

Food choice and intake: towards a unifying framework of learning and feeding motivation

Jon E. L. Day¹, Ilias Kyriazakis² and Peter J. Rogers¹

¹*Institute of Food Research, Reading Laboratory, Earley Gate, Reading, RG6 6BZ, UK.*

²*Scottish Agricultural College, West Mains Road, Edinburgh, EH9 3JG, UK.*

Abstract

The food choice and intake of animals (including humans) has typically been studied using frameworks of learning and feeding motivation. When used in isolation such frameworks could be criticized because learning paradigms give little consideration to how new food items are included or excluded from an individual's diet, and motivational paradigms do not explain how individuals decide which food to eat when given a choice. Consequently we are posed with the question of whether individuals actively interact with the food items present in their environment to learn about their nutritional properties? The thesis of this review is that individuals are *motivated* to actively sample food items in order to assess whether they are nutritionally beneficial or harmful. We offer a unifying framework, centred upon the concept of exploratory motivation, which is a synthesis of learning and paradigms of feeding motivation. In this framework information gathering occurs on two levels through exploratory behaviour: (i) the discrimination of food from nonfood items, and (ii) the continued monitoring and storage of information concerning the nutritional properties of these food items. We expect that this framework will advance our understanding of the behavioural control of nutrient intake by explaining how new food items are identified in the environment, and how individuals are able to monitor changes in the nutritional content of their food resource.

Introduction

'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 which 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' (Emmans, 1991).

Address to which all correspondence should be sent: Dr. J. E. L. Day, Consumer Sciences Department, Institute of Food Research, Reading Laboratory, Earley Gate, Reading, RG6 6BZ.
Telephone: 0118 935 7000
Facsimile: 0118 926 7917
E-mail: jon.day@bbsrc.ac.uk

Most animals have evolved in environments in which the quality and availability of their diet is unpredictable, and are consequently posed with the challenge of selecting a blend of foods from those on offer which best meets their nutrient requirements (Emmans, 1991). In such environments, the choices made by animals do not seem to be random or purposeless, but rather their food choice and intake appears to be directed towards attaining some defined level of nutrient intake (Kyriazakis, 1994, 1997; Tolcamp *et al.* 1998). The ability of animals to solve these types of nutritional problems stems from the evolution of behavioural mechanisms which enable them to effectively exploit and utilize heterogeneous food sources.

The study of feeding behaviour has fascinated scientists for decades because while animals make apparently quite simple feeding choices such as 'when', 'what' and 'how much' of a food to eat, the nutritional outcome of such choices and the underlying mechanisms which control them are rather complicated. The factors which underpin these feeding decisions are now known to be numerous, with both metabolic (endogenous) and environmental (exogenous) factors being involved in the decision set (Toates, 1981; Weingarten, 1985; Booth, 1992). The complexity of feeding behaviour, therefore, makes a suitable framework a prerequisite to the study of food choice and intake. Many of the frameworks currently used in behavioural nutrition are centered upon intervening variables such as feeding motivation (e.g. Lawrence *et al.* 1993), feedback (e.g. McFarland, 1971) and learning (e.g. Provenza & Cincotta, 1993) because they help to clarify the relative interactions between the many endogenous and exogenous factors which determine food choice and intake (Day *et al.* 1997). However, for an animal to make an informed selection when posed with a choice between two or more foods, it is necessary for that individual to have some knowledge of the properties of the foods on offer. For many years frameworks of learning have been used to explain how animals are able to select foods with positive post-ingestive consequences and avoid foods with negative ones (Revusky & Bedarf, 1967; Kalat, 1974; Booth, 1985; Provenza & Cincotta, 1993). While animals may learn very quickly to associate the sensory properties of a food with its post-ingestive effects and remember these for long periods of time (Green *et al.* 1984; Ralphs, 1997), learning paradigms alone give little consideration to how new food items are included or excluded from an individual's diet. Therefore, we are posed with the question, do animals actively interact with the food items present in their environment in order to learn about their nutritional properties? The thesis of this review is that animals are *motivated* to actively identify and sample the available food items in order to assess whether they are nutritionally beneficial or harmful. We believe that the rules animals follow are general rather than specific and propose that this information gathering occurs on two levels through exploratory behaviour: (i) the discrimination of food from nonfood items, and (ii) the continued monitoring and storage of information concerning the nutritional properties of these food items.

The first level of exploratory behaviour creates the opportunity to identify new food items, for example during behavioural development and in environments where the food resource exists in transitory patches. It is known that this type of discrimination can, in part, be socially mediated in familiar environments because naive animals are known to learn what to eat from their mother (Thorhallsdottir *et al.* 1987; Mizra & Provenza, 1990, 1992) and other experienced conspecifics (Provenza & Burritt, 1991; Biquand & Biquand-Guyot, 1992; Galef, 1996; Ralphs, 1997). However, social learning *per se* cannot wholly account for how animals learn what to eat because the nutritional requirements of the young are quite different from the requirements of their mothers or more experienced peers. In addition, animals clearly also learn what to eat in unfamiliar environments where there are no experienced conspecifics (e.g. Hogan, 1973 *a,b*). Therefore, we regard this type of social input as merely priming the identification of food items by exploratory behaviour. The second level of exploratory behaviour allows an individual to

modify its feeding behaviour in response to variations in the nutritional quality and other relevant properties (e.g. level of toxins) of the food resource and also acquire knowledge of alternative food sources. It occurs during ongoing feeding behaviour and is characterized by individuals actively sampling food items to acquire and retain relevant nutritional information. In this respect our thesis differs from the current accepted view that learning occurs passively during feeding.

Our aim is to expand upon this thesis, first by discussing the strengths of existing frameworks of feeding motivation, feedback and learning, second by exposing their weaknesses when they are used in isolation, and third by proposing a unifying framework which overcomes these weaknesses through the study of motivated exploratory behaviour. During the review we will use contrasting examples from the farm and laboratory animal literature, but will also refer to other species including humans as interdisciplinary information transfer is often valuable (see Day *et al.* 1997). It is expected that the framework proposed in the review will advance our understanding of the behavioural control of nutrient intake by explaining how new food items are identified in the environment, and how animals monitor changes in the nutritional content of their food resource.

The goals of food choice and intake within an evolutionary context

Before reviewing the frameworks currently used to study food choice and intake, it is useful to briefly consider what animals are trying to achieve through their feeding behaviour. It is now widely accepted that the feeding behaviour of animals (Kyriazakis, 1997), and partly of humans (Mela & Rogers, 1998), is directed towards achieving a goal. Although it is beyond the scope of this review to discuss the nature of this goal, or goals, or whether they are best served or achieved within the short or longer term (Kyriazakis, 1997; Tolkamp *et al.* 1998), it is useful to stress the general principles which underlie them. Natural selection has acted so as to favour animals which make best use of their environment, which includes their feeding environment, since this allows them to optimize their fitness in terms of survival and reproduction (Stephens & Krebs, 1986). It is accepted in the study of food choice and intake that animals can be viewed as 'possessing the desire' or 'seeking' to achieve this goal through their feeding behaviour (Emmans, 1991; Emmans & Kyriazakis, 1995).

It is clear that one has to consider or take in to account the environment within which animals have evolved when studying feeding behaviour. Although this might be regarded as stating the obvious in the ecological field, it has frequently been disregarded in the literature dealing with laboratory and farm animals and humans (for discussions see Tolkamp & Kete-laars, 1992; Kyriazakis, 1997; Mela & Rogers, 1998; Tolkamp *et al.* 1998). A negative consequence of this is that confronting an animal with certain experimental conditions can produce spurious results. For example, rats become massively obese when they are 'cafeteria' fed a series of highly palatable foods (e.g. Rogers & Blundell, 1984), and broiler breeders become overweight when they are fed *ad lib.* and suffer a reduction in their reproductive output (Hocking & McCormack, 1995). These animals have not evolved in environments where they have had experience of foods of such high nutrient density and consequently appear to behave 'inappropriately'. We should consider, however, that overconsumption in the short term may be adaptive in evolutionary terms as it increases an animal's ability to survive periods of future food scarcity (Mela & Rogers, 1998). Therefore, it is important that we examine food choice and intake within an evolutionary context (Siegel, 1993).

A second factor which must be considered when studying feeding behaviour is that the food resources available to most animals can vary both spatially and temporally. The composition of a food item could change within a day both in terms of nutrients and secondary compounds (e.g. toxins). For example, the concentrations of nutrients and toxins in plants change relatively rapidly over time as a result of plant growth processes and previous herbivory (Freeland & Janzen, 1974). The exception of course is the food items available to specialized animals. For example, the food resource of carnivores does not vary greatly in its composition. A third consideration is that animals are seldom in a 'steady-state' as a result of the ongoing processes of growth and reproduction, and consequently their requirements in relation to their goals also change very rapidly with time (Tolkamp *et al.* 1998). Furthermore, their physiological state also adapts to challenges, such as the adaptation of the digestive system to cope with the existence of toxins in food plants (Duncan *et al.* 1997). Therefore, taking these considerations into account, the problem of diet selection originally stated by Emmans (1991) may be restated as: how has the animal evolved to select its diet in response to both a continuously changing feeding environment and a varying physiological state?

Existing frameworks of feeding motivation, feedback and learning

Feeding motivation

It cannot be doubted that animals have adapted, through evolution, to make decisions on when and how to express specific behaviour patterns. These decisions may be made regarding a range of activities such as foraging, exploring and drinking which are integral parts of an animal's behavioural repertoire. The factors which cause animals to make these types of decisions are extremely complex, with both metabolic and environmental factors being involved in the decision set (for reviews see Toates, 1981; Booth, 1992). Therefore intervening variables such as feeding motivation have often been used to help clarify investigations (Fraser & Broom, 1990). Motivational theory states that an individual's behaviour is under the control of a variety of motivational systems (e.g. feeding, mating, exploring, etc.) which are viewed as reversible brain states controlled by both endogenous and exogenous factors (Bolles, 1975; Toates, 1986; Lawrence *et al.* 1993; Day *et al.* 1997). Each motivational system governs the tendency to perform a unique pattern of behavioural elements which tend to reduce the level of motivation through negative feedback (see Fig. 1).

As an individual can give priority only to one behaviour at a given time, motivational frameworks dictate that the behaviour expressed reflects the strongest motivation (the final common path: McFarland & Sibly, 1975). For example, if feeding were the dominant motivation, an individual would express feeding behaviour until: (i) eating reduced the underlying level of feeding motivation to a position subordinate to that of another motivation (e.g. motivation to drink), or (ii) the level of a competing motivation became elevated to a level superior to that of feeding motivation (e.g. motivation to flee a predator).

Through the use of motivational frameworks endogenous factors such as malnutrition (specific nutrient deficiency), undernutrition (general nutrient deficiency) and gutfill have reliably been found to affect feeding motivation (e.g. Balleine, 1992; Jensen *et al.* 1993; Lawrence *et al.* 1993; Day *et al.* 1996a). It is also known that exogenous factors, such as the perception of external stimuli (e.g. a highly preferred food item), can reliably elicit elevations in feeding motivation and even cause an apparently 'satiated' individual to initiate a feeding bout (Weingarten, 1983, 1984; Day *et al.* 1998). The emphasis placed by the different scientific

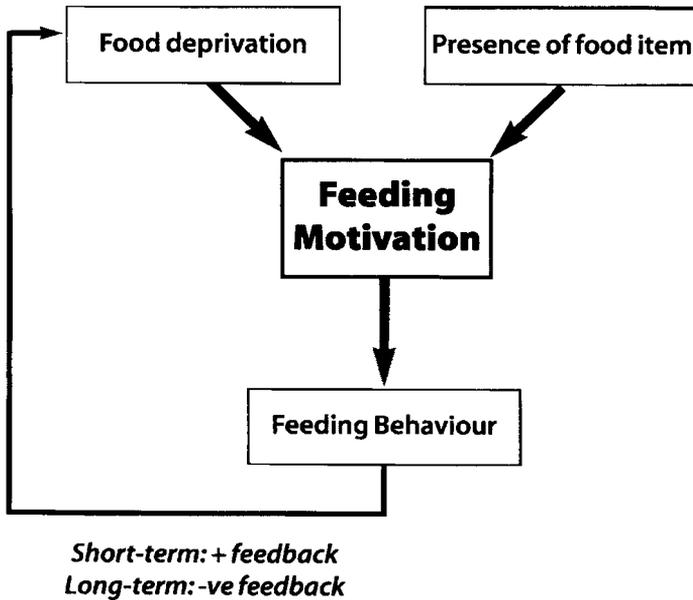


Figure 1. The motivational system associated with the control of short-term feeding behaviour. The level of feeding motivation is a function of both endogenous factors (e.g. food deprivation) and exogenous factors (e.g. the presence of a food item). Feeding motivation results in feeding behaviour which, through eating, is self-regulating via feedback control. Positive feedback maintains eating in the early stages of a meal, and negative feedback is responsible for the termination of meals.

disciplines on the relative importance of endogenous and exogenous factors varies considerably. For example, ecologists may focus primarily on exogenous factors such as the environment the animal is placed in, or inter- and intra-specific interactions, but only give broad descriptions of the animal's nutritional environment. A consequence of this is that food is frequently seen as having only the single nutritional dimension of energy (Castonguay, 1985). Conversely, nutritionists may exhaustively describe an individual's nutrient requirements, but give less attention to the exogenous factors which also affect its level of feeding motivation. The danger associated with this bias is that we forget that feeding motivation is a function of *both* endogenous and exogenous factors. Sibly (1975) commented that it is precisely this relationship between exogenous and endogenous factors which is important in determining feeding motivation. For example, the feeding motivation of an individual which perceives a highly preferred food item in a low state of deprivation could be the same as an individual which perceives a less preferred food item in a higher state of deprivation.

Feedback

Feedback can be defined as information (sensory or visceral) which directly affects the underlying level of motivation, and is described as having either a positive or negative effect. Positive feedback tends to increase the underlying level of motivation (Wiepkema, 1971; Houston & Sumida, 1985), whereas negative feedback tends to reduce the underlying level of motivation (McFarland, 1971). These two types of feedback determine the short term micro-structure of feeding as they control the level of feeding motivation both within and between

meals. In the initial stages of a feeding bout, the ingestion of food is thought to elevate the level of feeding motivation through positive feedback, perhaps in response to the hedonic (pleasurable) components of eating (Wiepkema, 1971; Yeomans, 1996). This initial elevation of feeding motivation is thought to play an important role in keeping ensuing behaviour 'locked in' to eating (Mela & Rogers, 1998), and simulations indicate that without positive feedback there is a tendency for behaviour to oscillate or dither between activities (McFarland, 1971; Houston & Sumida, 1985). However, while positive feedback is necessary to successfully initiate feeding, it is also necessary to determine how eating bouts are terminated when an individual becomes 'satiated', and this is achieved by negative feedback. During a meal, negative feedback is thought to begin to arrest and consequently inhibit the ingestion of food, as food enters the stomach and intestines and is subsequently absorbed (for reviews see Forbes, 1992; Mela & Rogers, 1998).

Learning

A foraging animal may encounter many food items of varying nutritional and toxic qualities which produce quite different effects when they are ingested. Therefore, an ability to associate the sensory properties of food items with their post-ingestive effects is of primary importance. Reviewing the role of conditioning in behavioural nutrition, Provenza & Cincotta (1993) indicated that animals learn to *increase* their intake of foods or non-nutritive flavoured water that are paired with: (i) calories (Mehiel & Bolles, 1984; Booth, 1985; Gibson & Booth, 1989; Ackroff *et al.* 1993), (ii) recovery from nutritional deficiencies (Garcia *et al.* 1967; Zahorik *et al.* 1974; Baker *et al.* 1987; Baker & Booth, 1989), and (iii) recovery from postingestive distress (Green & Garcia, 1971). Similarly, animals learn to *decrease* their intake of foods or non-nutritive flavours that are paired with: (i) toxins (Olsen & Ralphs, 1986; Garcia, 1989), (ii) abdominal discomfort (Pelchat & Rozin, 1982; Garcia, 1989), and (iii) nausea (Coil *et al.* 1978; Provenza *et al.* 1994). Such food preferences and aversions provide clear evidence of the role of conditioning in shaping the long term food choice and intake of animals and arise, as a consequence of feedback, through a learned association between the sensory properties of the food and its postingestive effects. However, such learning paradigms imply that animals eat discrete meals in terms of their composition (i.e. they don't 'mix' different food items), which is clearly not always the case. To clarify this area Provenza & Cincotta (1993) suggested that animals cautiously include novel food items in their diet. The corollary is that if the consequences of such a food choice is positive the new food may be eaten in increasing amounts, and if they are not then the animal will try an alternative choice. Such choices are retained (as they involve an element of safety) until a significant change in the animal's internal state occurs to force it to take action by modifying its feeding behaviour (Kyriazakis, 1997).

The weaknesses of existing frameworks

While frameworks of feeding motivation, feedback and learning are widely used in behavioural nutrition owing to their predictive power, they do not address some very important areas when used in isolation. For example, frameworks of feeding motivation alone provide no information about how an individual decides *which* food to eat when posed with a choice. Motivational frameworks would be unable to predict whether a protein deficient animal possesses a 'general' tendency to feed, or a 'specific' tendency to eat a protein-rich food item. Similar problems are

encountered when using frameworks of feedback and learning in isolation. Positive and negative feedback are important factors in explaining the short term microstructure of feeding bouts, but separate frameworks of learning are required to explain how feeding behaviour is related to longer term changes in internal state where close control over food choice and intake is often observed. Despite the power of learning paradigms to explain what food items should be included or excluded from an individual's diet, it is still unclear if animals actively seek opportunities in which this learning can occur. For example, it is often proposed that animals learn about the nutritional qualities of their food resource during ongoing feeding behaviour (Provenza, 1995). However, an explanation based on passive information gathering is diametrically opposed to the possibility that animals may actively seek opportunities in which useful learning can occur. Such a motivation to learn would be evolutionarily adaptive as it would ensure that an animal had the best possible information to change its feeding behaviour in response to changes in its physiological state.

Overcoming the weaknesses of existing frameworks of feeding motivation, feedback and learning

We propose that current frameworks of feeding motivation and feedback efficiently explain the short term control of feeding behaviour, and that frameworks of learning clearly explain the formation of food preferences and aversions. However, the weaknesses of these types of framework are: (i) they do not explain whether animals are motivated to identify new food items in their environment, and (ii) they do not explain whether animals are motivated to sample known food items to monitor changes in the nutritional content of their food resource. We are, therefore, posed with the challenge of devising a unifying framework which combines feeding motivation, feedback and learning around a new central concept of information gathering. In general it is agreed that a motivation to learn is of utmost importance to the life of animals in the wild because it allows them to gain the information about their home range which is vital for survival (Inglis, 1983; Wood-Gush & Vestergaard, 1989; Renner, 1990; Renner & Seltzer, 1994). For example, many animals have special sites for feeding, and preferred food sources (e.g. Frädrieh, 1974; Dardaillon, 1989). However, to gain such a comprehensive knowledge of their feeding environment, animals must have actively explored their home range to learn the locations and nutritional value (including toxicity) of the food items in their feeding niche. This review proposes that exploratory behaviour provides the means to devise a unifying framework; it facilitates the integration of existing frameworks and is centred upon the concept of information gathering.

Exploratory behaviour and its role in a unifying framework

In 1960 Berlyne defined two categories of exploration: 'intrinsic' exploratory behaviour which is directed at stimuli of little or no biological significance, and 'extrinsic' exploratory behaviour which is directed at obtaining information about conventional reinforcers such as food. The extent to which it is profitable to erect subcategories of behaviour is often debated (see Hinde, 1970), but Berlyne's definitions are both experimentally separable and of distinct use to the study of behavioural nutrition (Day *et al.* 1995). The thesis of this review is that intrinsic exploration is the means by which new food items are identified, whereas extrinsic exploration is the means by which the nutritional properties of existing food items are monitored.

Intrinsic exploratory motivation

Intrinsic exploration is viewed as a distinct category of behaviour which is not linked to any other motivational system (Toates, 1983; Wood-Gush *et al.* 1983; Toates, 1986), and is thought to create situations in which there is an opportunity to acquire biologically useful information (Renner, 1988; Renner & Seltzer, 1994). We propose that intrinsic exploration is under motivational control, and therefore the motivation to perform it competes with other systems such as feeding for its ultimate behavioural expression. In the study of behavioural nutrition this provides a motivational explanation of how new food items are identified from a range of stimuli which are originally of no biological significance to an individual. This stresses that individuals can be actively engaged in identifying new food items (see previous Section), and that intrinsic exploration is of equal importance to feeding itself. The discrimination of food from nonfood items is essential because, while there are some innate food preferences and aversions present at birth (Leathwood & Ashley, 1983; Steiner, 1983), most naive animals have to learn ultimately what is food and what isn't (Hogan, 1973*a,b*; Wright, 1991; Salvatierra *et al.* 1997). It is no coincidence that in many species intrinsic exploration involves placing novel stimuli in the mouth, thereby providing the feedback necessary to assess the substrate's nutritional properties (Wright, 1991; Renner & Seltzer, 1994; Day *et al.* 1996*b*). Without intrinsic exploration the animal does not learn to exploit new food resources and is thus placed at a disadvantage.

Extrinsic exploratory motivation

Extrinsic exploration does not compete for behavioural expression with other motivational systems, but is always present in conjunction with the dominant motivational system (Wood-Gush & Vestergaard, 1989, 1991). Therefore, the motivational system which is linked to the expression of extrinsic exploration will always accompany the dominant motivation (Day *et al.* 1995). For example, extrinsic exploration may obtain information about food items when it is linked to feeding motivation, and information about water sources when it is linked to drinking motivation. The motivational alliance between extrinsic exploration and feeding motivation is of central importance in maintaining the plasticity of feeding behaviour because it allows individuals to monitor the nutritional properties of known food items while they are feeding, and also acquire information about less exploited food items in their environment. Extrinsic exploration has the goal of constantly monitoring the properties of food items in the environment such that informed alterations in food choice and intake are possible when an individual is forced into modifying its feeding behaviour. As such, extrinsic exploration is a motivated behaviour which actively creates the situations where useful learning can occur.

A critic of this proposition may argue that extrinsic exploration merely represents an unnecessary intervening variable. For example, it could be argued that food items are sampled through the action of sensory, nutrient and toxin specific satieties which cause animals to ingest a variety of foods. This explanation implies that animals eat a food item, become averse to it and then eat a different food item and so on (Provenza, 1995). However, highly controlled experiments with human subjects make this view untenable as the hedonic ratings of food items have been found to be unchanged throughout a meal (Hill & Blundell, 1990; Rogers & Blundell, 1990). Furthermore, without frameworks of extrinsic exploration, an individual's food choice and intake would be based on a series of chance events which somehow allow it to learn to meet its nutrient requirement, rather than through mechanisms which actively seek the

information to facilitate informed nutritional choices. A consequence of this would be that animals would select rather inflexible diets, which would be associated with obvious disadvantages in a varying nutritional environment. Put more simply, frameworks of learning alone do not explain how animals solve the problem of diet selection. Toates (1997) commented upon a similar issue, that 'either an exceedingly fortuitous sequence of stimulus-response connections lead an animal to a 'functional end-point' that is not even present at the time the sequence starts, or a high level goal must be postulated'. The high level goal absent from conventional frameworks is that of information gathering.

The unifying framework explicitly defined

Intrinsic exploration is a motivated mechanism which facilitates the identification of new food items and extrinsic exploration is a motivated mechanism which facilitates the monitoring of the properties of existing food items. The goal of these behaviours is to acquire nutritional information which enables an animal to make informed modifications to its feeding behaviour when it experiences a significant change in its internal state. Taken together, these factors make the incorporation of intrinsic and extrinsic exploration into existing frameworks of learning and motivation highly desirable. Its consequences are:

1. Intrinsic exploration is under motivational control and facilitates the identification of new food items because its goal is seeking information about originally novel stimuli (see Fig. 2).
2. The intensity of intrinsic exploration will decline, through negative feedback, when information concerning a novel stimulus is gathered (i.e. a novel object is identified as a food item).
3. Extrinsic exploration is always present in conjunction with the dominant motivation system and facilitates the monitoring of the properties of known food items because its goal is to maintain current information about known food items, or items whose properties may change over time (see Fig. 3). Information concerning the properties of food items will be retained in an animal's memory as learned associations.
4. The level of extrinsic exploration will decline, but not be abolished, as a new food item becomes more familiar (partial negative feedback: see Fig. 3), thereby ensuring that learned associations are up to date.
5. Learned associations will decay as a function of the strength of positive or negative postingestive effect (e.g. animals will retain a conditioned food aversion which caused a highly severe malaise for longer than one which was associated with a relatively milder illness). Learned associations decay because it would be maladaptive to retain too much information in an ever changing environment.

The unifying framework in practice

The nutritionally naive individual is posed with two feeding imperatives: (i) it must learn to discriminate between food and nonfood items in the environment, and (ii) it must learn to select a diet which meets its nutrient requirements and avoids harmful toxins (Emmans, 1991; Rogers & Blundell, 1991) by acquiring the nutritional information which enables it to respond to changes in its internal state. This information is not retained as learned associations indefinitely, but rather decays as a function of its biological utility (Kyriazakis *et al.* 1998). Within the

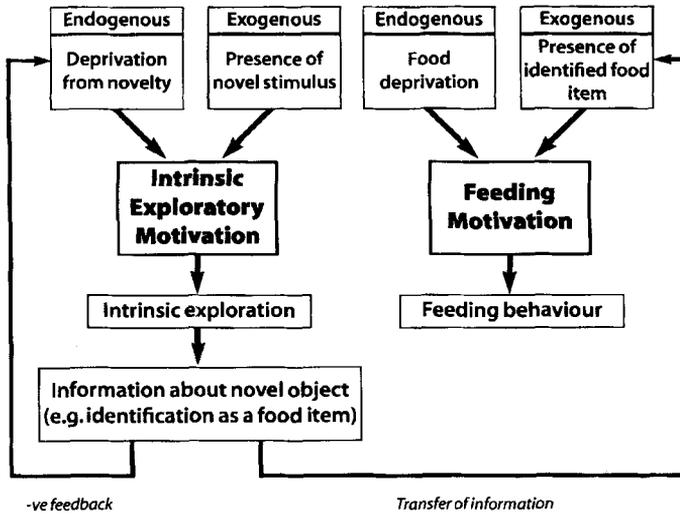


Figure 2. The motivational system associated with intrinsic exploration can be utilized to identify new food items in the environment. Once identified by intrinsic exploration, new food items are able to be exploited by the feeding motivational system. As information is gathered about a novel object, the level of intrinsic exploratory motivation declines through negative feedback, and the information acquired can be used by another motivational system (e.g. feeding motivation).

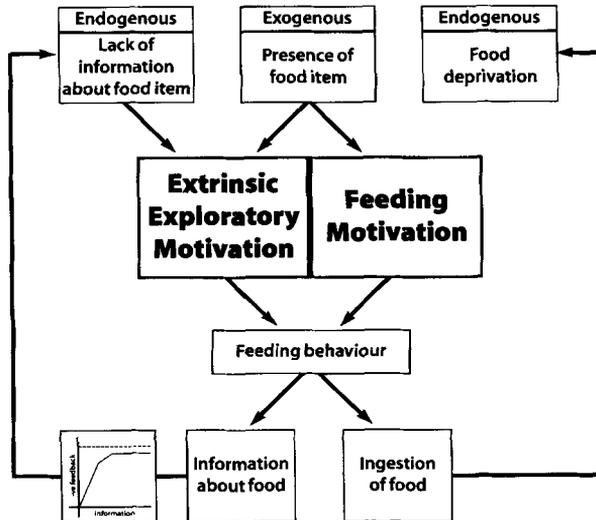


Figure 3. The interface between extrinsic exploration and feeding motivation is used to gather nutritional information concerning the food items in an animal's environment. As a food item becomes more familiar through extrinsic exploration, the underlying level of extrinsic exploratory motivation will decline, but not be abolished.

unifying framework proposed in this review, the first imperative is achieved through intrinsic exploration and the second through extrinsic exploration.

Intrinsic exploration and the identification of new food items

The development of a feeding repertoire by the naive individual could be likened to the acquisition of a dynamic 'menu' which stores current information concerning the identity and nutritional properties of known food items. This progressive learning process, initially using intrinsic exploration, would be most active during infancy, but would also be retained in later life (Almeida *et al.* 1994; Huang *et al.* 1994; Salvatierra *et al.* 1997). It would be short-sighted, however, to suggest that intrinsic exploration was the sole means by which individuals learn to discriminate food from nonfood items, as the role of social factors in priming intrinsic exploration is well documented (see Introduction; Galef, 1977; Laland & Plotkin, 1990; Laland, 1992). While the degree to which intrinsic exploration is utilized will depend upon the identity of the species and feeding niche in question (Cowans, 1983; Renner & Seltzer, 1994), there are many commonalities in the literature of how intrinsic exploration can be utilized by the learning individual (e.g. Asahida & Mimura, 1972; Hogan, 1973*a,b*; Renner, 1990; Nicol & Pope, 1994; Day *et al.* 1996*b,c*; Bolen & Green, 1997; Edwards *et al.* 1997; Salvatierra *et al.* 1997; Watanabe, 1997). For example, we investigated the role of intrinsic exploration by providing energy restricted pigs with a choice between two novel objects to chew: one which exuded a sucrose solution, and the other exuding only water (Day *et al.* 1996*b*). We found that there was initially no difference in the chewing activity between the sucrose exuding and water exuding objects. However, after only one session (equating to 6.5 h of total experience time), the pigs had identified, through intrinsic exploration, the sucrose exuding object as a food item (see Fig. 4). Similar results were found by Hogan (1973*a,b*) and Salvatierra *et al.* (1997) who showed that very young chicks have to learn to discriminate food grains from inedible objects. The discrimination occurred within 1–2 d from the start of the test and is in accordance with other studies which have found that young chicks do not show any evidence of meal patterns until they have learned to exploit effectively their feeding environment (Asahida & Mimura, 1972). The rapidity of discrimination observed in these experiments is typical of intrinsic exploration which characteristically declines as soon as the novel stimulus has been identified as being either biologically useful or irrelevant.

Extrinsic exploration and the monitoring of the properties of known food items

As soon as an individual has learned to discriminate food from nonfood items in its feeding niche, it is posed with the second imperative of learning to select a diet from these food items which meets its requirements, and acquiring the nutritional information which enables it to respond to changes in its internal state. This type of learning is important for an individual to meet its nutrient requirements, and also to alter its feeding behaviour in response to variation in the quality of the food resource (e.g. an increase in the level of toxin—see Provenza & Cincotta, 1993). For each animal this learning process can only be effective if there is continuous monitoring of the nutritional quality of the food items present in the environment through extrinsic exploration (Inglis, 1983; Illius & Gordon, 1993; Inglis *et al.* 1997). The persistence of the learned associations formed as a result of this monitoring is likely to be related to the intensity of the postingestive consequences. For example, an aversion to a plant which caused a

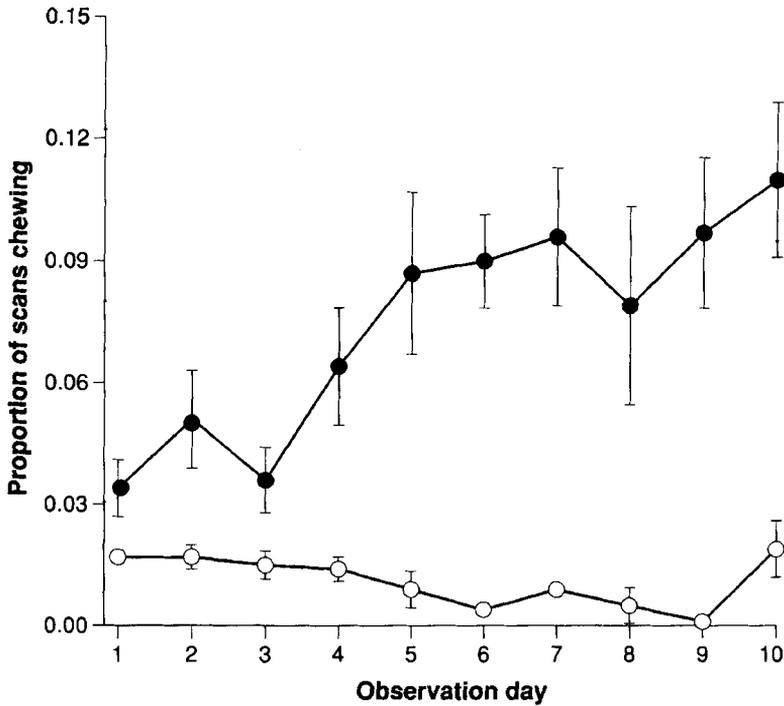


Figure 4. The mean level of chewing activity directed towards a novel object which exuded either sucrose (●), or water (○) by energy restricted pigs. The behaviour directed towards the water exuding object represented intrinsic exploration. Values given are means (\pm standard error of the mean).

highly severe malaise is likely to be retained by a sheep for a longer period of time than to a plant which caused a less serious malaise (Provenza, 1996). This will be discussed further later (see Section on 'Issues Raised by the Framework').

To support the insertion of extrinsic exploration in a behavioural nutrition framework, it is necessary to demonstrate that individuals have a concurrent motivation to gather information while they are feeding. Perhaps the most persuasive illustrations of this phenomenon have been achieved using an experimental paradigm termed *contra-freefeeding* (Jensen, 1963; Duncan & Hughes, 1972; Inglis & Ferguson, 1986; Forkman, 1993; Inglis *et al.* 1997), where animals are observed to 'work' for food even though the same food is freely available. It has been hypothesized that *contra-freefeeding* represents the gathering of information concerning the alternative food source (Inglis & Ferguson, 1986; Forkman, 1993; Inglis *et al.* 1997). Inglis & Ferguson (1986) found that starlings preferred to obtain 72% of their food by working (extrinsic exploration) even though identical food items were freely available. A similar result comes from the work of Forkman (1993). He provided 9 adult male Mongolian gerbils with the choice of digging for 30 sunflower seeds buried in a dish of sand, or eating from 1000 identical seeds which were freely available in another dish. In a similar fashion to the former experiment, he found that the gerbils preferred to obtain, on average, 67% of their food by digging. While this behaviour could be interpreted in a number of ways, the most plausible explanation is that *contra-freefeeding* is representative of an animal's level of extrinsic exploratory motivation in an unpredictable environment (for a systematic review of alternative explanations see Inglis *et al.* 1997).

A second line of evidence to support the existence of extrinsic exploration during feeding comes from the study of food choice. When individuals are posed with a choice between two or more foods, intake appears to follow some rules (for reviews see Rogers & Blundell, 1991; Rose & Kyriazakis, 1991; Wright, 1991; Hughes, 1993). This should not be surprising since all behaviours, including feeding behaviour, seem to be serving a purpose, or be part of a behavioural repertoire which served such a purpose in the individual's evolutionary history (Kyriazakis, 1997). There are some instances, however, when animals appear to make 'inappropriate' food choices (Forbes & Kyriazakis, 1995). Kyriazakis *et al.* (1990) found that when pigs were offered a choice between two nutritionally imbalanced feeds, they did not opt to consume exclusively the feed with the least penalties, but while feeding took a significant number of bites from the feed associated with the most penalties. Illius & Gordon (1993) outlined a similar finding from an unpublished experiment by Clark *et al.* where the grazing behaviour of groups of cattle, sheep and goats was observed. These animals were placed in plots in which the grass had been mowed to two different lengths. The taller grass, which maximized intake, was strongly preferred by all the species; however, the animals were observed to make frequent (every 3–6 minutes) trips to the shorter grass. These 'partial preferences' could be interpreted as the grazer's conflict between exploiting a depleting food resource, and moving to a new potentially replete food patch which gives greater rewards but costs time and energy to travel (marginal value theorem: Charnov, 1976). However, Illius & Gordon (1993) commented that such grazing movements appear to be a natural part of the herbivores' foraging tactics and are not apparently related to depletion of the food resource; they interpreted these findings as evidence of information gathering concerning the nutritional properties of the shorter grass.

Similar 'partial preferences' have been reported by Young (1940) in studies of rats, and have also been found to occur where choices are made between foods which differ only in their flavour (Rozin, 1969; Holman, 1973; Morrison, 1974; Treit *et al.* 1983; Le Magnen, 1986). 'Partial preferences' are interpreted by some as being mediated by foods becoming 'aversive' the more they are eaten (Provenza, 1996). However, as was outlined earlier (see Section entitled 'Intrinsic exploratory motivation'), this view is untenable as studies of human subjects indicate that the hedonic ratings of foods are unchanged during a meal (Hill & Blundell, 1990; Rogers & Blundell, 1990). Observations on freely feeding rats showed that 'partial preferences' were not evident within meals, but there was a strong tendency for the animals to alternate food choices between eating episodes separated by long inter-meal intervals (Rogers & Blundell, 1984). Similarly, rats which have been trained to obtain food in a specific location will often be seen to express exploratory behaviours even though they delay consumption (Whiting & Mowrer, 1943). In their authoritative review Richman *et al.* (1986–87) concluded that this behaviour is best considered to be a manifestation of 'exploratory motivation' (page 361).

The interface between extrinsic exploratory motivation and feeding motivation

One of the predictions made by Inglis (1983) is that exploration (now explicitly defined in the present review as extrinsic exploration) for information about food declines with increasing levels of feeding motivation. In their experiment, Inglis & Ferguson (1986) observed the contra-free-loading behaviour of starlings, and found that, on average, 72% of the food consumed originated from the search-board when the birds had not been food deprived, but this percentage decreased with increasing levels of feeding motivation (52, 35 and 23% for 2, 4 and 8 h food deprivation respectively). Similar reductions in the use of extrinsic exploration with

increasing levels of feeding motivation have been revealed in many studies of foraging behaviour (Charnov, 1976; Rechten *et al.* 1983; Snyderman, 1983; Bence & Murdoch, 1986; Perry, 1987). Inglis & Ferguson (1986) concluded that at low levels of feeding motivation, the starlings were adopting a foraging strategy which 'satisfied', but also allowed for the acquisition of information concerning the cryptic food source. Only with increasing levels of feeding motivation did the birds spend more time foraging in a manner which maximized food intake. Related to these observations, Levitsky (1979) argued that food deprivation in the neonatal period can reduce the expression of extrinsic exploration and can lead to subsequent impairment in learning. Studies directly testing this hypothesis have generally provided evidence in its favour. For example, in one study rats were undernourished during their suckling and early post-weaning periods and were at the same time exposed to stimuli (triangles and circles) later used in a discrimination learning task. Although they were well nourished during discrimination learning, they failed to show any benefit from the prior exposure to the stimuli, unlike control animals (well nourished throughout life) which learned the discrimination significantly faster if they had been exposed to the stimuli during their early life (Rogers *et al.* 1986). Taken together, these findings indicate that extrinsic exploration is indeed reduced with increasing levels of feeding motivation. This is intuitive, as in times of undernutrition or malnutrition it would be logical to cease gathering information and exploit well known food items to redress nutrient deficiencies.

Issues raised by the framework

The framework proposed in this review, we believe, allows research to proceed in some rather valuable areas. By integrating conventional frameworks of learning and feeding motivation around the central concept of exploration, it becomes possible to understand better the behavioural mechanisms which determine food choice and intake. This understanding is not just of academic interest because a knowledge of the rules used by animals during feeding directly underpins our ability to predict diet selection and food intake. Therefore, the purpose of this final section of the review is to discuss briefly some of these issues in relation to the proposed framework.

In the preceding section it was outlined that animals reduce their level of extrinsic exploration in response to increases in feeding motivation in order to exploit familiar food items and redress nutrient deficiencies. One of the predictions of the unifying framework proposed is that the intensity of intrinsic exploration will decline, through negative feedback, when information about a novel stimulus is gathered (see section entitled 'The unifying framework explicitly defined'). However, this prediction initially appears to be at variance with the literature concerning food neophobia. Many animals exhibit an initial reluctance to ingest novel foods (e.g. Revusky & Bedarf, 1967; Kalat, 1974; Birch & Marlin, 1982; Pliner *et al.* 1995; Provenza, 1995; Inglis *et al.* 1996; Cheney & Miller, 1997; Brigham & Sibly, 1998). What should be considered, however, is that intrinsic exploration is a motivated behaviour which competes for its behavioural expression. As such its expression would be terminated if the level of another competing motivation were to become dominant - a process termed 'active suppression' (Toates, 1980). When an animal encounters a novel stimulus for the first time, its behaviour may also be affected by other competing motivations such as those which arise through fear; for example it has been hypothesized that animals exhibit a fearful response when presented with a novel food item in unusual circumstances which makes them reluctant to eat

(Hull, 1943; Pliner *et al.* 1995; Brigham & Sibly, 1998). Thus an individual could be motivated to interact with a novel food item but its expression of intrinsic exploration suppressed by a stronger motivational tendency.

A second issue of interest concerns the quality of the food resource. For example how does the quality of the food resource available to an animal affect the expression of extrinsic exploration in times of elevated feeding motivation? If the food resource is abundant in nutrients, it makes little sense for it to express extrinsic exploration when exposed to periods of undernutrition (as is seen in the experiments of Inglis & Ferguson, 1986 where birds had access to a high quality food after testing); however, it is unknown whether extrinsic exploration would be depressed by undernutrition if the food resource were impoverished. These types of issues provide new areas in behavioural nutrition which could be addressed using the unifying framework proposed in this review. For example, if we apply the Weber-Fechner relation, the sensitivity of extrinsic exploration may be affected by the nutritional content of the foods on offer, with exploration being more sensitive to differences between food items when food resource is nutritionally poor than when it is nutritionally rich. In impoverished environments, the expression of extrinsic exploration could be especially important to allow individuals to identify the food items which optimize their intake of nutrients, and less important when nutrients are abundant.

These two areas provide an example of how the unifying framework raises some issues new to behavioural nutrition. We accept that we have not validated this framework in a quantitative manner; however, our main aim was to offer suggestions for how research may proceed in this area. These areas are not of insignificant scientific value and the utility of the framework will quickly become evident through its use. Therefore, we believe that future work must be rapidly focused on issues related to the use of intrinsic and extrinsic exploration during feeding.

Conclusions

The ability of an individual to meet its nutrient requirements through feeding behaviour is largely learned, and a wellnourished animal will persist in exploiting successful food items until a significant deviation in its internal state forces it to change its food choice. However, learning paradigms alone give little consideration to how new food items are included or excluded from an individual's diet. It is currently unclear whether animals actively interact with the food items present in their environment in order to learn about their nutritional properties. To overcome this problem we propose a unifying framework of food choice and intake which is centered upon the concept of information gathering through intrinsic and extrinsic exploration. This framework helps to explain how new food items are identified in the environment, and how animals monitor changes in the nutritional content of their food resource. While there are many examples supporting the existence of intrinsic and extrinsic exploration during feeding, it is now necessary to validate the framework in a quantitative manner to understand better how feeding motivation affects an individual's level of extrinsic exploration, and how the information gathered by exploration is utilized by the individual.

This review would not have been possible without intellectual input from A. B. Lawrence. The authors would also like to thank F. D. Provenza, S. Webster and G. Finch for comments on the manuscript. This work was financially supported by the BBSRC Competitive Strategic

Grant at the Institute of Food Research, and the Scottish Office, Agriculture, Environment and Fisheries Department at the Scottish Agricultural College.

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