 00    0000
   !0000000000000000000000 00 00 0000 00  0 0         0
 0 ++----+----+----+----+----+----+----+----+----+----+
    0    1    2    3    4    5    6    7    8    9   10
                  VELOCITY - CMS/SEC.
```

respect to time, especially with respect to the times at which a grain was eaten.

c) A frequency distribution of vole speeds (Fig. 5.5.2.3-3). This was needed to see if a simple criterion could be established for separating movement made during searching periods from smaller movements made during periods of "inactivity". During these latter periods, the vole would frequently shift around on the same spot, and it is clearly important not to include this movement in estimating the vole's speed under the brushes.

Visual analysis of frequency distributions of speed indicated that there was no evident bi-modality which could be attributed to a resting and an active phase. Consequently, there was no single speed which could be used to distinguish the resting from the active phases. This may seem slightly anomalous, but is explained by the fact that the resting phase was marked by small movements as the vole settled down. In addition, the active phase did contain instances when, over a half-second period, the vole was not recorded as having moved, either because of a brief pause to sniff an object, or because of lag effects on my part in operating the pointer following the vole.

However, it was easy to detect on the graph of speed versus time those periods of prolonged resting, during which times a speed of 0.6 cm./sec was only rarely exceeded. Consequently, I decided upon the following criterion to be used for deciding that a particular value for speed should be classed in the active phase. According to the criterion, the value was to be included if its own value was greater than 0.6 cm./sec, or if either of the two preceding values and of the two succeeding values was greater than 0.6 cm./sec. Thus, a very low value would still be included if it was deemed to have occurred between values greater than 0.6 cm./sec.

Except for earlier runs, when the duration of the interval between runs and the number of seeds eaten in each run had not been recorded during the session, an estimate was made of the vole's short-term hunger level at the end of each run, so that the mean speed for a run could be compared with the assumed hunger level operating at the time of the run. The arbitrary selection of the end of the run as the reference time for the hunger level is not critical, since each run only lasted for a maximum of four minutes, during which time the hunger level would not change greatly in the absence of food intake; but it does mean that the seeds eaten during that run would have been included in the estimate of hunger operating at the time of that run.

The model used for estimating the current short-term hunger level is that referred to in section 5.2.2.1. It assumes that the short-term hunger level is numerically equivalent to the amount of spare capacity in the vole's short-term food store, which is assumed to be the stomach. Then the rate of increase of hunger is taken to equal the rate at which the stomach empties, described by the equation:

$F_{12} = a_{12} . X_1$ where: F_{12} = flux of food from stomach to gut,

a_{12} = rate coefficient, and

X_1 = current amount in stomach

The value of a_{12} was taken as 0.41/hour, as a representative value obtained from the experiments described in section
The actual value chosen for a_{12} is not critical, however, since the eating of seeds made a much greater contribution to the change in hunger level during the course of a series than the emptying of the stomach described by the above equation. This was because, in most cases, the duration of a series was not greater than twenty minutes, during which time there would be only a change of 10% in the hunger level, which is equivalent to only one groat grain assuming a hunger level of half the maximum.

The initial value for the short-term hunger level at the start was calculated assuming that the hunger level was zero at 1.5 hours before the start of the deprivation period preceding the series. This is based on two assumptions, that the vole's short-term hunger is zero at the end of a feeding bout, and that interval between bouts is on average three hours. Since the deprivation period was started without regard to when the vole had last eaten, the last bout would then have occurred on average 1.5 hours ago. In those cases where the vole was deprived overnight and left with a small amount of food, it was assumed in addition that the vole ate food at a rate of 0.1 gm/hour and the start of true deprivation calculated on this basis.

While these assumptions are reasonable, small changes in the timing of the deprivation period are not important, since the rate of change of hunger decreases as the deprivation period continues, and is only about 0.02 gm/hour after five hours; an error of an hour either way would then only affect the initial hunger level by about this amount.

5.5.2.4 Results

The speed of movement of the vole can be investigated in relation to three factors. The role of the short-term and long-term hunger levels are important, because of their possible effect on the functional response. In addition, sufficient data was obtained for two voles (both male) to check for a difference in mean speed of movement between them.

a) Short-term hunger

For one vole, there was sufficient data on both consumption patterns and speed-of-movement trials to test for a relationship between the short-term hunger level for each run (estimated as described in the previous section) and the mean speed for each run. Fig. 5.2.2.4-1 shows the relationship between these two variables. It can be seen that there is a small positive correlation between mean run speed and short-term hunger level. Since hunger level decreased during each series of runs, this positive correlation could not be an artefact arising from the vole using tracks opened up in earlier runs of the series; this would bias the results in the opposite direction. It is possible,

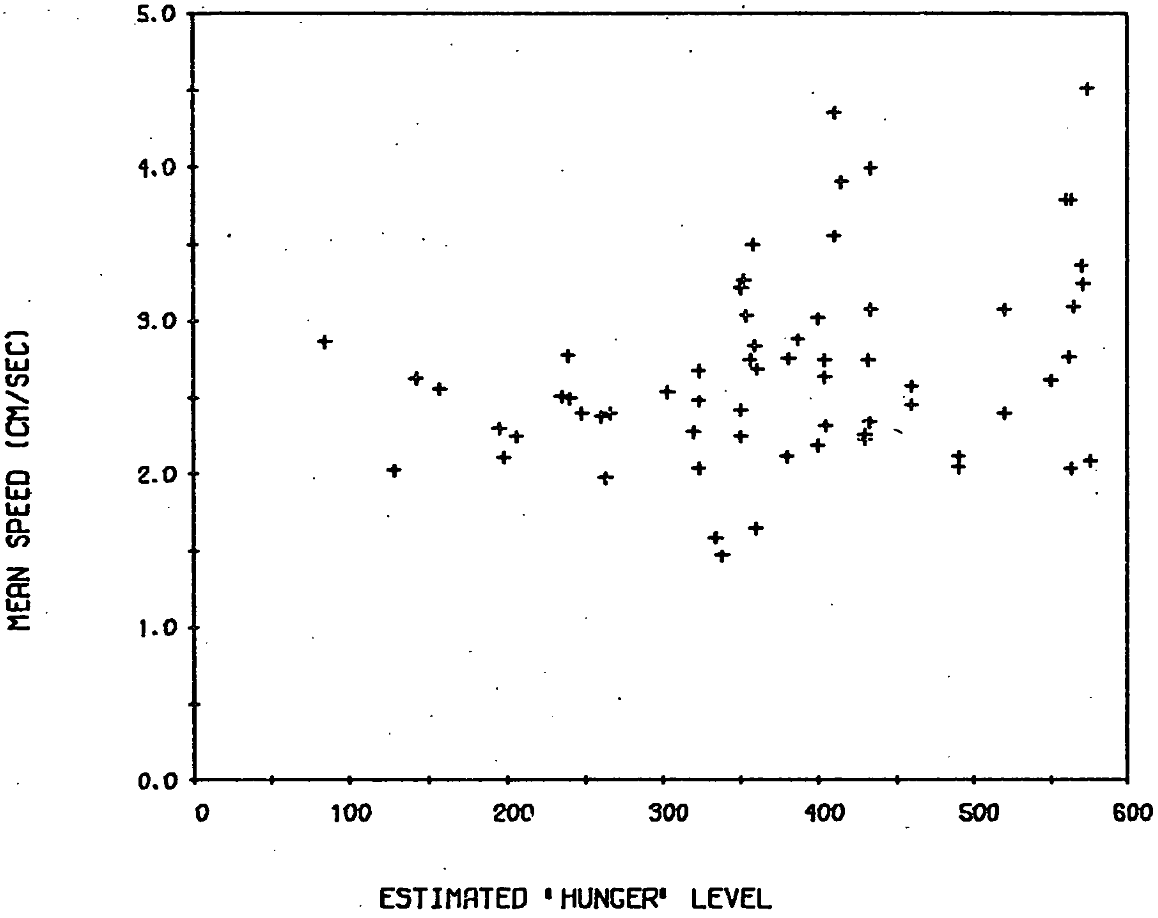


Fig. 5.5.2.4-1

Relationship between mean run speed and estimated short-term "hunger" level.

however, that the first runs of a series may tend to be along tracks used regularly in previous series, and therefore easier to penetrate.

It may thus be concluded that even if the apparent correlation between short-term hunger level and speed is a genuine one, the effect is nevertheless quite small.

b) Long-term hunger

Within a series of runs, lasting under 45 minutes, the vole's long-term hunger level would not change by very much. Therefore, the search for a possible effect of the long-term hunger level requires a comparison between series, rather than between runs. Fig. 5.5.2.4-2 shows the distribution of mean run speeds for consecutive series, for two voles. It can be seen that there is little evidence for differences between series. In one case (arrowed), the series was begun without a preceding period of deprivation, and it can be seen that this had no effect on the mean run speed. In view of the difficulty in estimating satisfactory values for the long-term hunger level, it can only be concluded that the data does not support the hypothesis that long-term hunger affects the vole's speed. If there is an effect, it is small enough to be masked by the inherent variability of the data.

c) Difference between voles

Comparison of the mean run speeds for the two voles on Fig. 5.5.2.4-2 indicates that there appears to be no difference

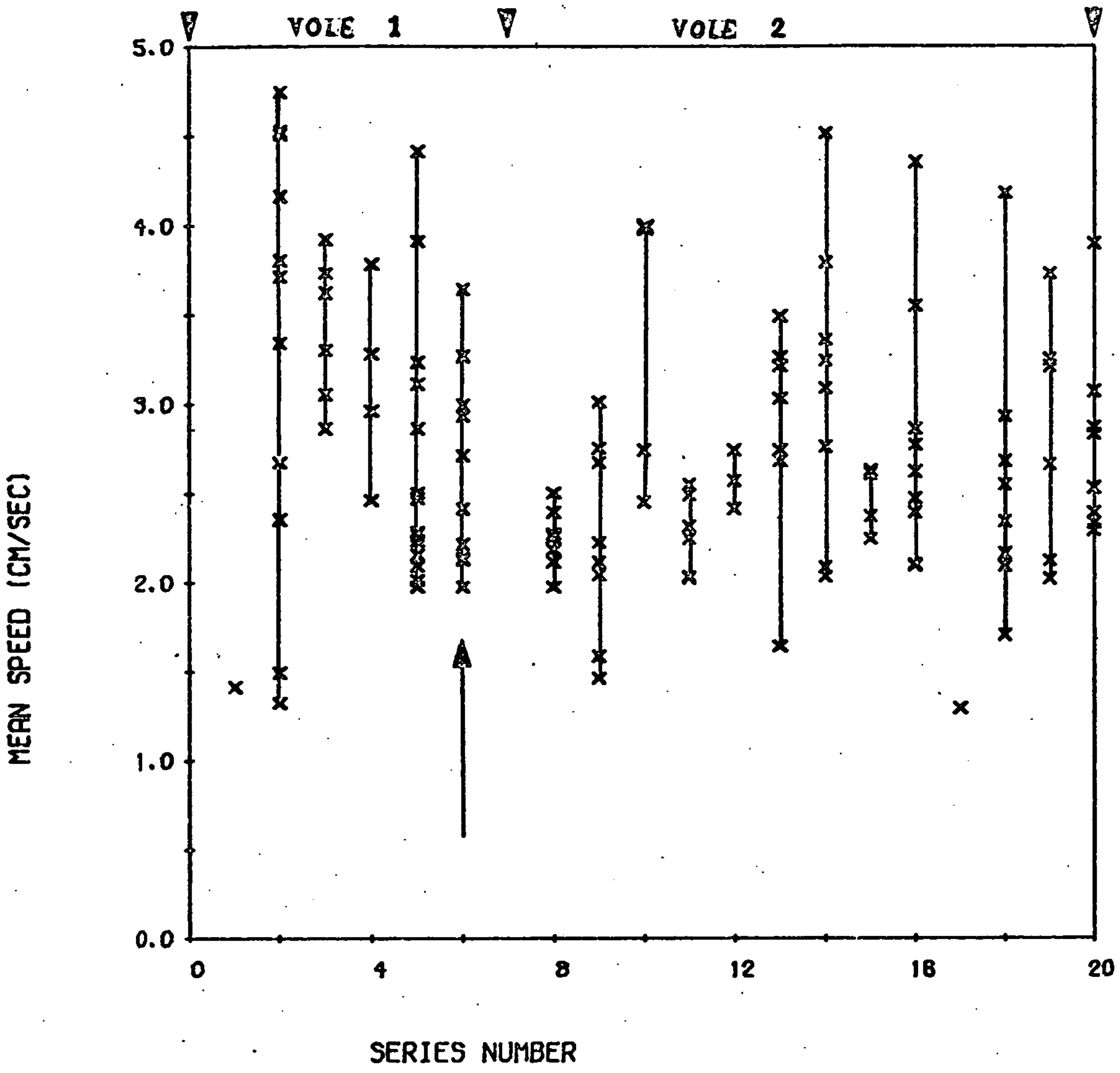


Fig. 5.5.2.4-2

Distribution of mean run speeds in successive series, for two voles.

in the distribution of mean run speeds for these two particular voles.

5.6 Handling time

The time that an animal takes to handle an item of food once it has been found is potentially an important factor in determining the functional response of an animal, since each item handled reduces the time available for feeding.

In the case of single-food systems, this component may determine the plateau value to which the functional response tends. This has been shown not only for model systems (Holling, 1959b) using a blind-folded human "predator" searching for discs on a table, but also appears to largely determine the maximum intake over a day for those animals equipped with a crop or its equivalent. Thus, Murton et al (1963), studying woodpigeons feeding on grain, present data for mean number of paces per minute and mean number of pecks per minute. Their data enable one to calculate that a pace takes on average 0.01 mins and a peck (the handling component) 0.03 mins. At the very highest density, it can then be calculated that the bird spends 75% of its time pecking at the grain. Since further increases in grain density do not cause a decrease in the mean paces per minute, the role of handling time appears to be even more important.

In single-food cases where the animal does not have a large food storage organ relative to food size, the role of handling time is likely to be less important, since the animal will then require to spend a larger amount of time in the digestive pause. Such a case is provided by the praying mantid system studied by Holling (1966). The average time to eat one fly was found to be approximately 0.01 hr, and a maximum of 35 flies were consumed per 16 hr. day at the highest fly densities, so that the actual handling time would then involve only 21 mins, instead of the full 16 hrs. It is for this reason that Holling, in deriving his analysis from the relationship: $N = a.D.(T-H.N)$ needs to define his handling time to include time spent in the digestive pause.

In the two-food or multi-food system, the role of handling time in shaping the functional response curve for a specific food is likely to be even less important. The reason for this is that time spent handling the particular food as its density increased would be compensated for by savings on the time spent handling alternative foods as less of these are consumed.

In some cases, the relative value of handling time for two food types has been used to develop a model of the optimal strategy for the feeding animal (Emlen, 1966; MacArthur and Pianka, 1966). Handling time can then be combined with values for the relative values of the two foods, and the relative times taken to find each, to indicate the proportion of the two foods that should be eaten. In many cases, especially with herbivores, it is unlikely that such limitations apply. First, many animals maintain a mixed diet even under conditions of ad lib. food and this would not be found if selection was made solely on the basis of which food gave the greatest return per unit time. Second, the problem for many herbivores is to obtain the optimum nutrient balance from a variety of foods, (Westoby, 1974) and the relative time spent handling each item is then less important. Third, handling time may again be a small proportion of the total time available for feeding.

Nevertheless, for the sake of completeness, the handling time for groats and wheat will be considered in the next section, after which the possible effect of hunger on handling time will be considered.

5.6.1 Handling time for groats and wheat

Handling time for groats and wheat were determined from the automatic feeder records. The method used was to measure the interval between the selection of one grain and that of the next: observations on the voles feeding from the apparatus had shown that one grain was usually taken as soon as the preceding one had been finishes, with any hesitation taking only a couple of seconds. Any error introduced by this method, rather than direct measurement of actual eating time, will be offset by the fact that the additional to move towards a food item, and to decide to take it, will be part of the handling time for each food item under functional response conditions as well.

Fig. 5.6.1-1a,b shows the interval length frequency distribution for two voles for intervals following the selection of a groat grain and following the selection of a wheat grain.

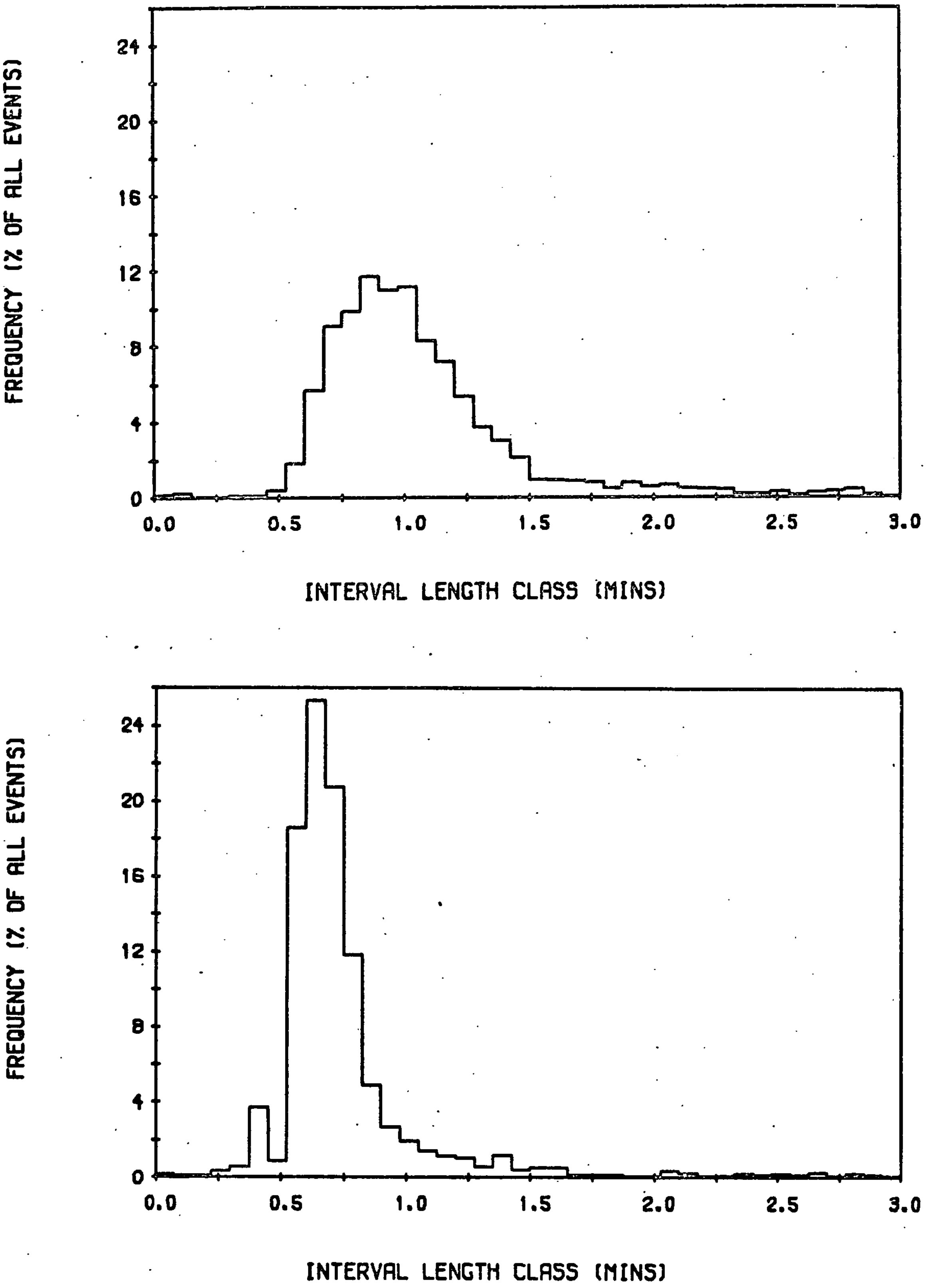


Fig. 5.6.1-1a

Interval length frequency distribution for groats, for two voles.

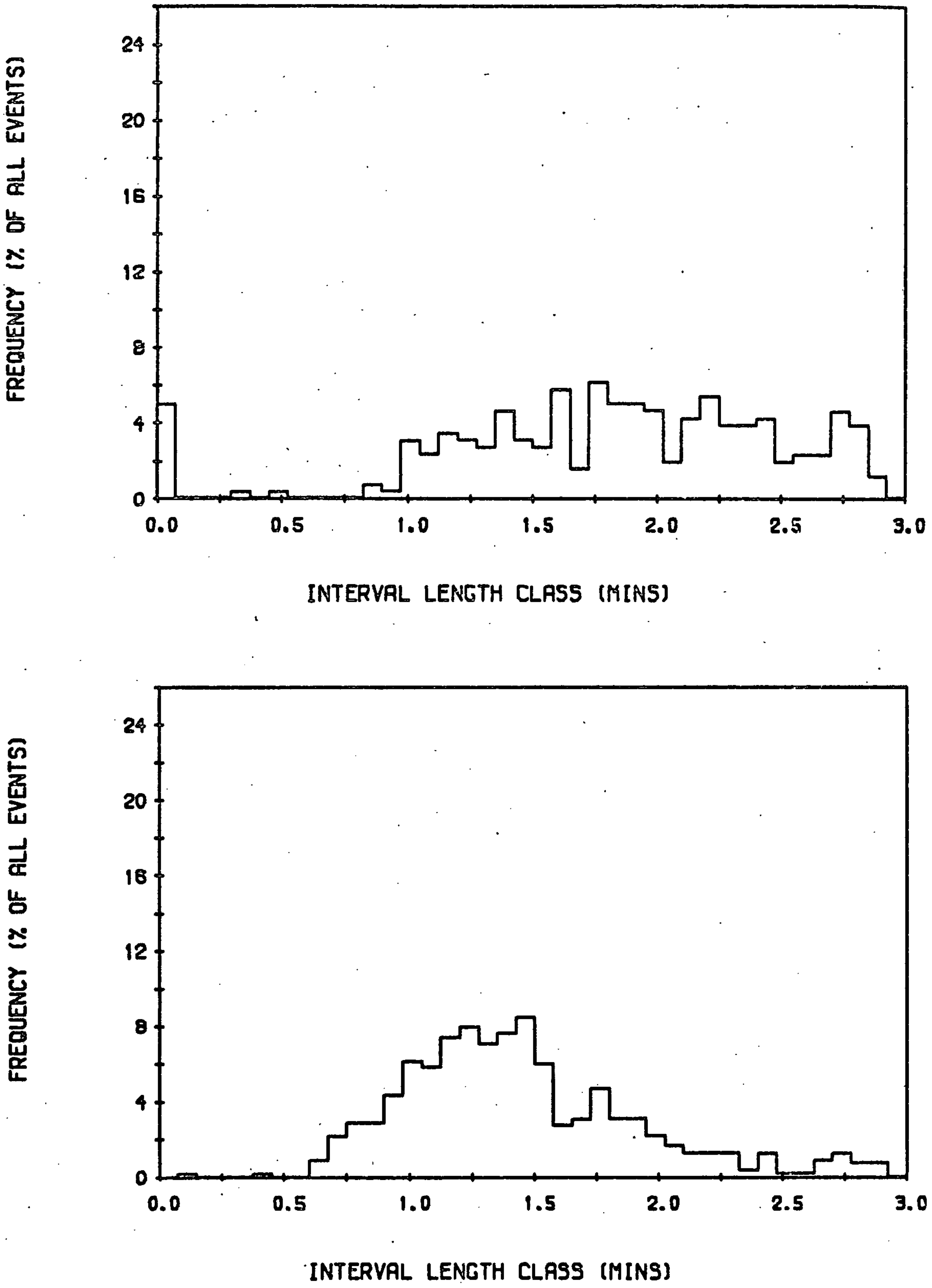


Fig. 5.6.1-1b

Interval length frequency distribution for wheat, for the same two voles.

First, it can be seen that the distribution has a relatively sharp cut-off at the lower end, since a limit will be set by physical limitations, but that the cut-off at the higher end of the peak is much less distinct, due no doubt to behavioural factors causing a delay before the selection of the next grain. For the purposes of the analysis, the distribution in handling time itself was assumed to be normal, with the distribution evenly distributed around the mode.

Second, it can be seen that the variability of the wheat results is greater than for groats; also the mean handling time for wheat is proportionally larger than for groats, considering that the mean weight for groats was 30 mg and the mean weight for wheat 45 mg. The larger handling time for wheat is due to the fact that the wheat grain is much harder than the groat grain. The increase in wheat variability is greater than would be expected from the variability in the grains themselves, and could be due to differences in grain hardness or it could be that slight differences in the vole's feeding motivation are amplified when the food is more difficult to handle.

Third, it can be seen that there are significant differences between voles in the mean handling time both for groats and for wheat. This makes it difficult to indicate a value for the typical vole; typically, the mean handling time for groats varies between 0.6 mins and 1.2 mins, while for wheat the corresponding values are 1.5 to 2.0 mins. Thus, if a vole typically ate 2.5 gm of food per day, it would spend between 0.83 and 1.66 hours per day actually handling food if it were feeding solely on groats, and between 1.4 and 1.85 hours per day if it were feeding solely on wheat. (These figures assume a mean weight per grain of 30 mg for groats and 45 mg for wheat). Assuming a preference for groats of 70% by weight, the vole would spend between 1.0 and 1.7 hours per day on a mixed diet, or between 4% and 7% of the day.

5.6.2 Effect of hunger on handling time

In view of the small proportion of potential feeding time actually spent handling food, any differences in handling time as a function of the intervening components would have very little effect on the functional response. Nevertheless, the data is available from the automatic feeder records to see if handling time is affected by short-term or long-term hunger; it is less easy to check the influence of the specific hunger or learning components. As with speed of movement, it is possible here to restrict the analysis for a qualitative test of the two hunger components, that is, we can see if handling time is different at the start of a bout, or at the end of a deprivation period, even though it may not be possible to express any effect in the form of a quantitative relationship.

Handling time has appeared to be insensitive to hunger changes in other studies. Thus, Holling (1966) found no effect of hunger level on the time it took a praying mantid to eat a fly, and Sterner (1968, quoted in Rosenzweig and Sterner, 1970) found that the time taken by rodents to husk seeds after a period of deprivation did not change as more and more seeds were eaten.

The effect of the short-term hunger component was investigated by comparing the interval lengths following the first and second-last groat for each bout. For each of two voles, 40 bouts, not distorted by deliberate or accidental periods of limitation to one food, were analysed by calculating the confidence limits for the difference between the two intervals. The results are summarised below:

	Vole 1	Vole 2
Mean difference (sec.)	-0.8	-2.1
95% confidence limits	-7.1 to 5.5	-8.8 to 4.6

It is clear that there is no evidence for the hypothesis that handling time should increase during a bout, as short-term hunger decreases.

In order to test whether long-term hunger affects handling time, the handling time for groats was estimated before and after three periods of food deprivation. The estimates of handling time were made for the two or three bouts preceding deprivation and for the first bout following. Two of the deprivation periods lasted 6 hours, and one 15 hours, but the results for all three are shown here. Fig. 5.6.2-1 shows the frequency distribution of interval lengths for groats taken before and for those taken after the deprivation. There is no apparent difference between the two.

We can thus conclude that handling time is not a function

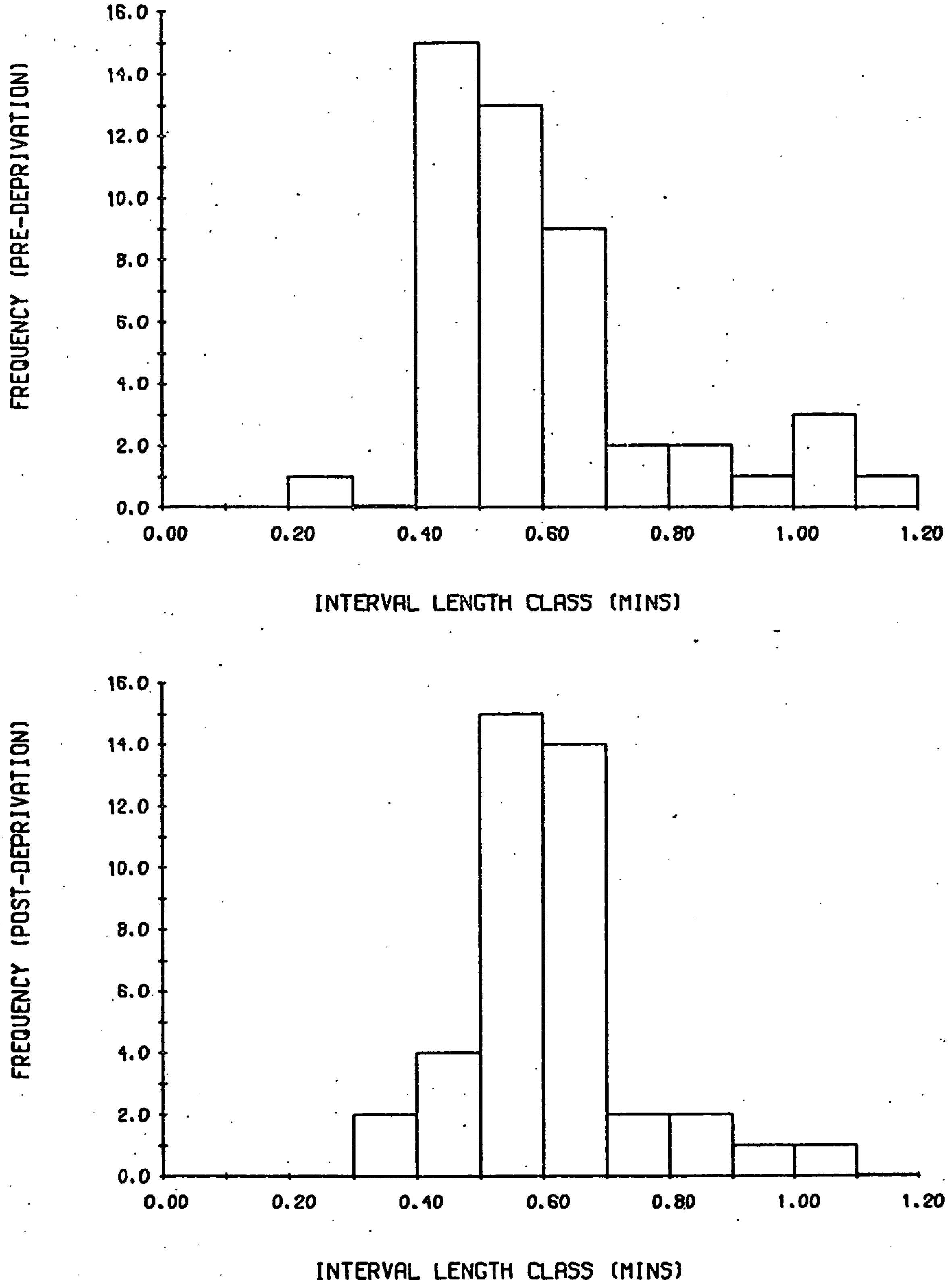


Fig. 5.6.2-1

Frequency distribution of intervals between selection of groats before (top) and after (bottom) a period of deprivation.

of the hunger component, though it could be affected by specific hunger. Voles differ in their mean handling time for groats and wheat, and also in the variability of handling time. Part of the variability is no doubt caused by variations in seed size; this is not the whole reason, because of the differences in variability between voles.

5.7 Reactive distance

The distance at which an animal can perceive a food item in the course of travelling over the area will affect the functional response through its effect on the rate of successful search. Thus, the larger the reactive distance - the furthest distance from the sensory receptor at which the food item can be detected - the greater will be the area swept out in a given amount of time at a certain speed.

Changes in the reactive distance will have proportional effects on the rate of successful search; for example, a 50% increase in the reactive distance would increase the rate of successful search by this amount, all other things being equal, and assuming no exploitation effect. This component is therefore a potentially important one in defining a particular animal's functional response, unlike the handling time component in which even large percentage changes would have quite a small effect on the feeding response.

In view of the importance of this component, it is unfortunate that it proved to be difficult to measure. Holling was able to measure the reactive distance of the praying mantid (1966) by gradually moving a dangling fly closer to a stationary mantid in various degrees of hunger and recording the distance at which stalking or striking began. This approach was not possible with voles in view of their sensitivity to disturbance, and the practical difficulties of getting the vole to remain still while food was moved closer.

Two methods were tried to estimate the vole's reactive distance. The first was based on the data obtained from the functional response experiments, since an estimate could be made of the width of the vole's track knowing the distance travelled per day and estimating the total area covered per day from the percentage of available food actually found. This method is described in section 3.4.4.6. The other method was experimental, in that food items were set up at various distances from the vole's track and the distance at which food items were taken non-randomly was recorded. This method is described in the next section. Neither method was able to be used to find whether the reactive distance was affected by the intervening components.

5.7.1 Experimental measurement of reactive distance

5.7.1.1 Method

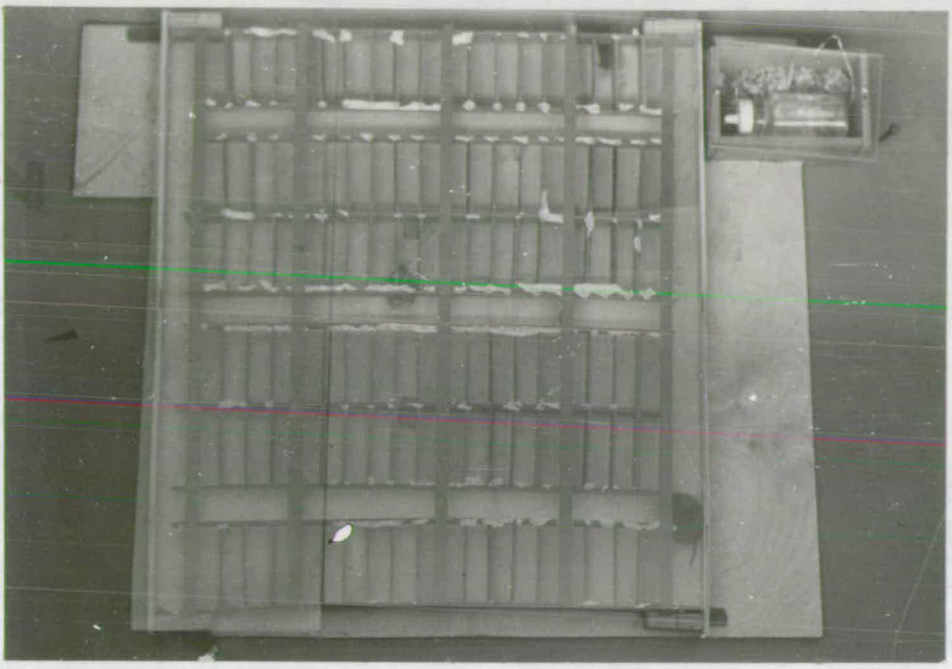
The experimental apparatus is illustrated in Fig. 5.7.1.1-1. The animal was able to travel along three corridors. On each side of a corridor their were 19 cells measuring 2 cm wide and 8 cms deep. Each cell could only be entered from the corridor, but in order to do so the animal was forced to pass under a lintel which left a gap of 1 cm between the floor and the lintel bottom. Thus, a cell could either be entered or not, with no intermediate option.

In order to detect whether a cell had been entered during a particular time period, the floor of the experimental area was made of fine wire mesh with peat scattered on top. On setting up the apparatus, the netting with peat was carefully placed on a base board which had marked on it the same pattern of cells. The action of the vole in entering a cell, or turning around in it to leave again, thus caused the fine peat to fall through the wire mesh under the particular cell, so that at the end of the experimental period all cells which had been entered were signified by corresponding patches of fine peat on the base board.

In order to test the distance at which the vole could detect food, single grains were placed at a fixed distance behind the lintel in some of the cells; the rest were left blank. The selection of cells to contain a grain was initially done pseudorandomly and later using random number tables, but in any case the vole appeared to show no pattern in its use of the cells.

Fig. 5.7.1.1-1

View of the equipment used for estimating the reactive distance. The two end-corridors and three cross-corridors can be seen. Each cross-corridor has openings into 19 cells on each side. The equipment is normally covered over, a fine-mesh wire gauze sprinkled with peat is placed between the walls and the baseboard during an experimental run.



In between actual experiments, which normally lasted for several hours, the vole was allowed to feed in the area with several grains placed in a few cells: thus, the vole would become accustomed to finding food in some cells and not in others.

The vole was not deprived for the experiment, since it was only necessary to allow the experiment to run for a certain length of time in order to ensure that enough grains were found. The experimental situation was similar to the brushes system used for determining the vole's functional response, since in both cases the food was resting on peat, the food itself was groats, and the area was in complete darkness, so that the animal would have to use the sense of smell in both cases.

5.7.1.2 Results

Table 5.7.1.2-1 shows the number of grains taken and not taken at each distance, and the number of blank cells entered and not entered. Even if several distances were used in a particular experiment, the results were analysed by setting up two-by-two contingency tables, containing the number of grains taken and not taken at a particular distance, and the number of blank cells entered and not entered in that run. The fact that these last two values may thus be used in several such tables, and the fact that the more cells entered the greater the homogeneity of the data, means that the use of Chi^2 is strictly

Table 5.7.1.2-1

Contingency tables showing number of cells entered and not entered, for cells either containing a groat grain at specified distance, or empty.

Grain distance from entrance		Entered	Not entered	Chi^2
1 cm	Groat	18	0	15.7
	Empty	38	40	
1 cm	Groat	11	13	20.5
	Empty	7	83	
2 cm	Groat	10	2	20.3
	Empty	19	71	
3 cm	Groat	15	9	10.8
	Empty	24	66	
4 cm	Groat	17	7	8.5
	Empty	34	56	
4 cm	Groat	6	6	4.8
	Empty	19	71	
5 cm	Groat	9	15	0.5
	Empty	27	63	
7 cm	Groat	7	11	0.5
	Empty	38	40	

speaking invalid. Nevertheless, since there was no correlation between the Chi^2 value obtained and the number of cells entered, and since the number of cells entered never exceeded 50%, the Chi^2 statistic will be used: the results were not sufficiently border-line to be affected by such factors. It can be seen from the Table that, when the grain is up to 4 cm behind the lintel, the vole tends to enter the corresponding cell significantly more frequently than would be expected if each cell had the same probability of being entered. At distances greater than 4 cm, those cells containing grains do not have a higher chance of being entered. It would thus seem that the vole can detect grains up to 4 cm away.

There is an indication in these results that the significance of the effect drops off as the distance of the grain behind the lintel increases. If this is correct, indicating that the vole has more difficulty in recognising a grain the further away it is, then the component of reactive distance must be viewed in terms of a probability distribution rather than as a fixed parameter, or as a variable which is a function of the intervening components. Once the form of this had been determined, the area under the probability distribution curve could then be calculated and the effective reactive distance determined.

Section 6 Discussion and conclusions

6.1 Introduction

The description of the vole's functional response to groat density (section 3), together with the analysis of the main underlying components (section 5), indicate that it is not yet possible to produce a quantitative model of the vole's functional response, nor justifiable to attempt one.

The descriptive approach showed that the response is quite complex. First, it can show both a positively-accelerated section and a negatively-accelerated section, in addition to the more basic linear rise and a plateau. Second, use of the index of distance travelled can reveal features not shown by the actual numbers of groats taken. Third, the results are complicated by the fact that the response obtained for a particular set of conditions is influenced by conditions on the preceding days.

Even if the response had not been complicated by these factors, it would still have been necessary to include at least one of the intervening components of hunger, specific hunger or learning, if the resultant model was to reflect the animal's feeding behaviour on a fine scale. For example, the factthat the vole feeds in bouts, and responds to periods of deprivation, means that a hunger component must be included, if only in a start-eating/stop-eating vole. The response of the vole to single-food conditions means that a specific hunger component is required.

In addition, the complexity of the functional response results support the need to include the three intervening components (see section 5.1). First, the POS segment of the functional response curve requires the inclusion of at least the hunger component on a learning component. Second, the NEG segment probably requires a specific hunger component. Third, the temporal changes in the response indicate the need of including a learning component.

It is thus clear that the functional response of the vole cannot be adequately modelled unless the action of at least these three intervening components is included. This action may either take the form of an effect on the direct components, as implied by the word "intervening", or the components may have a more direct effect, as the "search/no-search" decision governed by the hunger component, or the act of specific selection governed by the specific hunger component. Holling's hunger component (1965) served both roles, since it determined when searching or attacking would take place, in conjunction with thresholds, and its value was found to affect the reactive distance. In either case, an intervening component can only be included if it itself can be satisfactorily modelled.

The act of modelling an intervening component falls into four stages. First, the variable or variables associated with the component must be identified. I have argued in section 5.1 that it is most satisfactory to consider an intervening component in terms of a hydraulic model, with compartments which get charged up and empty. Such an attitude is common in discussion of these components, although it may not be explicit. Then, the variables associated with an intervening component would represent the level of the corresponding compartments, and could be called state variables (Patten, 1971). The state variables associated with the hunger system, for example, could be the level of sugar in the stomach, gut, blood and long term stores.

Second, the way in which each variable can be increased needs to be known. In the case of the hunger system, the input into the first variable is simply the intake of food, and the input into the subsequent variables is equivalent to the output from the preceding one. The problem may be greater for the other components: thus, for example, although it seems likely that there is a variable in the specific hunger system which is affected by each contact with a groat, it cannot be assumed that this effect is constant.

Third, we need to know how the value of a variable declines over time, and whether this decline is at a constant rate or a function of some other variable in the system. Again, this is easy to visualise in the hunger system, as the rate at which food passes out of a particular compartment, but is more difficult to see in the case of the specific hunger or learning components.

Fourth, for those intervening variables which also have a direct effect, it is likely that the variables of that component will operate over one or more thresholds, as was deduced for the hunger system (section 5.2.2). These thresholds are needed to determine when a particular activity should begin and when it should stop. A threshold may have a constant value, it may be a function of a longer-term variable in thesame system (section 5.2.2), or it may depend on the value of a variable in another intervening component, as Holling (1965) suggested for the action of learning on the attack threshold.

It will be seen from the foregoing discussion that there is simply not enough information in the present study to construct reasonable sub-models for the three intervening components, in particular the components of specific hunger and of learning. Although it is perfectly possible to fabricate sub-models which may or may not be rough approximations of the true action of these components, I felt that the large number of assumptions required, and the fact that any information used to test the sub-model would also have been included in its original formulation, did not justify such an attempt.

For this reason, the information gained from the analysis of components will be used to make qualitative rather than quantitative predictions relating to the functional response. As Levins (1966) has pointed out, such an approach can generally yield "robust" models, whose predictions are in terms of directions rather than values, and which are not so susceptible to errors in formulation. In the present case, the qualitative predictions required deal with the shape of sections of the functional response curve, the plateau level, and the dependence of the response for a particular density on prior conditions.

The following section will consider the four possible segments of the functional response curve, and discuss the explanations which have been put forward for each one. These explanations will be considered with regard to their compatability with the results obtained from the functional response experiments with voles.

The four segments of the functional response curve are as defined in section 3.3.4.7, and will be presented in the following order:

6.2.1	LIN	segment of linear rise;
6.2.2	plateau	plateau level, relative to total intake;
6.2.3	NEG	negatively-accelerated rise to plateau;
6.2.4	POS	initial positively-accelerated rise.

6.2 Possible explanations for segments of the functional response curve

The factors to be considered in the following subsections are specific to particular segments of the functional response curve. Thus, the time required to handle each food item can only be used to account for a NEG segment. In most cases, these factors are assumed to operate in a time-independent way, that is, the response to a particular density level does not depend on antecedent density conditions and does not change with time; though some factors, such as searching image, may have a time-dependent effect.

The functional response of the vole showed very strong time-dependent effects. Sharp drops in groat density from a high level to zero density resulted in an increase in distance travelled for the first day only following the drop (section 3.3.4.3). The response during the period of decreasing groat density tended to be higher than during the period of increasing groat density, irrespective of which period preceded the other (section 3.3.4.7).

We need to account for these effects over and above explanations for the shape of the individual segments.

The concept of "expectancy" has been used for this type of situation by animal psychologists (see Hinde, 1966), and by ecologists (Gibb, 1962). Amongst the former, Skinner (1938) has shown that when a rat is conditioned to obtain a reward by pressing a lever, removal of the reward results in a temporary sharp increase in the rate of bar pressing; and Cowles and Nissen (1937) have shown that rats and chimpanzees used to finding food in a particular situation will decrease its searching effort when food is not present. Gibb studied the predation of tits on larvae of _Ernarmonia conicolana_, and found that the birds did not eat a constant proportion of larvae from the pine cones in which they occurred. Rather, when a few trees contained cones with a high intensity of larvae in an area in which most trees contained low-intensity cones, relatively fewer larvae were taken from the high-intensity cones. Gibb argued that the birds would expect to find a certain number of larvae per cone, and stop their searching once this number had been found. This idea has been strongly criticised (see Krebs, 1973), since it is only the proportion of larvae found that is reduced at high intensity, and the absolute number found is still much greater than for the low-intensity cones. Nevertheless, the idea has some attraction: it is the spatial analogue of the effect of novelty (see section 6.2.4 - Possibility 6), in which a food may not be exploited as much as it could be because it had previously been scarce.

The idea of expectancy has been used above to account for an increasing in searching when previous experience was of higher food densities, and for a decrease in searching when previous experience was of a lower food density. It is assumed that the response under these conditions is being compared with the results that would be obtained if each density level was maintained for a long period of time. In the case of the bank vole, this control is not available, so the difference between the periods of rising and of falling groat density could be due to the expectancy effect operating in either period or both. The results obtained from the sharp decrease in groat density certainly indicate that expectancy should operate when groat density is falling; it is moreover more likely that the vole would put in more effort to finding the preferred food when its density had previously been high, than that it should be influenced by previous low groat densities even when it now finds groats more frequently. Thus, the reason for the vole's response being greater during falling groat density probably results from expectancy operating during the falling period, though there may be an initial lag when groat density is raised from zero to a low value in which chance encounter of groats may not be sufficient to stimulate the vole to increased searching.

Expectancy is clearly a learning process. As such, it needs to be included as a component in the functional response as part of the learning component, which was more fully discussed in section 5.4.2.

6.2.1 The LIN segment of the functional response curve

The LIN segment of the functional response curve covers that range over which an increase in the density of a specific food results in a proportional increase in the amount of that type eaten. This segment has normally only been identified with Holling's (1965) Type 1 response - a linear rise to a plateau. But, as pointed out in section 3.3.4.7, the advantage of considering segments of the functional response curve, rather than trying to classify the whole curve, is that different mechanisms can be seen to operate over different density ranges. Therefore functional response curves normally classified as Type 2 or Type 3 may include a LIN segment.

The simple Type 1 responses, which have been found for some invertebrates, are discussed in section 2. In addition, casual observation of response curves classified as Type 2 usually show an initial section which is as well represented by a linear rise as by a section of a negatively-accelerated curve rising to a plateau: this is not surprising, since most explanations for a complete Type 2 response generate relatively slow rates of change in the slope of the response curve at low densities. The functional response curves for the bank vole, however, clearly showed in some cases a definite linear section, despite evidence for a preceding POS segment and a following NEG segment.

The only explanation ever put forward to account for the LIN segment is based on the simple search model:

$N = a.D.T.$ where N = number of items found;

a = a constant;

D = food density;

T = time spent searching.

The basic form of this model has been proposed in one form or another by Lotka (1923) and Volterra (1931), (both quoted in Holling, 1965), and Nicholson (1933). In addition, the model has been taken as a starting point by Tinbergen (1960) and Holling (e.g. 1965), amongst others. The coefficient $\underline{a}$ has the units of areas per unit time, and measures the rate at which the animal searches the area. From the equation, $\underline{N}$, has the units of number, but as usual when used in the functional response situation, both $\underline{N}$ and $\underline{T}$ are expressed in terms of per day or some large unit of time.

For this model to produce the LIN segment, the coefficient $\underline{a}$ and the variable $\underline{T}$ must be constants. In order for these conditions to be satisfied, the effect of the intervening components (see section 5.1) must be zero, and the direct components must have constant values. The following sections will be concerned with the cases in which these are not constants.

It should be noted that, in order for the effect of the intervening components to be zero, it is not necessary to discount them altogether; the fact that for example the hunger component regulates food intake does not in itself mean that intake should not be directly proportional to food density.

6.2.2 The plateau of the functional response curve

There are two aspects relating to the plateau level for the consumption of a particular food type. The first deals with the proportion of intake made up by the one food type; the other deals with the factors which determine the absolute level of intake.

Factors determining the absolute level of intake are beyond the scope of this study. They include species-specific factors and long-term changes in body weight resulting from past eating history. Differences between animals in total intake should appear purely as differences in scaling for the plateau levels of consumption of the available foods.

Of more interest is the plateau value for a specific food relative to total intake. This is basically a question of what determines an animal's preference for a specific food under ad lib. conditions, and is still a largely unresolved question. There have only been a limited number of mechanisms proposed which can account for the maintenance of a mixed diet.

Possibility 1 - Self-imposed non-feeding periods

An animal may have daily periods of feeding and non-feeding which are not controlled by hunger levels. At the end of a non-feeding period, the animal's hunger level will be high, and it may then be willing to eat a less-preferred food.

> There is evidence that rats are less selective as their hunger increases (review in Young, 1948). Ivlev (1961) found that carp showed an increasing preference for chironomid larvae over other foods as they became more satiated.

It is unlikely that this can account for the vole maintaining a mixed diet. First, the records from the automatic feeder (described in Appendix A3) showed no diurnal cycle in the vole's feeding pattern, yet both foods were taken. Second, even if an inter-bout interval is considered to be a "non-feeding period", wheat should only be taken at the start of a bout, and this was not found (section 5.3). Third, depriving the vole of one food increases its subsequent consumption of that food, and this finding is not consistent with such a model.

Possibility 2 - Short-term operation of specific hungers

The more that is eaten of a particular type of food, the less one additional item of the same type may be preferred to one item of an alternative type. Eventually, the alternative food should become more preferred, and would be selected. This selection of the alternative food would decrease its relative attractiveness, while at the same time the attractiveness of the first is increasing, so the animal would again select the first type.

> Work with rats has shown that the more that is consumed of a particular type of food, the less the amount eaten when a choice is given (Holman, 1973; Morrison, 1974). This is found even when the two foods differ only in flavour, and not in nutrient composition. The aversion to the no-choice food is short-lived; it decays with the passage of time, and its decrease does not depend on the consumption of alternative foods.

This model in its simplest form predicts that the animal should take a run of the preferred food type, followed by a single item of the alternative type. Although the run lengths for groats tend to be more uniform in length than would be expected on a random basis (section 5.3), the run length distribution for wheat did not show more runs of one grain than expected. However, the model can be readily modified by the inclusion of lag effects to generate these results.

Possibility 3 - Optimum diet model

For each animal, there may be an optimum ratio of the various nutrients required (Westoby, 1974). Each of the available foods will contain the required nutrient in non-optimal ratios. Linear programming techniques exist for determining the ratio of the various *foods* the animal should consume in order to obtain the optimum ratio of the various *nutrients*. Only if one food contains all nutrients in the correct ratios should this be eaten to the exclusion of all others; otherwise the animal should maintain a mixed diet.

> The evidence that animal's can show self-selection of a balanced diet from basic nutrients, and can respond appropriately to changes in their internal environment, is discussed in section 5.3.1. The persistence of the bank vole's response to single-food conditions also suggests that metabolic rather than peripheral sensory factors are involved.

This model says nothing about the behavioural mechanisms involved in such a process. However, as discussed in section 5.3, the same mechanism for assessing foods as used in the short-term specific hunger model could serve the prupose, provided that a relationship had been built up between an awareness of the nutritive value and composition of a specific food and its taste. The experiments described in section 4.5.5, in which voles were limited to one food type for long periods, support the contention that metabolic effects are important as well as short-term changes in palatability. Presumably the short-term mechanism of spontaneous alternation is adapted to provide approximately the correct nutrient balance, with the metabolic effects operating only to occasionally correct small errors in balance; in this case, the short-term mechanisms will be most important under ad lib. conditions. It would not then be necessary to know the metabolic reasons or mode of operation of the long-term specific hunger mechanism in order to construct an adequate behavioural model for the maintenance of the mixed diet.

6.2.3 The NEG segment of the functional response curve

The negatively-accelerated segment of the functional response curve for the bank vole was not particularly marked, and it was necessary to lump the data for most voles in order to demonstrate its existence (section 3.3.4.7). The presence of a NEG segment has been clearly shown for invertebrate predators and parasites - Holling (1959b) gives several examples from other authors, and a further example is given for the preying mantid feeding on house-flies (1966).

Although there is considerable literature on the functional response of birds (see Krebs, 1973), it usually does not enable the presence of a NEG segment to be confirmed, either because of too few density levels under controlled conditions (e.g. Smith and Dawkins, 1971), or because of the variability of data obtained under natural conditions and the impossibility of controlling the densities of alternative food (e.g. Tinbergen, 1960; Royama, 1970). The functional response curves for small mammals (Holling, 1959a, 1965) do not definitely show a NEG segment: it is equally possible to fit an initial POS segment followed by a LIN segment to the data points given.

Possibility 1 - Handling time

If the feeding animal has a fixed amount of time available for feeding, and if it takes a finite amount of time to handle each item encountered, then only a limited number of items can be handled in the time available. At very low densities, virtually all the available time will be spent searching, so the area covered per unit of available time will be large; at higher densities, much of the available time will be spent in handling items, so the overall rate of search will decrease. Thus the number of items found in the available time will drop off as density increases to the point where the animal can spend all its time eating and very little time searching.

> This idea was first proposed by Holling (1959b) as discussed in section 5.6, and the equation derived from it was found to produce curves which could be made to fit the functional response results for invertebrate predators and parasites.
> However, the model in its simple form has two basic deficiencies. First, knowing the handling time per food item and the total time available for searching, it is possible to calculate the expected plateau value for the functional response curve: for many animals, this value is much too high.

The vole takes 0.5 to 1.0 mins to eat one groat grain, and could thus eat 1,440 to 2,880 in 24 hours, whereas it rarely eats more than 120. Holling went on to include the digestive pause - the time following consumption when the animal may be too satiated to eat - in handling time; handling time thus becomes very variable, and can only be investigated by an analysis of the components of the feeding system. This is in essence a different model from the one initially proposed, and is considered in more detail next. The initial model is thus only applicable in full to those situations in which there is little satiation. These include parasite systems, and those feeding animals which have a large crop. For example, Murton et al (1963) have found that woodpigeons can feed at near maximum rates for most of the daylight hours during winter.

The second problem with the handling time explanation for the NEG segment arises when there is an abundant supply of an alternative food. Then, an increase in the time spent handling the relevant food will be compensated for by time saved by not eating the alternative. This is evident from the extension, by Lawton et al (1974), of the handling time equation to a two-prey system. It is only if the handling time per unit of alternative food is less than that for the food under consideration that a

NEG effect could be found in the functional response curve.

MacArthur and Pianka (1966) have argued that the opposite is more likely to be true, with preferred foods having shorter handling times.

Possibility 2 - Effect of hunger on components of feeding

If there is only one available food, or if total intake is greater at higher densities of a preferred food, then the animal will be less hungry at higher densities of the food being considered. The term "hungry" is used in terms of the model proposed in section 5.2, and indicates lower levels in the hunger model compartments. The level of hunger may then affect one of the components of search, and reduce the rate of food intake.

Holling (1966) found that at high prey densities a praying mantid spends more time in a digestive pause, and therefore has less time available for searching. In addition, the reactive distance of the fly decreased as its hunger fell. The speed of movement of rats, for example, decreases as hunger decreases, and Beukema (1969) has found that hunger levels in the three-spined stickleback affect the probabilities of grasping and eating an envountered prey item.

When several foods are unavailable, however, it is much less likely that there will be large changes in hunger at different densities of a particular food (subject to the proviso in the first paragraph). However, there could be significant changes in the average value of the short-term hunger component if this hunger level needs to rise to a high level before alternative foods are eaten. For the bank vole, there was no evidence that its total intake was greater, the higher the proportion of groats, nor that the short-term hunger level affect the speed of movement (section 5.5) or on handling time (section 5.6). The possible effect of short-term hunger on reactive distance could not be determined. (section 5.7).

Possibility 3 - "Unutilised opportunity for attack".

Gause (1934, quoted in Holling (1959b) proposed that each predator is capable of generating a maximum number of attacks per unit time. As food density increases, rate of increase of number eaten with increasing density is proportional to the difference between this maximum and the current rate of attack. This model has also been proposed by Ivlev (1961), and Watt (1968), who modified it to include interference effects between predators and exploitation of the food supply by the individual predator. This model is essentially one way of representing hunger (Holling, 1959b), but as such it has no basis in observation and no explanatory value.

Possibility 4 - Specific hunger

The more that is eaten of a specific food, the lower may be the incentive to search for, or to accept, that particular type of food.

> The evidence for the existence of specific hungers is discussed in section 5.3, and considered in relation to the maintenance of a mixed diet in section 6.2.2 (possibility 2).

It is clear that, if there are nutritional and taste differences between foods, then all the evidence suggests that at low densities of a particular food, its specific hunger will be high. This is true whether or not specific hunger is considered to operate on the peripheral sensory or the metabolic level. It cannot yet be stated, however, whether a high specific hunger results in a higher probability of the food being accepted when encountered, causes the animal to increase the time spent in an appropriate area, or can affect the direct components of reactive distance, handling time or speed of movement. In addition, any effect of specific hunger may be swamped by other effects, such as the avoidance of rare food items (section 6.2.4 (possibility 4)).

On balance, however, this explanation appears to be the most likely to account for the NEG segment of the vole's functional response.

6.2.3 The POS segment of the functional response curve

The POS segment of the functional response curve is invariably assumed to occur in the region of low density, if it occurs at all, so that as the density of a specific food type rises above zero, the amount eaten increases more rapidly than the relative increase in density. This feature has been widely reported in bird and mammal species, and also in relation to the response of an insect parasite to host density although often evidence for this effect comes from a comparison of the response at a limited number of densities rather than from sufficient data to show a definite curve.

Although this segment may only extend over a small fraction of the rising part of the functional response curve, as I found with the vole, and may thus be of minimal importance to the feeding animal itself, nevertheless this effect may be extremely important to the food species. First, it may be a factor in the density-dependent regulation of population size, since it is the only feature of the functional response which can perform this role (Holling, 1965; Huffaker et al, 1968), although when the food species is an insect, the numerical response may be of much greater importance. Second, the decrease in predation at very low densities may enable a species to persist where otherwise it would have become extinct. Third polymorphism may be maintained within a species through the process of apostatic selection (Clarke, 1962), where the density of each morph may then lie in the POS segment of the functional response curve for the predator. Croze (1970) has demonstrated experimentally that crows are more efficient predators in a single-food than in a multi-food situation, so a prey species would do better (suffer less predation) by having several morphs.

The problem of what causes the POS segment has generated a large amount of discussion in the literature in the last fifteen years. This has been largely in relation to predation by birds, following the pioneering work of Tinbergen (1960), mainly because they are in general convenient to work with. Krebs (1973) has reviewed the possible mechanisms which may apply to bird predation; below I will discuss these and other possible mechanisms in more general terms, and relate them to the information available on the functional response of the vole.

The possible causes for the POS segment can be considered under three headings. Possibilities 1 to 8 are based on observations on the feeding animal, even if these were not originally related to the functional response. Possibilities 9 to 12 are based on observations of the food species in relation to their density, and possibilities 13 and 14 are derived from theoretical considerations. The list below is an attempt to provide a comprehensive list of the possible causes of the POS segment, and is not restricted to particular types of feeding or food species; the possibilities are not mutually exclusive, so more than one mechanism may operate at the same time (Alcock, 1973). Possibilities are included even if they have no relevance to the present series of experiments with bank vole.

The phenomenon of "switching" (Murdoch, 1969; Lawton et al, 1974) has not been included since it is a description of the presence of the POS segment in particular predator-prey or parasite-host systems, rather than an explanation of why the response curve includes a POS segment.

Possibility 1 - Searching image

When the density of a particular food is low, the feeding animal may be less likely, or unable, to detect it. As the food density increases, the animal learns to detect it, and is said to have developed a specific searching image for this food type.

The term was first used by Tinbergen (1960) to account for the fact that great tits ate fewer larvae of Acantholyda at low density of this prey compared with the number predicted by a simple search model. Royama (1970) has pointed out that this hypothesis is not the only nor the best explanation for Tinbergen's results. To be of any use, the term should be restricted to learning to detect a specific prey (Dawkins, 1971a), and should not be used to cover any change in behaviour which alters the prey risk (Beukema, 1968), nor to describe a preference for one food type over another (Brown, 1969).

Evidence for the formation of searching images comes mainly from experimental work under artificial conditions using cryptic prey for predators hunting by sight, and is reviewed more fully in Krebs (1973). De Ruiter (1952) found that, when jays and chaffinches were kept in cages with twigs on the floor, they only learnt to find stick caterpillars (Geometridae) once they had stumbled across one caterpillar. Dawkins (1971 a,b) found that, once chicks had chanced across several cryptic food items (coloured grains of rice on a background of the same colour), these grains were subsequently found at a much higher rate. Experiments which show a lower intake of cryptic than of non-cryptic food (Den Boer, 1971; quoted in Krebs, 1973), although indicating a failure to detect the cryptic food, do not provide support for the searching image hypothesis unless this failure is greater when the food is rare.

The formation of a searching image will result in a time-dependent (temporary) POS segment if the effect of each contact with the prey does not decay over time. (The terms time-dependent and time independent are introduced in section 6.2). If, however, the searching image tends to decay in the absence of contact with the prey, then a time-independent (permanent) POS segment will result. Dawkins (1971a) found that, when chicks were exposed to cryptic and conspicuous prey on three consecutive days, the rate of eating the

> cryptic grain type was less at the start of one day than at the end of the preceding day, but greater than at the start of the preceding day. Thus, the searching image appears to have decayed to some extent between the periods. However, in less extreme situations, where the food is not so cryptic and only one encounter is needed for the formation of a searching image (e.g. de Ruiter, 1952), it would be expected that the image would decay much more slowly.

It seems unlikely that the searching image hypothesis can account for the POS segment of the bank vole's functional response. First, it appears very unlikely that the vole could fail to detect grains which it normally detects by smell, when the grains would share aromatic compounds in common with other foods, and when they are not presented against a background of other, similar odours. Second, the searching image hypothesis would predict that the distance travelled per day at very low densities should be the same as at the upper end of the POS segment, since it is merely the animal's ability to detect food which changes. In fact, it was shown in section 3.3.4.7 that some voles show a definite decrease in the distance travelled per day at the low groat densities.

Possibility 2 - Niche hunting

In a mosaic habitat, with different foods in different areas, the profitability of each area is assessed through sampling, and the area is left if it is less profitable than another. Therefore, less time is spent in an area of relatively low food density, and the functional response for the corresponding food includes a POS segment.

This hypothesis was proposed by Royama (1970) to account for his observation that great tits took proportionally fewer prey of some species (e.g. the caterpillar of Tortrix viridana) at low prey densities. He rejected the searching image hypothesis since some prey species were taken in inverse proportion to their density (e.g. the caterpillar of Operophtera brumata), the diet of adults and nestlings was different, and the sequence of prey selection showed runs of one type followed by runs of another. The profitability of an area is the number of items found per unit of searching time: Royama used Holling's (1959b) disc equation to develop the theory, but it can be shown that a variety of simple search models generate the same result.

There is good experimental evidence to support the hypothesis. Hassell (1971) found that the hymenopteran parasite, Nemeritis canescens, of the larvae of Ephestia cautella tended to spend more time in artificial containers with the highest host densities. Smith (Smith and Dawkins, 1971) set up an experimental arena for great tits, consisting of four feeding areas, each of which was made up of 256 little pots. When prey density was varied by placing 1, 4, 8 or 16 meal-worms in each area, the tits spent most time in the area of highest density. Goss-Custard (1970) in a field study of predation by redshank on the burrowing amphipod, Corophium volutator, found that the birds tended to spend more time in the areas of highest prey density.

Royama's hypothesis should have a time-independent effect, with relatively less food being taken at low food densities even if the density remains low for a long period of time.

The model is not very suitable to account for the vole's POS segment for three reasons. First, the bank vole shows a POS segment even when the wheat was scattered with the groats under the brushes, i.e. not in separate areas. Second, the vole should only eat wheat, since this is always more abundant than groats. Third, even if wheat is considered to be at some intermediate density, because of its lower palatability, the functional response curve should have a particular shape, with an initial LIN segment followed by a vertical rise to the plateau, and such a shape was not found.

Possibility 3 - Cue hunting

A specific food type may be associated to a variable extent with particular cues or stimuli. The animal may only respond to a cue if it has learnt that there is a fairly high probability that food will be associated with it. If the occurrence of the cue is constant and the food density variable, then the response to the cue will be greater at higher food densities, and there will be a POS segment in the functional response curve.

> Unlike niche hunting, this possibility does not require that the total area be split into smaller areas of differing profitability; but there must be heterogeneity on a much finer scale within the area, to permit the development of an association between a food type and some feature of the area. Krebs (1973) appeared to be aware of the distinction between the two hypotheses when he talked of an animal "learning to go to a particular place to find food", and "learning to look in a particular type of place.
>
> Evidence for this hypothesis comes from Gibb (1962), who found that great tits associate pine cones with the presence of larvae of _Ernarmonia conicolana_, and feed in regions where the intensity of larvae (the number per cone) is large. Alcock (1973) reports that, when an experimental area is covered in a checkerboard of sand and gravel squares, redwing

blackbirds search preferentially in the type of square that had previously been associated with food. In analagous experiments, animal psychologists using probability learning trials (for example, MacKintosh, 1969) have shown that rats and birds respond preferentially to one of two stimuli when one stimulus is rewarded 75% of times and the other only 25%. The preference never reaches the optimum 100%, though this failure to maximise is due more to the influence of irrelevant cues than a persistence effect from the stimulus last rewarded.

As with niche hunting, cue hunting should operate in a time-independent manner, since it also does not depend on time lags in learning. The distance travelled per day should also decrease at low food densities, though, unlike niche hunting, this is not because the animal spends more time in another area.

This hypothesis has some relevance to the vole's functional response, if we assume first that abundant, less-preferred wheat is equivalent to intermediate groat density, and second that each centimetre of brushes represents a cue, or stimulus, with a given probability of yielding a grain. However, none of the other studies involved an abundant supply of an alternative less-preferred food, and this model again predicts that the functional response curve should contain a vertical segment when the animal switches from eating both foods to groats only.

Possibility 4 - Rarity

The rarer of several food types may be avoided, irrespective of differences in conspicuousness.

Several studies have shown that a food species may be avoided at low density simply because it is rarer than other food types. While "avoidance of rarity" is a description of the action of any of the mechanisms for generating the POS segment, it is used here as a mechanism in its own right, though the actual psychological basis for this mechanism is not considered.

Manly et al (1972) placed pairs of quail in an artificial arena with pastry cylinders, coloured red or blue, scattered on the floor. The proportion of red and blue prey was varied, with a constant total number, and the birds allowed to feed until half the available prey had been eaten. An index of preference for red was derived, and it was found that the value of this index was positively associated with the frequency of red prey, whereas its value should remain constant if selectivity did not depend on relative frequency. In addition, the index of preference fell smoothly as relative frequency dropped to 0.1, so that the avoidance of red was not confined to the very low frequencies. Similar results have been shown by Allen and Clarke (1969) working with tits, and by Coppinger (1969) for the response of blue jays to insects.

Although this mechanism has been mainly investigated in relation to the maintenance of a polymorphic situation (apostatic selection; Clarke, 1962), it is clearly equally applicable to a situation containing several food species, rather than several morphs of the same species. However, there will be smaller nutritional differences between morphs than between species; it would therefore be expected that specific hunger effects (see section 5.3) would be greater when the food consisted of different species, and this should lessen the avoidance of rare items.

This effect should be time-independent, since it does not depend on a delay in the animal's realising the true food situation. It can also be expected the distance travelled per day should be less when the density of one food becomes lower, since its relative preference should also drop, and less effort would be put into searching for it.

Although the results obtained for the functional response of the bank vole are thus consistent with this mechanism, it is unlikely that this is the main reason behind the vole's POS segment on the functional response curve. First, the above results were obtained with both food types in the same area, and it is not clear whether the same effect would be expected when the two foods were in separate places, for instance when the wheat grains were not placed under the brushes. Second, the mechanism is more appropriate for a rapidly-searching predator than for the relatively slow-moving bank vole feeding under the brushes. Third, specific hunger effects are very marked in the vole situation, especially in relation to absence of groats in the diet.

The remaining possibilities based on knowledge of the behaviour of the feeding animal (5-8), and those based on changes in the food as its density changes (9-12), are not relevant to the present study of the bank vole's functional response, owing to the design of the experiments. They are included here because of their relevance to field studies of the functional response.

Possibility 5 - Area-restricted searching

Area-restricted searching refers to the tendency of some animals to concentrate their search in the area where a food item was recently found. It is possible in some cases that such behaviour may reduce feeding efficiency at low absolute food densities.

Two situations can be envisaged. First, if the animal always manages to eat out a clump, then it will find a relatively larger number of prey items per unit time at higher densities only if the time taken to find the next clump decreases as the size of the clump increases and if the total searching and handling time is independent of the number of items within a clump. Second, the change in the circumference-to-area ratio of a clump could result in the percentage of food items eaten increasing as clump size increases, since the probability of learning the clump would be lowered. A plot of number of items eaten per clump against clump size would then have a positively-accelerated curve tending to an asymptote of 45° passing through the origin. The functional response curve would then also contain a POS segment provided that the time needed to find the next clump was not too great.

The process of area-restricted searching is well documented. Chandler (1969) recorded the movements of syrphid larvae before and after they had made contact with an aphid. He found that the rate of turning increased by up to 200 degrees/min more than the pre-contact rate, the amount of casting (lifting and striking out the front part of the body) also increased, and the speed of movement tended to decrease by about 12%. These three factors would contribute to area-restricted searching. Smith (1971) studied the movements of thrushes searching for natural prey (earthworms) and artificial prey (pastry "larvae"); the earthworms showed a clumped distribution naturally, and in some experiments the artificial prey were distributed in a clumped manner. The birds showed area-restricted searching, mainly through turning more frequently in one direction rather than alternating the direction of their turns. If the artificial prey were distributed in a regular distribution, then the birds no longer showed area-restricted searching, indicating that the behaviour is plastic and readily learnt or de-learnt.

This mechanism would clearly operate in a time-independent manner, since it does not depend on lags in a learning process.

Possibility 6 - Novelty

A food type may be avoided when it first appears due to its unfamiliarity. Once experience has been gained with the food type, it should not consequently suffer proportionally less predation at low densities

Von Uexhull (quoted in Hinde, 1966) records that a hungry toad will only eat earthworm-like objects once it has been forced to eat one earthworm; there is no suggestion that the toad cannot see the earthworm like objects, and the result cannot therefore be explained by the concept of searching image. Rabinowitch (1968) fed captive herring gull and ring-billed gull chicks on one of three foods for five days, then gave a choice of the same food and one other; for both species, about 90% of the birds

showed a preference for the original food, even though two of the foods were the same food dyed different colours. Coppinger (1969) found that blue jays tended to avoid novel insects.
This effect is a time-dependent one, since it would only be expected to operate following an increase in the abundance of a food species from zero, and, at low densities, should eventually be lost as experience with the prey accumulates.

Possibility 7 - Handling experience

The efficiency of handling a food type may increase with experience. Therefore more time is spent handling each item, and less available for searching, when the food type first appears.

Morgan (1972) found that the dogwhelk, Nucella lapillus, took 5 days to drill a mussel when it had had no previous experience, but only 3 days after one month's exposure to the mussels. Norton-Griffiths (1968) studied the feeding technique of oyster catchers, Haematopus ostralegus, feeding on crabs, cockles, mussels and limpets, and found that the speed of opening the shell increased with experience. Similarly, Orians (1969) found that while adult brown pelicans, Pelecanus occidentalis, were successful in 69% of dives on fish, juveniles only succeeding in catching a fish in 49% of dives.

This is a time-dependent effect, but will only result in a POS segment under certain conditions. These depend on the difference between the naive and experienced handling times, the rate of increase in food density, and the rate at which efficiency increases with experience.

Possibility 8 - Social facilitation

A specific food type may only be accepted by an individual if a member of the same species is observed to feed on it. The probability of making this observation depends on the frequency with which the other individual is feeding, which in turn depends on the food's density. Thus, the food will only be consumed by the observing animal at reasonably high densities.

Murton (1971) observed wood pigeons, Columba palambus, feeding in groups on fields containing clover, tic beans, maple peas and sugar beet. Birds were seen to feed on a particular type of food only if another bird could be seen eating the same type.

This process would produce a time-dependent POS segment if the animal perfectly retained a willingness to accept a food type. The effect

> would be time-independent if feed back from other feeding animals was necessary to maintain the willingness to accept the particular type of food.

The next four possibilities involve possible changes in the food supply itself. These possibilities have been largely ignored in field studies of the functional response, though they could be of some importance.

Possibility 9 - Changes in food distribution with density

Predators tend to be more successful when food is distributed in a clumped than in a regular distribution (Tinbergen et al, 1967; Horn, 1968). Therefore a feeding animal will be relatively more successful at higher food densities if the food's distribution becomes more clumped at higher densities.

> Kershaw (1959) found evidence which can be interpreted as showing that Dactylis glomerata becomes more clumped in distribution as its density increases. Dixon and Logan (1972) found that aphids tend to be more closely packed together on leaves at higher densities, both in the field and the laboratory.

Possibility 10 - Changes in prey anti-predator responses

Many prey show anti-predator responses. If this response becomes less efficient at high prey densities, the predator will be able to eat relatively more at the higher densities.

> Wellington (1964) found that the Western tent caterpillar is more sluggish at high densities, and therefore more susceptible to predation.

Possibility 11 - Changes in degree of prey protection

If the prey population normally occurs in an area which is relatively inaccessible to the predator, and only extends into more exposed areas as the density increases, then the predator's searching efficiency will increase at the higher food densities.

> This possibility has been discussed by Andrewartha and Birch (1954), and Wynne-Edwards (1962), and there appear to be many instances when surplus individuals are forced to occupy less favourable areas.

Possibility 12 - Changes in the density of alternative foods

If the density of an alternative food source decreases at the same time as the density of the food under consideration increases, then this will cause relatively more of the latter to be eaten as its density increases, because it will be encountered relatively more frequently, or because it will become less worthwhile to search for the alternative.

That the composition of an animal's diet varies because of fluctuations in the availability two or more food species has been recognised by many workers studying the feeding habits of animals in the field (e.g. Watts, 1968 for voles; Hunter, 1954 for sheep; Royama, 1970 for tits). However, the explanation of, for example, a POS segment in the functional response has usually been put forward in isolation from variation in the density of other foods. There is in fact no accepted method for dealing with a multi-food situation with the density of several foods changing simultaneously, apart from Holling's (1965) model based on specific attack thresholds, and a nutrient optimisation approach (Westoby, 1974), which only applies if all foods are easy to find in the required quantities. Changes in the density of an alternative food could result in a POS segment in the response to a specific food, though the quantitative way in which this happened would depend on other response mechanisms.

The remaining two ways of accounting for the POS segment of the functional response are not based on known biological facts, but rather are derived theoretically from assumptions about how the feeding animal could behave, or in the case of optimisation models, about how the animal should behave in order to maximise some factor.

Possibility 13 - The free-time feeding model

Any model, such as that of Royama (1960), which results in an animal spending more of its total feeding time searching for a specific food type as the density of the food increases, will generate a POS segment on the functional response curve for that food. The model proposed below shows that such a response can be generated from very simple assumptions about the animal's behaviour.

If it is assumed that the animal has a certain number of hours per day that it can devote to feeding (the total feeding time), and that a certain number of hours (the minimum feeding time) would be needed if the animal fed only on an abundant, less preferred food, then the difference between the two represents time which is available for feeding on a preferred food of variable density. This difference is termed the free time. If preferred food is found during this time, then less time needs to be set aside for eating the less preferred food, since part of the animal's daily requirement would already have been satisfied. This effectively creates more free time, during which the animal can again search for preferred food, thereby creating more free time, and so on. For any day, the total amount of free time will represent the sum for an infinite number of terms of a series, each term of which represents the additional free time created by the food found in the preceding free time.

It is clear that if each free time period creates an even larger subsequent amount of free time, then the series has terms which increase in magnitude, and the sum of the series is infinity. Even if succeeding terms get smaller, the sum of the series could still be greater than the total feeding time. Thus, total feeding time imposes a constraint on the total amount of free time. What is of interest is the behaviour of the model when the sum to infinity is less than the total feeding time. In particular, does a doubling in food density result in a precise doubling in the amount of free time, and therefore in the amount of the preferred food eaten (assuming a simple search model)? The answer is that the increase in free time is relatively greater than the increase in food density, and the model thus predicts that the functional response curve should contain a POS segment, rising to the density corresponding with the point at which free time equals total feeding time; above this point, the functional response curve should rise linearly until a maximum limit set by the plateau rate of intake.

The model as proposed above is intuitively pleasing, since it would be to the animal's advantage to behave in this manner, but it is unlikely that animals can operate in this way. It is therefore interesting to find that the model can be re-cast in terms of a precise physiological mechanism. Let us assume a simple model of the hunger mechanism, such as that proposed by Holling (1965), with a single hunger variable moving across attack thresholds, one for each food type; the more preferred the food, the lower its threshold. Let us further assume that the hunger level is always above the threshold for the variably-abundant preferred food, so that it will always be eaten when encountered, but that it starts off below the threshold for the abundant less preferred food. For the sake of simplicity, the hunger level is assumed to rise linearly in the absence of intake, but the results of the model do not depend on this. Then any decrease in the rate of rise of hunger with time, resulting from an increase in food density, means that it takes longer before the threshold for the less preferred food is reached; therefore fewer items of the less preferred food will be eaten in the course of a day, and the time that was required for that is now released for feeding on the preferred food. Thus, this version of the model also predicts that the functional response curve should contain a POS segment.

It should be noted that the criticism of Holling's model of hunger and thresholds (section 5.3) does not apply here; the model is not being used here to generate individual feeding events, but in a qualitative way, to represent the fact that less preferred foods are more likely to be eaten when the animal is hungry (Ivlev, 1961).

Possibility 14 - Optimisation models

In attempting to predict how an animal should behave, rather than making deductions from known facts about the animal's behaviour, the optimisation model reflects the belief that an animal species, as the product of natural selection, behaves in a way which is most advantageous to members of the species. There are five features of optimisation models which are worth emphasising.

(i) the approach is normally limited to one aspect of the animal's behaviour, in this case its feeding behaviour. Since the justification of the optimisation is through the assumption of fitness through natural selection, we need to be sure that the optimum values determined by such a model do not lower fitness in other areas; for example, increase susceptibility to predation.

(ii) normally one factor is optimised, usually net calorific gain (Krebs, 1973). It seems likely that in practice the intake of many nutrients is crucial to the animal; to accomodate these would require re-stating the factor to be optimised as "gain in body weight" or "number of offspring reaching maturity", which renders the problem intractable using current models.

(iii) in assuming that the animal has perfect judgement (MacArthur and Pianka, 1966; Emlen, 1966), no account is taken of the way that the animal adjusts to a new situation, nor of the fact that the animal's strategy may require sampling unprofitable areas in order to be able to respond to changes when they come (Royama, 1970).

(iv) following from (i) above, parameters whose values are assumed to be fixed during feeding, for example, total time available for searching, may themselves be subject to optimisation in the wider context of an animal's fitness.

(v) the more obvious biological features of a system are readily accepted, for example, handling time and speed of movement are not thought to be capable of further improvement. If this assumption was not made, optimisation would require zero handling times and infinite speed of movement. How many other biological realities of a system are ignored?

The main parameters in such models are the animal's speed of movement and energy expenditure per unit distance, and, for each food type, its calorific value, its handling time (pursuit and consumption time), and its density (or some correlate of density). The parameter set to be optimised is the probability that a particular item will be selected when encountered, which is a continuous variable in the model of Emlen (1966), and a binary variable in the model of MacArthur and Pianka (1966); or, as in the latters' patchy environment model (ibid) and Royama's (1970) model, the probability that a particular patch or niche will be exploited.

Optimisation models can be used to generate a variety of quantitative and qualitative predictions. The discussion will be limited here to qualitative predictions related to two features of the present experimental studies. In cages, voles were presented with groats and wheat in ad lib. conditions. All models, apart from the linear programming type of Westoby (1974) which is not relevant to the POS segment, predict that only one food should be eaten. In fact, very few voles restrict themselves to groats only (section 4.5.1); most take between 10% and 40% of daily intake as wheat. Thus, optimisation models based entirely on energy balance are inadequate.

The other situation is the one used in the functional response experiments, in which wheat was always very abundant, and the density of groats was varied. The model of MacArthur and Pianka (1966), when adapted to this situation, predicts that, at low groat densities, the animal should eat both foods when encountered, but should eat groats only at higher densities, since then the increase in handling time associated with the decision to eat wheat would be greater than the decrease in mean search time arising from such a decision. The functional response for groats should then have an initial LIN segment followed by a vertical rise to the plateau level. It should be noted that the response to groats is constant, and that wheat is either always or never taken when encountered; in addition, this version of themodel only applies to the case of wheat distributed with the groats, and the sharp increase in groats eaten is due entirely to the saving in wheat handling time. An extension of this model to deal with a patchy environment in the same paper also predicts that the functional response for groats should include a POS segment, this time in connection with the wheat distributed outside the brushes. In this case, the model predicts that the groat "patch" will be avoided at low groat densities, used together with the wheat at higher densities, and used exclusively at higher densities; this should accentuate the POS segment. Similar results are predicted by Emlen's (1966) model for non-patchy distributions, except that in this case the transitions between the different strategies is not abrupt.

The predictions of optimisation models thus are in broad agreement with these experimental results. It is unlikely that the whole of the POS segment can be attributed to this: the transitions are not sharp as predicted, and it is unlikely that the time for extra searching under the brushes comes entirely from time saved on handling wheat grains. In addition, such models do not indicate mechanisms, (Krebs, 1973), and if the models do agree with observation, it is still necessary to determine the behavioural mechanism involved.

6.3 Conclusions

This study of the bank vole's functional response has revealed several features of interest. First, the addition of the index of distance travelled to the description of functional response has provided information which is incompatible with the qualitative predictions of some of the models discussed in section 6.2.

Second, the careful planning of the groat density schedule has permitted the detection of lag effects which can significantly affect the vole's response. These are most dramatically seen following a large step decrease in groat density, but can also be seen as differences between periods of rising and falling groat density.

Third, the study of various aspects of the vole's feeding has revealed a large amount of detail (for example, on hoarding and drinking) of potential relevance to the formulation of an adequate functional response model.

Fourth, the ease with which the main components of the functional response can be identified (section 5) contrasts with the difficulty of constructing sub-models of the three intervening components with any degree of confidence. Only in the case of the hunger component was it possible to develop such a sub-model in outline, and this relied for its structure more on odd pieces of information gathered from the literature than on a formal set of experiments.

Fifth, the qualitative models for segments of the response curve (section 6.2) are either found to be untestable in practice, because of their vagueness (Krebs, 1973), or else are found to be wanting when tested against descriptions of the functional response involving supplementary detail. Nevertheless, the approach of considering the response curve as consisting of a number of segments appears to be useful, and the qualitative models do provide an indication of which aspects of the animal's behaviour to analyse in more detail.

The question then arises: How much detail in a model of the functional response is needed in order to provide a satisfactory model? As with any other model, the first stage in the modelling process is to state one's objectives. In section 1, it was argued that the ultimate function of a functional response model is in the context of population dynamics, both in terms of the direct effect on the food species, and the indirect effect of food quality and quantity on the survival and reproductive success of the feeding animal. So the minimum requirements for such a model are that it should be capable of predicting the number of food items consumed per unit time; from these it is simple to calculate the benefit to the feeding animal.

By making the description of the response more complete (by, for example, including the index of distance travelled), the possibility of detecting the operation of important factors may be increased, but there is the danger that the model may then be expected to do more than is needed. Similarly, the analysis of feeding behaviour and of the components of the functional response may provide more than the minimum information required. Thus, we can ask whether the model should be capable of generating the vole's feeding bout patterns in order to provide a satisfactory model of the functional response system.

Paradoxically, it is likely that the more realistic a model is, in terms of representing "irrelevant" aspects of feeding, the more general it becomes, since it is then formulated in terms of behavioural and physiological mechanisms common to a range of species, rather than simply being an elaborate curve-fitting operation.

A reasonable approach would be to obtain a fairly full description of an animal's response, using more than one measure of the response, and then to analyse this in a qualitative manner to decide which of the potential response components need to be included. Only then need one undertake the additional experimental work required adequately to represent the particular components.

The present study has indicated that the distance travelled per day - and thence the time spent searching per day - is the main determinant of the bank vole's functional response. Analysis of the distance-travelled response curve and the functional response curve itself showed that all four segments of the response could be present: a positively-accelerated segment, a linear segment, a negatively-accelerated segment and a plateau. In addition, the vole's response on any day could be influenced by the food conditions on preceding days. These results can only be satisfactorily modelled if the three intervening components of hunger, specific hunger and learning are included. More work needs to be done on the modelling of these components, in a realistic but economical manner.

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Appendix A1

Rejected methods for measuring the functional response of the bank vole.

The following methods were tested in the same room as was used with the "brushes" system (section 3.3.2).

Method 1 - The barley-straw method

The floor area was covered in eight frames of wire-netting, filled to a depth of approximately 10 cm with barley straw. Each day, groats were scattered under the straw, and an abundant supply of wheat was placed near the nest-box. Grain from the previous day was recovered by lifting the frames, sweeping up all the debris on the floor, then sorting out the grain.

The following difficulties were encountered:

a) Barley grains were recovered for the first 15 days.

b) The vole readily found over 90% of the groats available.

c) It was difficult to ensure that the vole was not nesting and hoarding in the straw.

The vole was exposed to groat densities ranging from 50/total area to 200/total area, but the fact that such a high percentage of groats was found means that little can be gained from presenting the results.

Method 2 - The grass/peat method

An area measuring 105 cm by 60 cm was covered in artificial (hessian) grass. The groats were placed in this, and covered with 5 cm of fine peat. Each day all the peat was collected and sieved to recover the groats.

A vole was tested for four days, with 100 groat grains under the peat and ad lib. wheat near the nest-box. After the first day, the vole found between 51% and 57% of the available groats.

There were three main draw-backs with this method:

a) The conditions were considerably different from the vole's normal feeding conditions.

b) A large amount of peat (c. $0.6m^3$) would need to be sieved each day, assuming an area of 3 m^2 was used in order to ensure that the vole found only 10% of the groats.

c) The danger of introducing a two-day cycle into the schedule, since two lots of peat would be needed owing to the time needed to sieve one day's peat.

This method was abandoned after the four days.

Method 3 - The wood-chippings method

The total floor area was covered by eight wooden frames. Each frame was covered with ½" nylon mesh on the sides and bottom, and filled to a depth of 10 cm with wood-chippings. The daily procedure was the same as for the barley-straw method. To separate the grain from the chippings which had fallen through the mesh, the recovered debris was put into water, with the grain falling to the bottom.

One vole was exposed to 6 density levels, ranging between 80 groats/total area and 1200 groats/total area. In the first period, each density was maintained for 3 days, 2 days in the second period, and 1 day in the third. Within each period, the density level was assigned randomly.

The resulting functional response curve is shown in Fig. A1-1. The curve appears similar to Holling's type 2, functional response curve (1965), though closer inspection would suggest an initial linear rise, followed by a slower rise to the plateau. At the two lower densities, an average of 40% of the groats are eaten, with a maximum of 63%. Since it is not known whether the vole is searching randomly, the results for these two densities could be an under-estimate of the vole's "true" response. However, applying a correction for random search should not affect the linearity of the initial rise.

There was no evidence for an initial positively-accelerated rise to the functional response curve, but this could be because the lowest density was too high.

This method was an improvement on the preceding two, but some problems still remained:

a) The vole still could find a fairly high proportion of the groats. Since there was no way of telling whether the vole was searching randomly (unlike the brushes system), this affected the interpretation of the functional response curve.

b) The relative ease of finding grains also meant that only one vole could be used in the room available at any one time.

c) The method of separating out the grain was time-consuming, and soaking the grains could have had an unknown effect on them.

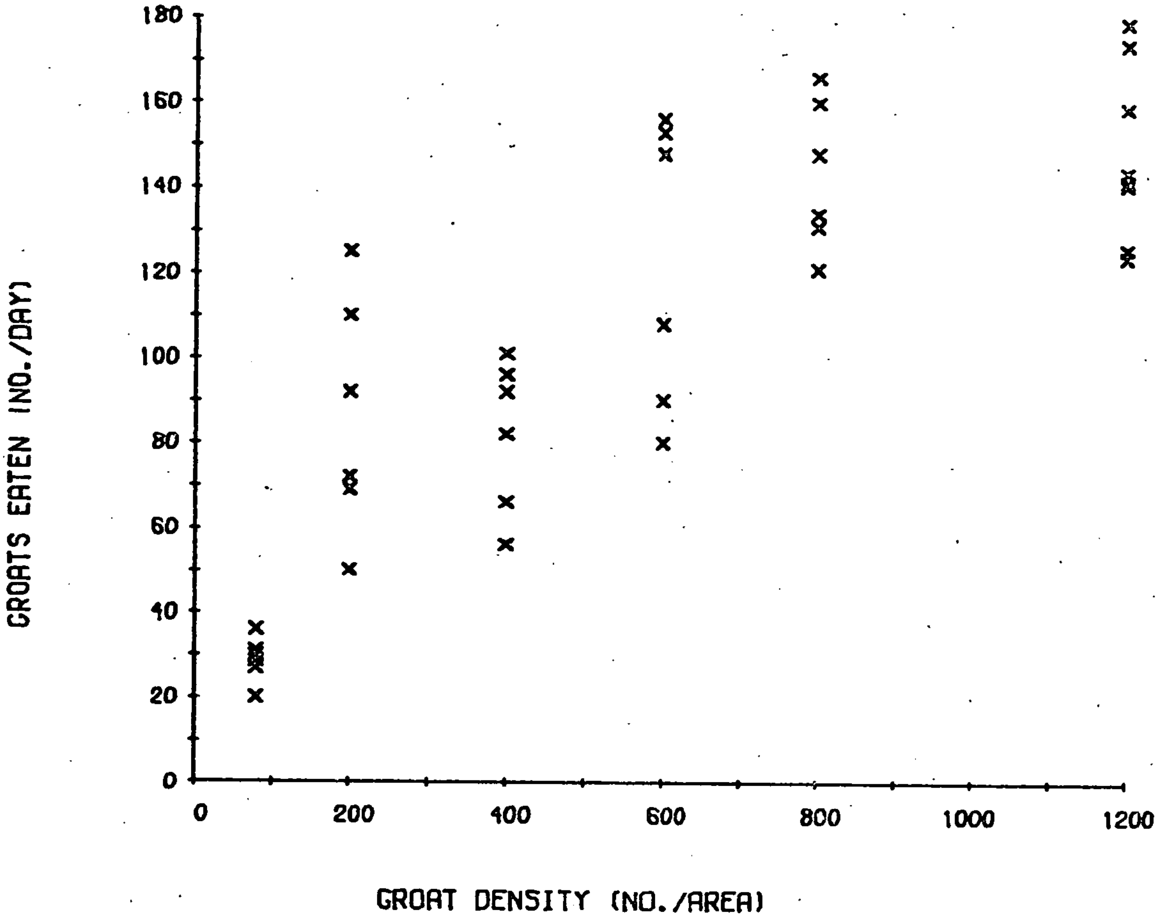


Fig. A1-1

Functional response curve for groats using the wood-chipping method.

d) Hoarding could have been difficult to detect, although the vole tested did not appear to hoard wheat or groats.

Appendix A2

Test for randomness of groat distribution in functional response experiments.

347 groats were scattered over an area measuring 80 cm by 110 cm. The area was divided into 88 squares, each measuring 10 cm by 10 cm, and the number of grains in each square was counted.

Results

1 - Overall test of homogeneity.

The frequency distribution of counts was compared with that expected from the Poisson distribution.

Count	Observed frequency	Expected frequency
0	0	1.70
1	7	6.72
2	16	13.25
3	14	17.43
4	18	17.19
5	14	13.56
6	14	8.92
7	2	5.02
8	1	2.48
9	2	1.09

Lumping counts (0,1) and (7+) gives $\mathrm{Chi}^2 = 6.19$, with d.f. = 6, which is not significant.

I conclude that on this basis the grains are distributed randomly.

2 - Edge effect.

The number of grains in the squares on the edge of the area was compared with the number in the internal squares.

	Number of squares	Number of seeds Obs.	Number of seeds Exp.	Mean number of seeds
Edge	34	99	134	2.9
Internal	54	248	213	4.6

$\text{Chi}^2 = 14.9$, with d.f. = 1, which is highly significant. I therefore conclude that the density of grains on the edge strip is significantly lower than further in, being approximately 63% of the internal density.

3 - Distance from position of dispersal.

I compared the number of grains in the half of the area nearest to me with the number in the other half.

	Number of squares	Number of seeds Obs.	Number of seeds Exp.
Near	44	165	173.5
Far	44	182	173.5

$\text{Chi}^2 = 0.84$, with d.f. = 1, which is not significant at the 10% level. I therefore conclude that there is no difference between the two halves.

Appendix A3

The automatic feeder.

The automatic feeder was designed to provide a continuous record of a vole's selection of groat and wheat grains. The equipment consisted of four functional blocks.

The seed holder

This consisted of two identical perspex units (Fig. A3-1). Each unit had a hole, U-shaped in cross-section, designed to hold one groat or wheat grain. A small aperture at the base of the hole led to a photocell, which was connected to the snap-action amplifier. Above the seed hole, a speed reducer broke the fall of a grain arriving from the dispenser. A light over the seed hole was capable of triggering the photo cell only when it was not covered by a seed.

The snap-action amplifier

The electronic circuit (Fig. A3-2a) was designed by Mr. Richard Scott. Input from the photo cell was thus amplified and passed on in an all-or-nothing manner to the seed dispenser and the event recorder.

The seed dispenser

When triggered by the photo cell via the amplifier, a reed relay provided mains current for a clock motor (12 revs/min). This rotated a drum, which contained up to several hundred seeds

(Fig. A3-3). Three holes were set in around the drum rim, which were capable of picking up a grain and then dropping the grain out in the top position. The grain landed on a slide from where it fell into a funnel, down a plastic tube and into the seed holder. The arrival of a seed covered up the photo cell, thus switching off the seed dispenser.

The event recorder

This was an eight-track recorder, with both motor and relays operating at 12 volts. Paper speed was approximately 15 cm/hr. The trace was recorded on the pressure-sensitive paper by a fine needle attached to each relay, permitting measurements to be taken to the nearest 0.1 mm. This gives a nominal accuracy of approximately 2.5 sec. All readings were made relative to clock marks supplied to each channel every hour, thus eliminating error caused by differences in the relative position of pins for the separate channels, and by variations in the paper speed.

Seed holders were constructed for four voles, requiring eight channels through the emplifier, eight seed dispensers and the eight channels on the event recorder. Fig. A3-4 shows a general view of the complete arrangement. Although the equipment was used continuously for three months, frequent malfunctions (seeds jamming in the delivery tube, debris over the photo cell) meant that few long uninterrupted records were obtained).

The wheat and groats used in the equipment were selected to be of uniform size, with approximate weights 45 mg and 30 mg respectively. The equipment was tested by taking 200 grains of each type from the seed holder, and recording whether

a) one seed was delivered correctly,

b) a grain fell from the dispenser but not into the seed tube,

c) two grains were delivered,

d) a grain fell into the seed holder but jumped out.

The results are summarised below.

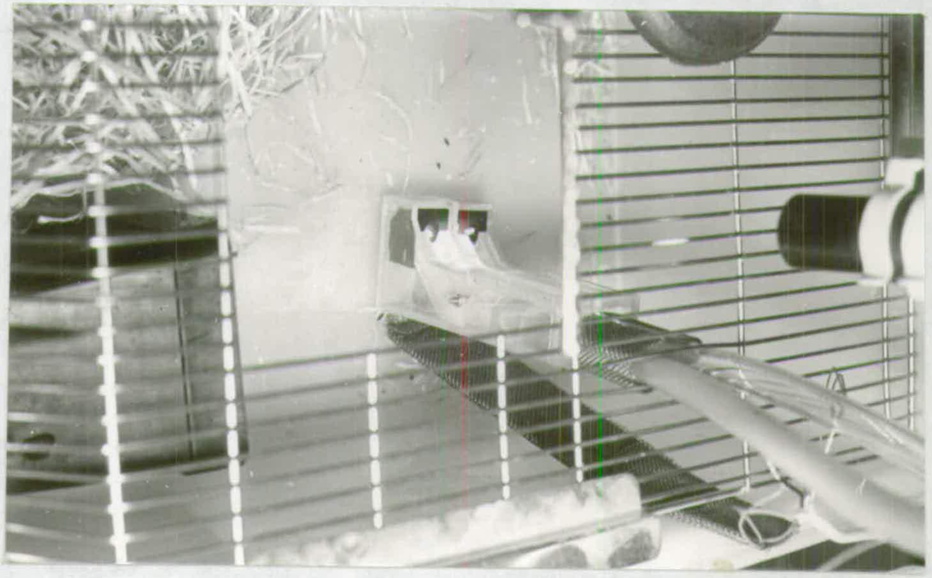
Result	Wheat	Groats
a	187	192
b	9	1
c	3	7
d	1	0

Grains in category (d) are unlikely to distort the vole's feeding pattern (only occasionally did a grain fall into the cage), so this represents a reasonable performance.

The event recorder could also be used for simultaneously monitoring drinking, as described in section 4.7.2. The circuit diagram for the circuit involved is given in Fig. A3-2b. In this case, output was to the two channels on the event recorder allocated to each vole, to avoid ambiguity between grain selection and drinking traces.

Fig. A3-1

View of seed holder, showing a wheat and groat grain in each seed hole, the grain delivery tubes leading into the speed reducer, and the light source.



Component list for snap-action amplifier.

Transistor	T1	BC107	Resistor	R1	4.7 K
	T2	BC107		R2	4.7 K
	T3	BC107		R3	4.7 K
	T4	BFY51		R4	10 K
Photocell	P1	P20		R5	4.7 K
Diode	D1	IN914		R6	15 K
				R7	1.1 K
				R8	220 K

A - A Output to event recorder and need relay.

Component list for drinking detector.

Transistor	T1	BCY70	Resistor	R1	680 K
	T1	BFY51		R2	100 K
Diode	D1	IN914		R3	4.7 K

A - A Output to event recorder.

B - B Input from terminals, one in water bottle and one connected to metal gauze under water bottle.

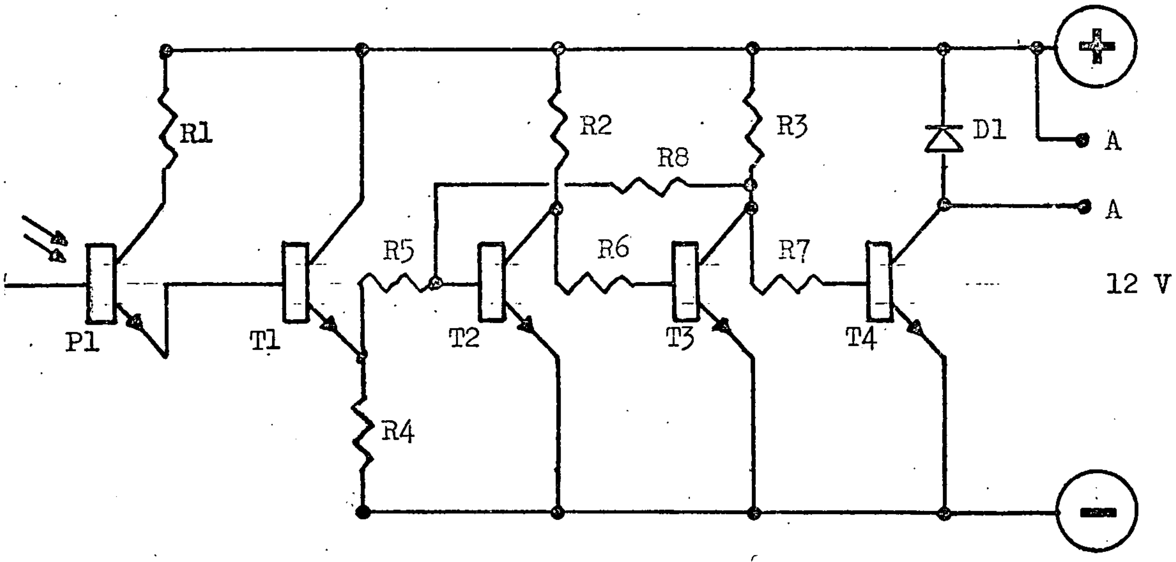


Fig. A3-2a

Circuit diagram for snap-action event-recorder and reed-relay operator, using input from photo cell.

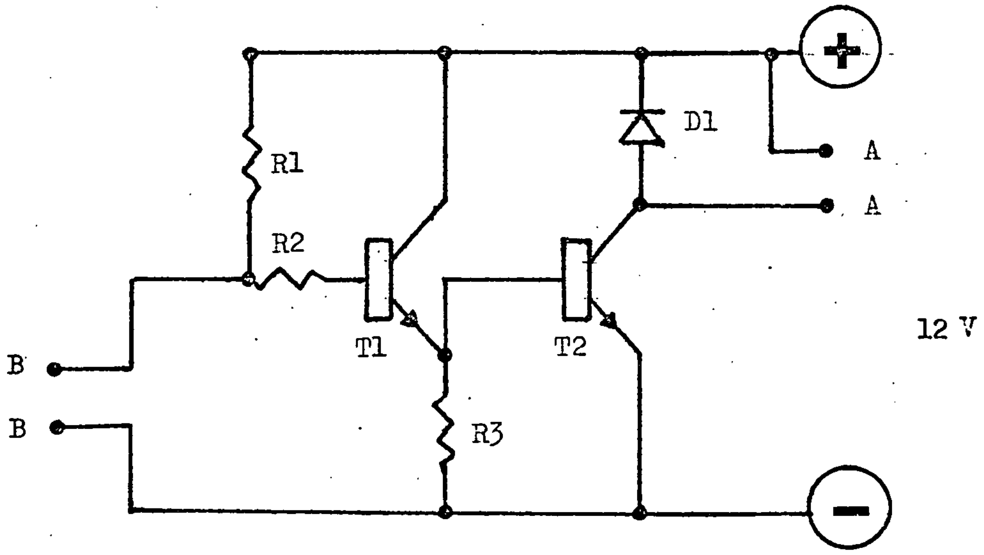


Fig. A3- 2b

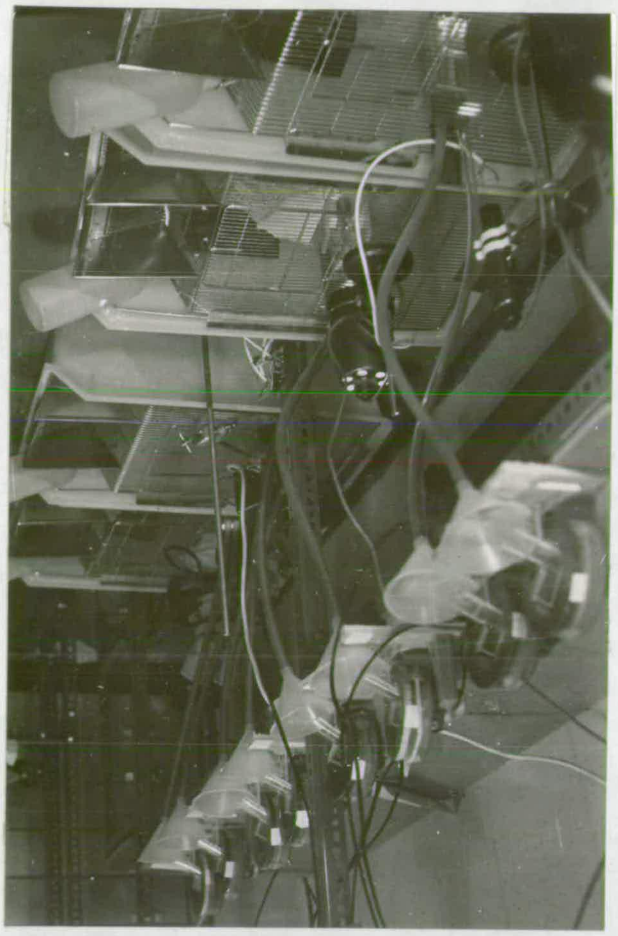
Circuit diagram for drinking detector.

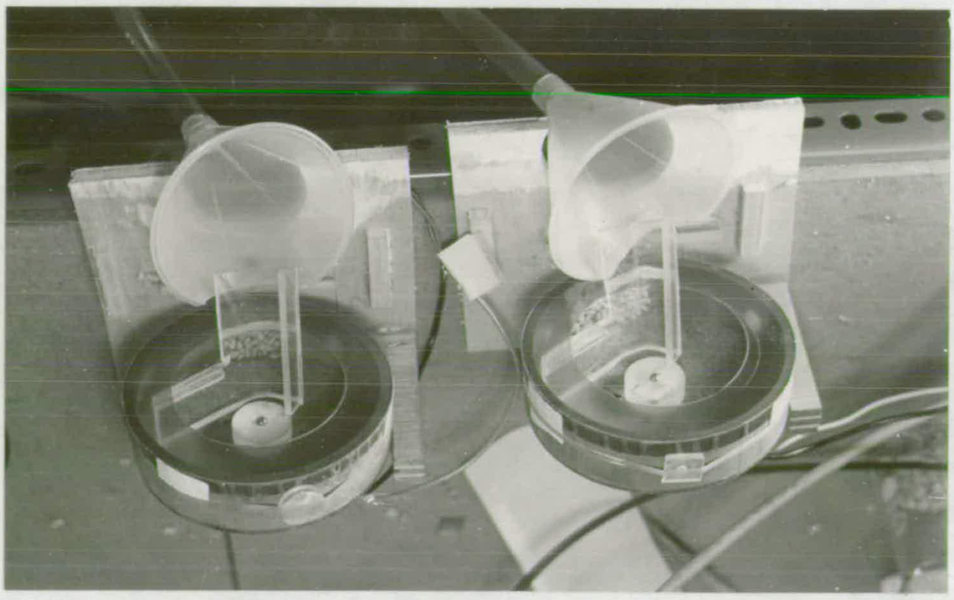
Fig. A3-3

View of a pair of seed dispensers, showing drum containing seed, pick-up points on drum rim, and funnel leading to delivery tube.

Fig. A3-4

General view of the automatic feeder arrangement, showing four cages each with a wheat and a groat channel.





ABSTRACT OF THESIS

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Title of Thesis The functional response of the bank vole, Clethrionomys glareolus (Schr.), to food density.

The aim of this work was to investigate the relationship between food consumption and food density in the bank vole, Clethrionomys glareolus (Schr.). This relationship is known as the functional response, and has importance for the population dynamics of the food and the feeding populations, and for the pattern of energy and material flow through a community.

The first part of this work was to describe the response of the bank vole to changes in the density of a preferred food (groats, or huskless oat grains), in the presence of an abundant supply of a less-preferred food (wheat grains). A system (the "brushes" system) was devised which met the opposing requirements of ease of handling by the experimenter, and difficulty of searching by the vole. This system also made it possible to measure the distance travelled by the vole in search of its food. It was found that voles settled to the system in 2-3 days, though some subsequently showed long-term changes over the course of the experiment. Voles responded to a sudden removal of groats by a temporary increase in the daily distance travelled; thereafter, travelling through the area was maintained at a low level. Voles appeared less willing to search for groats when wheat was scattered with the groats, rather than separate. The data could be used to estimate the vole's reactive distance for groats, at 2-4 cm. The functional response curve showed four features, for some or all of the voles: a region of constant groat intake, and regions of a linear rise, a negatively-accelerated rise, and a positively-accelerated rise in the response curve. Distance travelled was depressed at low groat densities. The response during periods of falling groat density was higher than during periods of rising groat density. At intermediate densities, differences were found between the first and last day at each density. Quantitative features of the response curve are also described.

To provide background information on the feeding mechanism, aspects of feeding behaviour are considered. Vole feeding and searching behaviour are described. Stability, regulation and temporal patterns on consumption and preference were investigated. Restriction to wheat was found to increase the subsequent relative preference for groats. Aspects of hoarding and drinking were studied. As a first step in analysing the functional response mechanism, the main components of the response were identified and investigated. Three intervening components (having an indirect effect on the feeding response) were considered - hunger, specific hunger and learning - and three direct components - speed-of-movement, handling time and reactive distance. A theoretical model of the hunger system was derived, and the component was investigated experimentally: at least two state variables were deemed necessary to represent this component. Fine-scale analysis of the pattern of selection following limitation to wheat led to the conclusion that specific hunger operates on the peripheral sensory, as well as on the metabolic levels.

Use other side if necessary.

The nature of the learning component was deduced from the functional response experiments, and the difference between extinction and forgetting of a learnt response is stressed. Speed-of-movement in the brushes system was found to be 2-4 cm/sec. Handling time for groats and for wheat was approximately 0.75 minutes and 2.0 minutes. The reactive distance for groats was measured experimentally as being approximately 4 cm. There was little evidence for a marked effect of the intervening components on the direct components, though it was not always possible to test for this. Various possible qualitative explanations for the presence of particular regions on the functional response curve are discussed, and a speculative but plausible model to account for the positively-accelerated region is proposed. It is concluded that the inclusion of the three intervening components greatly increases the difficulty of modelling the functional response.