PROCEEDINGS OF THE NUTRITION SOCIETY
A Scientific Meeting was held at the University of Strathclyde on 29/30 March 1990

Symposium on 'Diet selection'

Diet selection by animals: theory and experimental design

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In nature many animals are faced with a variety of foods some of which they are able, and prepared, to eat. As the foods may differ in their nutritional value the diet that the animal attains will vary with the selection made from the foods on offer. Diet selection is thus a problem that the animal has to solve. The scientific problem is to invent a theory which will successfully predict, across a set of relevant cases, the solutions that the animal will find to its problem.

The relevant variables to be considered in the theory of diet selection are the animal, the environment within which the animal is kept, and the characteristics of the feeds on offer. In the present paper attention is concentrated on the food variables which may be relevant to experiments on domestic animals which are kept in homogeneous environments and given two, or more, homogeneous feeds of different composition. The geometry of feed mixtures, following Parks (1982), is emphasized.

FOOD COMPOSITION

A conventional description of the chemical composition of a food is shown in Fig. 1. It is set out in a way that emphasizes that the food is a mixture. The food is, first, a mixture of dry matter and water with the water as a homogeneous component. The dry matter is a mixture of ash and organic matter with the ash seen, in turn, as a mixture of particular

Water			
Dry matter:	Ash		
	Organic matter:	Protein	
		Fat	
		Carbohydrate	
Ash: Specific minerals			
Protein: Amino acids			
Fat: Specific composition			
Carbohydrate: Specific carbohydrates			
Vitamins			

Fig. 1. Conventional food composition as a mixture.

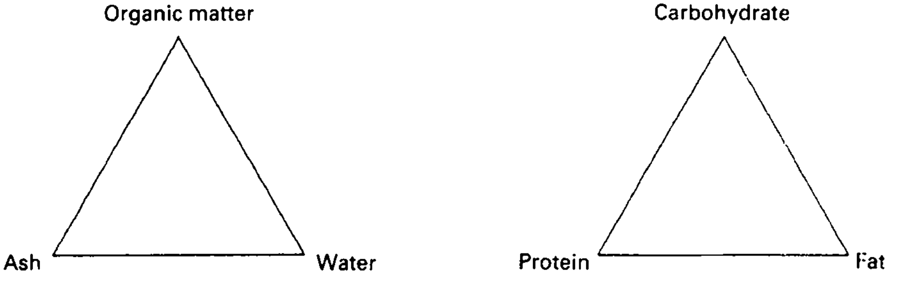

Fig. 2. Three-component food mixtures.

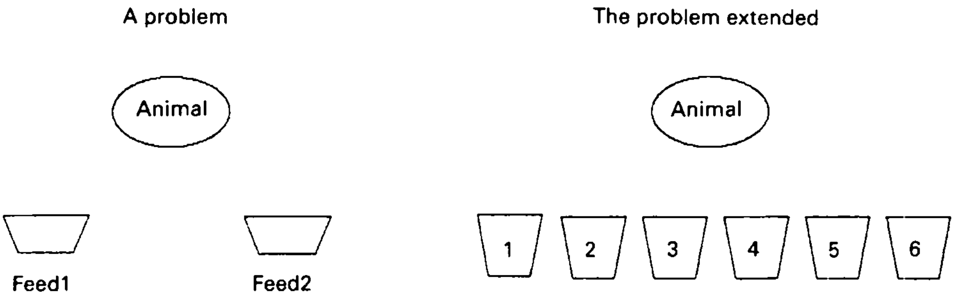

Fig. 3. The simplest, and a more complex case of the problem of diet choice.

minerals. The organic matter is a mixture of protein, lipid and carbohydrate with all three components seen, in turn, as mixtures of particular sub-components. An important point about a mixture is that no one component is independent of the others. It is not possible simply to increase the proportion of a component: its content can be increased only by substituting it for one, or more, of the other components of the mixture.

A one-component mixture can be represented as a point and a two-component mixture as a line. Where the mixture has three components it can be seen as an equilateral triangle (Fig. 2). Examples of such three-component mixtures which are relevant are: water, ash and organic matter in the total feed; protein, fat and carbohydrate in the organic matter and these three as digestible components in the digestible organic matter (Fig. 2).

FOOD CHOICES

The simplest case to consider is that where an animal is given free and continuous access to two foods as shown in Fig. 3. More complex cases are produced by increasing the number of foods as is also shown in Fig. 3. It is sensible to try to invent theories about the simplest system before moving to the more complex but, to make a point, a three-food system is considered first to relate the idea of the food as a mixture to the problem of diet selection.

Fig. 4 shows food as a three-component mixture (the dimensions could be seen as water, ash of a given composition and organic matter of a given composition, where an animal is given no water other than that in the food).

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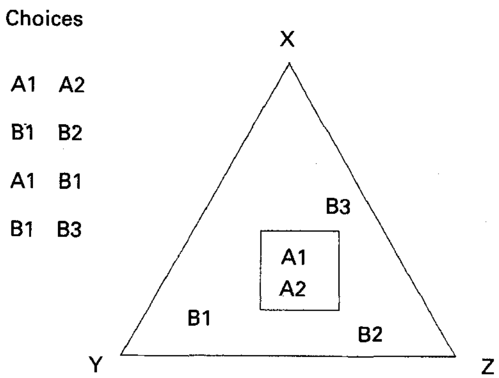

Fig. 4. Two-way choices between foods in a diet composition space.

When foods are given alone it may be found that those in some sub-space of that in Fig. 4 allows the animal to be successful while those outside this sub-space do not. (Where the dimensions are sensibly chosen it seems intuitively obvious that the adequate sub-space will be a single area rather than a set of non-contiguous areas.) The animal is now given free and continuous access to two foods the compositions of which are represented as points in the total space; a given food may be in the adequate sub-space, or not. As shown in Fig. 4 there are several possible kinds of food pairs:

(1) foods A1 and A2 are both in the adequate sub-space and the composition of the diet selected must be an adequate one whatever choice the animal makes,

(2) foods A1 and B1 lie in two different sub-spaces. The animal could choose a diet of adequate composition,

(3) foods B1 and B2 both lie in the inadequate sub-space and the line joining them does not pass through the adequate sub-space. The composition of the diet selected by the animal will be an inadequate one whatever choice it makes,

(4) foods B1 and B3 both lie in the inadequate sub-space but the line joining them passes through the adequate sub-space. It is, therefore, possible, but not certain, that the diet selected by the animal will be adequate in its composition.

TWO SIMPLE THEORIES OF DIET SELECTION

We can imagine two very simple theories of diet selection. The first states that the animal, when given two foods, will always eat equal amounts of each and hence, that the composition of its diet will be (0·5A + 0·5B) where A and B are any two foods. The theory applies to all experiments where an animal is given two foods. It has the considerable merits of being simple, explicit and extremely powerful. Unfortunately it is false. Since it has no general validity it is important to examine carefully experiments where the outcomes are consistent with it.

The second simple theory states that when an animal is given free and continuous access to two foods it will always show an absolute preference for one over the other. The composition of the diet that it selects will be (1·0A + 0·0B) or (0·0A + 1·0B). It is a powerful theory, but not as powerful as the first one as it does not state which of the two outcomes that it allows will occur. It can be made richer by adding the condition that all

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choices are transitive, i.e. if food A is preferred to food B and food B to food C then food A will be preferred to food C and so on. Were this theory to hold then the problem of diet selection would become that of finding some rule, or rules, for ranking foods in terms of the animals' preferences. Given such a rule, or rules, the more preferred of any food pair could be predicted and the outcome of any choice feeding experiment with two foods also be predicted.

The second simple theory is also false. In at least some cases an animal given two foods will eat some of each of them: it appears to behave as if its preference were for some mixture of the two rather than either of the foods alone. A simple example is that of an animal given a dry food and water which it would be expected to both eat and drink.

THE ANIMAL

One of the components in the system of interest is the animal. In order to predict the outcomes of an experiment using some theory it is necessary to have descriptions of the system which are sufficient for the theory to be used. Those working in the field of diet selection have, in general, given much more attention to describing the foods used than to the animals. Descriptions of the foods used may occupy several tables in a paper; the description of the animal may only be as a species name although an initial age and weight are often given. It would appear necessary to give as much attention to the description of the animal as to the foods used if theories of diet selection are to be invented that are useful. As with the foods the description of the animal needs to be one that is sufficient in the light of some theory and will depend on the theory that is being used or invented.

It is not appropriate to the present paper to do more than suggest at least some components of such a description of an animal. The problem has been approached elsewhere (Emmans, 1988). It needs to be a means of predicting, for a given animal in a given state, its rates of maintenance, growth and production, and the compositions of the growth and production, where neither the diet nor the environment are such that the animal is constrained by them. The diet that the animal needs is then that which it needs to attain that performance; this diet will have a particular composition.

It would appear that, without such a description of the animal, it is not possible to make quantitative predictions of the composition of the diet that it will select when given a choice between different foods. During the course of an experiment the state of the animal, in the usual case, will be continually changing. If the composition of the diet that it selects is presumed to be some function of its state, as would seem to be reasonable, then the composition of the diet selected will also change with time. Fig. 5 shows the change in the composition of the diet selected by an animal given a food A and another one. The composition of the diet selected is expressed as the proportion of A in its total intake. As Fig. 5 is drawn there is a time, or animal state, at which the animal eats equal quantities of each food. Since it can clearly detect a difference between the two foods before and after this time it is to be expected that it can also detect a difference at this time. That it eats equal quantities of the two foods is then most simply interpreted as its having a preference for a diet which contains half of each feed. The alternative explanation, given that it can detect a difference, that it simply has no preference for one feed over the other, seems less satisfactory.

A picture of the change in diet selection over time, such as that in Fig. 5, is clearly

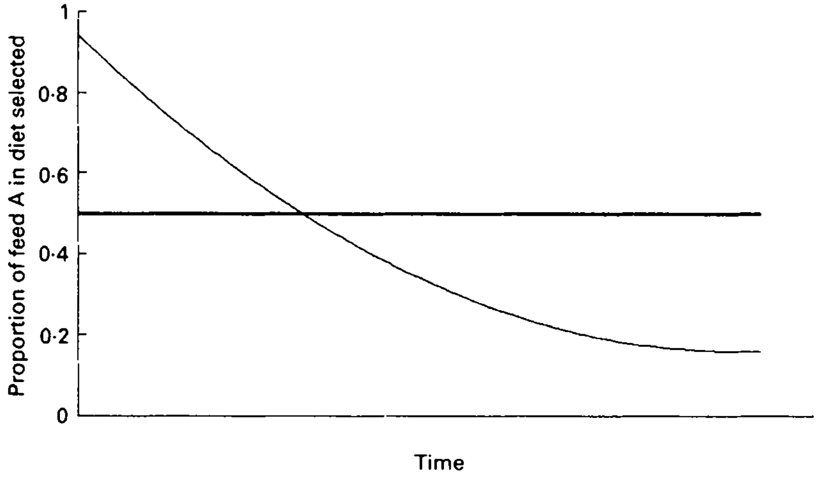

Fig. 5. Possible change in diet selection over time.

richer than an observation of the composition of the diet selected at a given time. It would seem to be sensible to allow animals to have a given choice of foods for long enough for any time effects to be seen. Many experiments on diet selection, in common with many other experiments on animals, do not last long enough.

A MORE COMPLEX THEORY OF DIET SELECTION

The two simple theories of diet selection presented previously had some merits but were false. An alternative theory distinguishes between two kinds of experiments in which an animal is given free and continuous access to two different foods. In the first kind the two foods are such that some mixture of them is a diet of adequate composition; in the second kind no mixture of the two is of adequate composition.

Where the compositions of the two foods are such that the animal can choose a diet of adequate composition the theory states that it will. There is no statement as to the time-course of the choice. It is implicit that the animal will see both the foods on offer as foods and will be prepared to eat at least some of both of them; it does not seem to be reasonable to expect an animal to eat something that it does not see as being food. The problem of predicting whether an animal will see a particular material as food is left on one side.

Where the compositions of the two foods are such that no mixture of them is of adequate composition the theory states that the animal will select a mixture of them of a composition such that its inadequacy is minimized. The main purpose of the theory is to act as a framework for the design of experiments and to emphasize the minimum requirements for such experiments. To test whether a diet of adequate composition can be selected from a given pair of foods, A and B, it is necessary to give like animals a series of foods made by diluting A with B to varying extents and measuring the performance of the animals on the foods of this dilution series. The number of such foods needed may vary with the case but at least four, and preferably more, should be used.

Given such a dilution series the experimental design is made more powerful by giving all possible two-way choices of the four, or more, foods in the series. With four foods there are six possible two-way choices and with five foods ten.

It is helpful to see the two basal foods as having compositions represented by two points in food composition spaces such as those shown in Fig. 2. Where the foods differ from each other in several, or many, dimensions the food composition space necessary to describe the foods will have several, or many, dimensions. Such mixtures are represented by points in spaces of increasing complexity. The first members of the family are: a point to represent one component, a line to represent two, an equilateral triangle to represent three and a tetrahedron to represent four. Where there are five, or more, dimensions the figure cannot be visualized.

DISCUSSION

The diet-selection problem that an animal in the wild faces is often one of great complexity. A theoretical approach, which sees the animal as a forager which is optimizing something, has been helpful in trying to give the problem a structure (Krebs & McCleery, 1984). This approach has, perhaps inevitably, been nutritionally naïve in that it is usual to see the foods that the animal eats as having just one quality. The nutritionist has come to see a food as a complex mixture of a large number of essential nutrients and potential energy and would need about fifty dimensions to give it a sufficient description.

While the problem of diet selection is one of considerable complexity it is not necessary that it is initially seen as being so in the development of theory and the design of experiments.

The aim of the present paper has been to show that an approach that simplifies the problem may be useful. Simple theories can then be proposed and suitable experiments designed to test them. Where the theories are found to be fruitful they are persisted with. Eventually a theory will cease to be fruitful; it should then be replaced by another.

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Printed in Great Britain