Theoretical developments in the study and prediction of food intake

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The purpose of the present paper is to review recent theoretical developments in food intake modelling applied to animal science and ecology. The models are divided into those that have been developed for intensive agricultural systems, and those which consider more extensive systems and natural systems. For the most part the present paper discusses models that predict the food intake of herbivores. The mechanisms of each model are discussed, along with a brief mention of the experimental support for the most popular models. We include a discussion of models that approach the study of food intake behaviour from an evolutionary perspective, and suggest that lifetime models are especially useful when food intake carries an intrinsic cost. These long timescale evolutionary models contrast with the more common food intake models, whose timescale is usually much shorter. We conclude that the 'eating to requirements' model highlights an important food intake mechanism that provides an accurate predictive tool for intensive agricultural systems. The mechanisms of food intake regulation in extensive systems are less certain, and closer links between the ideas of animal science and ecology will be helpful for improving our understanding of food intake regulation.

Food intake model: Eating to requirements: Ingestion constraint: Digestion constraint

Food intake is one of the most important aspects of an animal's life history. Explaining food intake behaviour has correspondingly generated a large amount of research interest in the fields of animal ecology, animal science and medicine. Despite studying the same basic subject, these different fields have developed independently of one another, possibly due to their different research goals. The present paper reviews the recent theoretical approaches in the study of food intake for animal science and ecology, but does not look at the medical literature.

The animal science and ecological literature associated with food intake is vast, and we review only the most recent literature (for reviews of animal science literature, see Forbes & France, 1993; Ingvartsen, 1994; Mertens, 1994; Allen, 1996; Poppi, 1996; Pitroff & Kothmann, 1999; Baumont *et al*. 2000, Illius *et al*. 2000; for reviews of the animal ecology literature, see Stephens & Krebs, 1986; Hughes, 1993; Perry & Pianka, 1997; Belovsky *et al*. 1999).

The role of food intake models

The role of models in the study of food intake depends largely on the desired research goal. A model that addresses the key questions in animal science may completely fail to answer the questions posed by animal ecology and vice versa.

The primary goal of research on food intake in animal science is to optimise the economic performance of the agricultural system. Intensive agricultural production systems are in the unique position of being able, if required, to control an animal's environment: the supply of food can be regulated and assured; diet can be monitored; external risks, such as predation or disease, can be combated; movement can be constrained; space and social conditions can be manipulated; even factors such as the environmental temperature can be controlled. This high degree of regulation has benefits for modelling, since it favours accurate model predictions by reducing the variability in the system, and allowing environmental variables to be

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accurately measured. Accurate predictions are important for agricultural systems, due to their tight profit margins. The most important cost in an intensive production process is often that of food (Table 1). The high food costs, combined with the fact that an animal's performance is strongly dependent on its food intake, provides a strong incentive to develop reliable predictive models of an animal's food intake requirements. Within a highly-controlled environment the primary requirement of a model is to predict food intake to within errors of a few per cent. If the error in an animal's predicted food intake requirement reached 10–15 %, the result would be an unprofitable agricultural production system (Table 1). In the face of these economic priorities, the requirement to understand the mechanisms of food intake regulation is of secondary concern.

For wild and extensively-farmed domestic animals, little or no control can be exerted on the feeding environment. In addition, the number of species and breeds of animal covered in this group is far greater than that of intensive agricultural systems. These two differences lead to an increased variability in the observed feeding behaviours and a decrease in the predictability of the system. Food supply may be highly variable spatially and temporally, and in quantity or quality. Environments vary on a diurnal and a seasonal cycle, whilst more stochastic factors, such as predation, disease, competition or reproduction, and behavioural variation between individual animals, may play an important role in determining food intake. In view of all these uncertainties precise predictions of food intake are viewed as unlikely, and the primary goal of a model is to investigate how different ecological factors may contribute towards the observed variability of food intake. Often studies are viewed in the light of evolution, where different factors can be compared in the common currency of Darwinian fitness. These more general models may focus directly on food intake, but other topics, such as spatial distribution (Kennedy & Gray, 1993), time spent feeding at a site (Charnov, 1976), and the implication of competing evolutionary forces for food ingestive behaviour (Van de Meer & Ens, 1997) are also relevant.

Whatever the ultimate goal, an attempt to model every causal link involved in the behaviour associated with food intake is futile. Models must synthesise the important concepts out of the mass of possible causal links, and minimise the number of parameters. Mechanisms of food intake regulation may be an unnecessary complication to a model whose aim is purely to predict. For accurate predictions the simplest approach is often an empirical model that provides a direct link between environmental

variables and food intake. Research that is driven by a desire to understand mechanisms may wish to break the direct coupling between the prediction of food intake and the empirically measured variables by adding in hypothetical mechanisms of the regulation of food intake. The resulting model is unlikely to improve on the accuracy of an empirical model, because errors may arise not only from uncertainties in parameter estimation, but also from an incorrect description of the regulation mechanism. However, the possible increase in generality and understanding can make the reduction in quantitative accuracy an acceptable cost, as long as the model can still be tested against data (Orzack, 1995; Orzack & Sober, 1996; Hutchinson & McNamara, 2000). The point is often made (for example, see Forbes & France, 1993) that a mechanism in one type of model can be represented by empirical relationships in another type of model. Neither type of model is superior, they are just addressing different issues. In the present paper, we shall review a diverse range of models. This diversity should not cause conflict, but instead should be seen as a strength, which allows the subject of food intake to be seen from many contrasting angles.

Models of food intake in controlled environments

Empirical models of food intake

With the importance of accurate food intake predictions in mind, the majority of food intake models intended for agricultural applications are statistical regression models (for reviews, see Ingvartsen, 1994; Poppi, 1996). Although these models do give accurate food intake predictions, they lack generality, since each model cannot be applied outside its original parameterisation. In practice a model may only be applicable to a particular method of production, for one specific breed, age-group and sex of animal, in a certain geographical region. These models do not try to represent the true regulation processes underlying food intake. Instead they demonstrate a correlation between variables and food intake, and so add to our predictive ability of feeding behaviour without furthering our understanding.

Eating to requirements

For controlled environments, where food is unlimiting and where an animal's genetic potential is known, the idea of 'eating to requirements' (the requirements model) has been remarkably successful in predicting the food intake of growing and reproducing animals (Emmans, 1997). The model has been applied to single-stomached animals, such as pigs and hens (Emmans, 1989), with some applications to growing ruminants (Amer & Emmans, 1998; Friggens *et al.* 1999). The requirements model assumes that an animal feeds in order to meet its genetic potential, subject to constraints such as gut volume, where genetic potential is defined as an animal's growth rate given that its environment has never been a limiting factor. An animal's total food intake requirement is therefore determined by the sum of two factors, its maintenance requirement and its growth requirement. A detailed description of the requirements model is given by Emmans & Kyriazakis (2001). If

Table 1. The marginal costs (£) of pig and broiler production per £100 market value (Chadwick, 1998) (Values do not include fixed overheads such as rent, machinery costs, and labour)

	Pigs	Broilers
Feed costs	73	74
Other costs	18	15
Profit	9	11
Profit/feed costs (%)	12	15

an animal is unconstrained by factors such as digestibility, availability of food and costs of thermoregulation, then the model predicts that an animal's food intake will be sufficient to meet its requirements, and no more.

Other requirement-type models, which bear a strong similarity to the model described earlier, have been conceptualised, first for non-ruminants (Webster, 1993), and more recently for ruminants (Pitroff & Kothmann, 1999). These models, which are yet to be clearly formalised in a mathematical framework, propose that food intake is determined by an animal's protein deposition requirements when the food supply is unlimiting.

Fig. 1 shows an application of the requirements model for male turkeys kept in an unlimiting thermoneutral environment. A turkey's energy requirement was calculated using the equation:

$$\text{energy requirement (MJ/d)} = M_E P_m^{0.73} P/P_m + 50 \, dP/dt + 56 \, dL/dt, \qquad (1)$$

where M_E (1·63 MJ/d) is the maintenance requirement per unit protein content of a mature bird, P_m (3·64 kg) is the mature protein weight, and the rate of protein deposition (dP/dt) and lipid deposition (dL/dt) are measured by weighing and analysing slaughtered birds at a series of weights (Emmans, 1989). From the energy requirement of equation 1, and knowing the energy density of the food, the turkey's food intake requirements could then be predicted (Fig 1). In this case, where efforts were made to remove all possible extraneous constraints on food intake, the close agreement between prediction and observation strongly suggest that the male turkeys are indeed eating to accurately meet their requirements.

If an animal is subject to physical constraints then the requirement model still assumes that a genetic potential is trying to be met, but the constraints may now prevent the animal from attaining this goal. In the case of a herbivore voluntary intake is reduced by the low digestibility of the diet and rate of passage, and it is therefore assumed that low rates of rumen digestion and passage lead to physical limitations on daily intake (Laredo & Minson, 1973). Highly-digestible feeds can potentially be eaten in greater quantities before the presumed physical constraints of gut clearance apply. In the case when food intake is constrained the accuracy of the model's prediction is determined by the accuracy with which the constraints can be specified. If the constraints are poorly determined, or are not the correct mechanism underlying the limitation of food intake (Ketelaars & Tolkamp, 1992a,b; Tolkamp & Ketelaars, 1992; Owen-Smith, 1994; Pitroff & Kothmann, 1999), then the predictive power of the requirements model is reduced.

The requirements model could, in theory, be extended to incorporate costs other than maintenance and growth (e.g. the effect of parasitic infection, or temperature regulation). By including the requirements of the offspring, assuming that the number of offspring is known, the requirements of a reproducing animal can be estimated (Friggens et al. 1999; Emmans & Kyriazakis, 2001). Recently, thermoregulation costs have been included in a requirements model which predicts the food intake of pigs with differing heat regulation costs (Knap & Schrama, 1996; Knap, 1999). Further possible extensions, which would be particularly relevant when predicting food intake in less-controlled environments, are factors such as variable reproductive effort, parasitic infection and disease. However, it is unclear if a requirements model could be applied to factors such as these, since it is debatable whether the concepts of genetic potential and energy requirement would always be easily definable and useful. For example, several requirements may be conflicting, and comparison between requirements may not be possible with a currency of energy or nutrients. In uncertain environments, where food availability is not assured, requirements may include a need to store reserves for use in the future, but this storage requirement is likely to be difficult to predict. Even the basic requirements model incorporates models for metabolic rates and growth rates that are empirically well determined under certain situations, but whose theoretical foundation is still unclear (Bajzer, 1999; Speakman, 2000). These kinds of issues present a challenge to the requirements model, and it is perhaps due to complications like these that the requirements model has not been adopted in ecology.

Models of food intake in poorly-controlled and natural environments

Wild and free-ranging domesticated animals do not live in a highly-controlled environment. The dominating paradigm, underlying the majority of thinking on food intake behaviour in these kinds of environments, is that natural selection has been a strong force in shaping an animal's food intake behaviour (Stephens & Krebs, 1986). If this is the case, then ingestive behaviour will have been selected towards maximising an animal's Darwinian fitness (where Darwinian fitness may mean lifetime reproductive success, reproductive success of all future offspring, population growth rate, or some other population quantity depending on
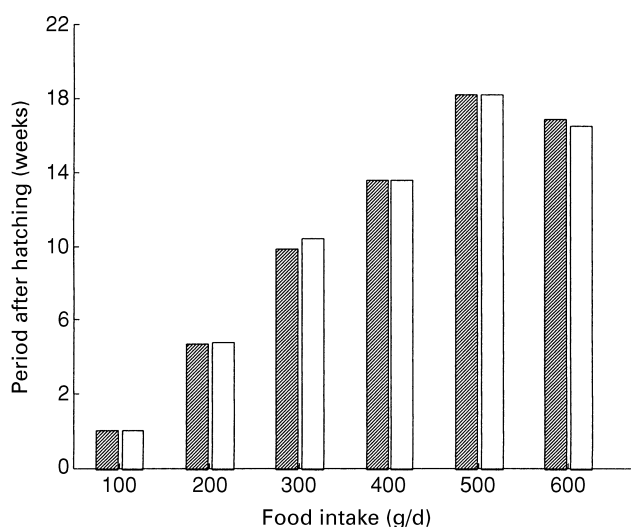

Fig. 1. The observed food intake (▨) and predicted food intake using the 'eating to requirements' model (☐) of growing male turkeys (Emmans, 1989; C Fisher, unpublished results). Birds were given *ad libitum* access to food and kept in a thermoneutral environment.

the ecological scenario being studied; Metz *et al*. 1992). Over 20 years ago this paradigm gave rise to optimal foraging theory, where a fitness-maximising animal was assumed to be maximising either its energy intake rate or its energy intake efficiency. Energy intake rate is often used as a currency because it is a simple concept that is universally related to survival and reproduction. However, alternative currencies may also be relevant when energy is not the crucial determinant of survival or fecundity. For example, nutrient intake or nutrient balance may be of prime importance (Rapport, 1980). Researchers now realise that ingestive behaviour is more complex than just maximisation of energy intake (Perry & Pianka, 1997). Factors such as stochastic resource availability, predation risk, reproductive costs, competition, parasitism, disease, variation between individuals and an animal's own state are some of the complicating factors which may influence feeding behaviour.

Models that predict food intake in wild or extensively-farmed environments have tended to concentrate primarily on herbivores, probably because herbivore food intake has important, worldwide economic implications, and the models described here will primarily concern large mammalian herbivores. In contrast to this emphasis on herbivores, the majority of ecological foraging theory has been developed without herbivores in mind. Carnivore food intake is assumed to be simply a matter of maximisation of energy intake. Nutrient balance is sometimes assumed not to be of great importance to a carnivore, because all essential nutrients can usually be obtained from any given prey, although even carnivorous diets may not be so simple. For example, it has been shown that the feeding behaviour of carnivorous birds depends to some extent on ecological constraints such as the nesting habitat and nutritional requirements (Pierotti & Annett, 1991) and the digestive physiology of carnivorous and piscivorous birds correlates with ecological constraints such as the method of foraging and the generality of a bird's diet (Hilton *et al*. 1998, 2000). It has long been recognised that compared with carnivores, herbivores face different feeding priorities (Owen-Smith & Novellie, 1982; Stephens & Krebs, 1986). Although herbivores are often surrounded by many food types that are relatively easy to locate and consume, each food type is likely to have different nutrient properties, making diet choice an important consideration. Food intake is therefore complicated by factors such as gathering sufficient nutrients and avoiding toxins.

Linear programming

A long-standing method for predicting intake rate and diet is to assume that an animal is trying to maximise some objective (usually either daily energy intake or the reciprocal of the time spent foraging) subject to a number of nutritional, physiological and possibly environmental constraints (Pulliam, 1975; Belovsky, 1978). Models that maximise a feeding objective relative to a set of linear constraints have been solved using linear programming, and are known as linear programming models. These models are simple, both conceptually and mathematically, and seem to give good predictions (Belovsky, 1984), making the method

very attractive. More recently, this method has been criticised on a number of fronts: for not incorporating a herbivore's digestive physiology (Hobbs, 1990); for being circular (Owen-Smith, 1996); for being too sensitive to the model's parameters (Hobbs, 1990; Huggard, 1994); for overlooking the possibility that a herbivore's feeding behaviour may not be optimal (Ward, 1992, 1993; Owen-Smith, 1993, 1994). Of all these criticisms, the most crucial is the claim of circularity. It is contended that the accurate predictions from the model are due to the way the constraints are estimated from the data rather than due to the model itself (Owen-Smith, 1996). If this is the case, then the agreement between the model and observation is not due to the mechanisms of the model but simply because the answer is in the data used to parameterise the model. This factor would explain another criticism of linear programming, which is that the accuracy of the model seems inconsistent with its sensitivity to the parameters (Huggard, 1994). The circularity issue, along with all the other criticisms, have been contested (Belovsky *et al*. 1999). Some studies have tried to avoid the problems of circularity (Edwards, 1997), although the predictive success of these models has also been questioned (Owen-Smith, 1997). In view of the criticisms, linear programming models must give proof that the mechanisms of the model are relevant for predicting the feeding behaviour of real animals.

Ingestion models

Ingestion models assume that intake rate is limited by an animal's ability to consume food. They have concentrated on the constraints of bite size, chewing and searching time to derive various functional responses that specify an animal's feeding rate as a function of one or more variables (Laca & Demment, 1992; Spalinger & Hobbs, 1992; Farnsworth & Illius, 1996, 1998; Pastor *et al*. 1999). In these models the feeding rate is determined either by the effort required to search for food, or by the morphology of the animal's mouth and the proportion of time spent chewing as opposed to cropping (Spalinger & Hobbs, 1992). By assuming that chewing and cropping are mutually exclusive, Spalinger & Hobbs (1992) derived three functional responses for the cases where food is: (1) dispersed and difficult to locate; (2) dispersed and clearly visible; (3) concentrated and clearly visible. Since a herbivore's food is often ubiquitous, interest has centred on the third process which predicts that competition between cropping and chewing will result in intake rate being a type II function (Michelis-Menten form) of bite size:

$$I = R_{max} S / (R_{max} h + S), \qquad (2)$$

where I is intake rate, S is the bite size, R_{max} is the maximum possible rate of plant processing, and h is the average time required to crop one bite in the absence of chewing. This mechanism was independently derived by Laca & Demment (1992). Competition between cropping and chewing has since been incorporated into a general contingency model (Farnsworth & Illius, 1996, 1998), by extending the original disc equation of Holling (1959) to allow for simultaneous searching and handling. Equation 2 has allowed a scaling

rule to be derived for food intake rate v. body mass (Shipley *et al*. 1994), with the prediction that maximum intake rate should scale as body mass$^{0.71}$. For short feeding bouts (less than 5 min) this scaling prediction corresponds to data obtained for a wide variety of free-ranging pasture herbivores (Shipley *et al*. 1994).

Short-term feeding experiments on numerous species of hungry herbivores have provided evidence that equation 2 describes an important proportion of the variability in intake rate. Bite size would therefore seem to be a useful predictor of food intake rate due to the competing processes of cropping and chewing (Shipley & Spalinger, 1992; Gross *et al*. 1993*a*,*b*). However, this relationship may be too simplistic, since cropping and chewing need not always be mutually exclusive (Laca *et al*. 1992, 1994). Ginnett & Demment (1995) have found that, although the type II functional response (equation 2) can explain 99 % of the variance in their food intake observations, the best-fit parameters of h and R$_{max}$ significantly underestimated those directly observed. In fact, their observations suggested that the parameters h and R$_{max}$ need not be constants, and may depend on bite size (S in equation 2). They further demonstrated that parameters h and R$_{max}$ could be described by linear functions of bite size, without altering the conclusion that food intake rate has a type II functional response. This finding implies that although the competition mechanisms underlying equation 2 are supported by the data, the interpretation of the parameters h and R$_{max}$ is not universal, since their dependence on bite size may vary from one application to another.

If the chewing v. cropping mechanism (Spalinger & Hobbs, 1992; Laca & Demment, 1992) is to apply over entire foraging bouts, rather than short-term intake rates, then it is required that: biting and chewing are independent events; there are no periodicities in the length of consecutive bite or chew sequences; the average bite size is constant; the bite rate does not depend on the number of bites in a sequence. Pastor *et al*. (1999) studied the feeding behaviour of two foraging moose (*Alces alces*) over periods of 25 and 39 min and found that all but the last of these assumptions were met. They then extended the cropping v. chewing model so that the bite rate could depend on the number of bites in a feeding bout by making the parameter h a type II function of the number of bites in a feeding bout. Observations of two free-ranging moose supported this extended model's predictions that bite size should be maximised subject to constraints of mouth volume and plant shoot size, whilst the number of bites per bout should be minimised. Woodward (1997) has suggested a further extension of the chewing v. cropping model, which calculates daily intake rate by using a daily time budget. The predictions from the model are yet to be rigorously tested against data.

At their base, all the ingestion models described here assume that food intake rate has an upper limit set by the rate of oral processing (represented by R$_{max}$ in equation 2). These models do not attempt to explain the upper limit of food intake rate. If we assume that this upper limit is determined by an animal's genetic potential, then these ingestion models reduce to being descriptions of a constraint in the framework of a requirements model.

Digestion models

Digestion models assume that food intake is determined purely by the dynamics of the gut and food digestion. Digestive models of food intake come in two forms: compartment models, which describe the digestive process by the rate of flow into and out of a series of compartments; gut-reactor models, which are also mass balance models based on the well-developed theory of chemical reactors (Penry, 1993). In theory these two types of model are equivalent; however, in practice gut-reactor models are strongly linked with the detailed biological processes of digestion, whilst compartment models have a more empirical formulation that allows a broad range of issues to be investigated, such as particle size or metabolic controls (Penry, 1993).

Gut-reactor theory was first studied by Penry & Jumars (1986, 1987) and the approach has been applied to polychaete worms and mammalian herbivores (Penry & Jumars, 1987; Hume, 1989; Alexander, 1991) as well as to fish (Horn & Messer, 1992) and insects (Yang & Joern, 1994). Recently, work has shown that gut-reactor theory can incorporate more realistic aspects of gut dynamics such as hydrolysis (Jumars, 2000*a*) and axial variation in the gut (Jumars, 2000*b*). Gut-reactor modelling looks in detail at the chemical transitions that occur during digestion, and has the advantage of being supported by a large body of literature on the theory of chemical processes and reactor design. Gut-reactor theory has broad applications to areas such as diet analysis (Alexander, 1991; Hirakawa, 1997), digestive tract morphology, processing patterns of digesta and food intake predictions (Jumars, 2000*a*). The optimal food intake rate or rate of throughput is calculated by assuming that the energy absorbed from the gut is being maximised. In general, gut-reactor theory predicts that when growth is limited by the acquisition of simple carbohydrates, ingestion rate should decrease as food quality decreases (Jumars, 2000*a*). This result is supported by evidence from various experiments on insects (Jumars, 2000*a*), and nectarivorous birds (Downs, 1997; López-Calleja *et al*. 1997). On the other hand, if growth is limited by protein acquisition, then maximal ingestion rate should occur for intermediate food qualities (Jumars, 2000*a*), which is consistent with experiments on the lug worm *Abarenicola pacifica* (Taghon & Greene, 1990) and polychaete annelids (Pandian & Marian, 1985). These results also suggest that animals are feeding to maximise absorption rather than feeding up to a target intake rate, although quantitative tests of the optimality theory are lacking (Jumars, 2000*a*).

Digestion compartment models of ruminant intake are reviewed along with metabolic models and some other approaches by Mertens (1994), Illius & Allen (1994) and Illius *et al*. (2000). Compartment models assume that food intake is governed wholly by the rate of digesta clearance from the rumen. Two such models, which have been compared against data, were developed by Illius & Gordon (1991) and Hyer *et al*. (1991*a*). Hyer *et al*. (1991*b*) tested their model with data from beef cattle, and found that their model underestimated food intake on low-quality diets and overestimated food intake on high-quality diet. When compared with intake rate data from low-digestibility

forages the digestion model of Illius & Gordon (1991) explained 61 % of the variance in intake rate. Furthermore, a sensitivity analysis showed that gut DM contents and the passage rate of small particles in the rumen were the two main determinants of food intake rate, in agreement with the model of Hyer *et al.* (1991*a*). The model of Illius & Gordon (1991) was also used to predict the scaling of DM intake with body mass. For high-quality forages, passage rate is a less important contributor than digestion rate to digestion turnover, and intake rate is predicted to scale as body mass[1]. As forage quality decreases, digesta passage rate becomes an important constraint and food intake tends to scale as body mass$^{0.73}$. These models apply when food is unlimiting and of low quality, which corresponds to the expectation of when digestive constraints should be important.

Rumen function has been modelled in greater detail (Danfaer, 1990; Dijkstra *et al.* 1992, 1998; Baldwin, 1995), but these models commonly include intake rate as an initial parameter, and require the estimation of a large number of parameters. Bannick *et al.* (1997) compared the rumen models of Baldwin (1995), Danfaer (1990) and Dijkstra *et al.* (1992), and showed that their outputs differed markedly, even though the same data sets were used for parameterisation. It is suggested (Bannick *et al.* 1997) that this inconsistency is partly due to the difficulties of accurate parameter estimation, which is a significant weakness of any complex modelling approach.

Integrated models

Digestion and ingestion models can be combined with other processes to give an integrated model (Parsons *et al.* 1994; Poppi *et al.* 1994; Sauvant *et al.* 1996; Armstrong *et al.* 1997; Illius *et al.* 2000). Poppi *et al.* (1994) extended a model of energy metabolism of absorbed nutrients originally developed by Gill *et al.* (1984). Poppi *et al.* (1994) integrated instantaneous intake rate, faecal output, rumen fill, genetic potential for protein deposition, heat dissipation and ATP degradation into one model in order to calculate the first limiting pathway on intake rate. Their results suggest that excess energy (represented by the ATP degradation pathway) is often the limiting factor, although importantly under certain circumstances (predominantly for forages of low digestibility) more than one factor may be limiting at the same time. The process of ATP degradation, which was required in the model in order to prevent the unrealistic build up of ATP (Gill *et al.* 1984), has been removed by Illius & Jessop (1995) whose modifications to the model cause excess energy intake to be represented by a build up in acetate.

Sauvant *et al.* (1996) combined a rumen digestion model with a model of feeding behaviour. Although this model could be parameterised to give 'acceptable' predictions of food intake rate, the behavioural feeding sub-model involves concepts such as feeding motivation which are difficult to associate with any physical quantity, and therefore requires careful parameterisation. The same comment is true for models that integrate hypothetical central nervous system signals (Forbes, 1996, 1999; Berthoud, 2000), making these models difficult to test in a rigorously quantitative manner.

With the development of the mechanistic models of digestion and ingestion comes the possibility of not only predicting food intake, but also diet composition and the impact of herbivores on their resources. By combining a mechanistic food intake model with a dynamic model of the plant species community, Parsons *et al.* (1994) were able to explore the physical constraints of intake rate and diet selection, and how these constraints vary with vertical and horizontal distributions of plant species. Their model showed that for grazers feeding on a single plant species the inclusion of the variable, time taken to chew, is necessary in explaining differences in food intake rate. However, when animals graze selectively among several plant species, searching time rather than chewing time might limit food intake. An applied model of sheep grazing on hill vegetation combined digestive and ingestive constraints in order to predict how vegetation utilisation depended on sheep stocking levels across seasons (Armstrong *et al.* 1997). The model incorporated seven dwarf shrub vegetation types and five grass vegetation types commonly found in hill areas of the UK, and assumed that food DM intake was limited either by digestibility or biomass availability of vegetation. The functional response for DM intake *v.* biomass was determined from empirical relationships for bite weight, bite rate and maximum grazing time. The model correctly predicted the rankings of a sheep's vegetation preference for all but two species, although further data were not available to properly validate the model's predictions of utilisation rate and seasonal variations. Such applied models may be useful management tools, but the integration of many regulation mechanisms makes their individual validity difficult to assess.

Cost–benefit models

A further approach towards modelling food intake moves away from the concepts of constraints used so extensively in the preceding models. In cost–benefit models, an animal's food intake behaviour is assumed to be an optimal strategy that balances the benefits of food intake *v.* its possible costs. These models allow intake rate to be a behavioural adaptive strategy (Newman *et al.* 1994), and unlike the digestion and ingestion models, they do not require the constraint of a maximum food intake rate, or gut passage rate.

Thornley *et al.* (1994) presented a model of herbivores grazing on a two-species grassland sward. Food intake was assumed to have a benefit, B, which was chosen to be a semi-empirical function for large ruminants (Agricultural Research Council, 1980):

$$B = b \ln [1 + \beta v (i - i_m)], \qquad (3)$$

and food intake was also assumed to carry with it a cost, C, proportional to the intake rate:

$$C = i E_0 (1 + \gamma), \qquad (4)$$

where i is food intake rate, i_m, is the intake required for maintenance, E_0 is the specific energy cost of obtaining DM, γ represents the cost of being selective, whilst β and b are constants. Since the benefits from food intake depend on

what is being eaten as well as the amount eaten, the relative value of one diet to another is quantified by the parameter ν. For a single food resource, the intake rate is predicted to have the functional form:

$$i = i_m - 1/\nu\beta + b/E_0, \tag{5}$$

which is consistent with experimental results (Penning *et al*. 1991). For two food resources (representing clover *Trifolum* spp. and grass), if the cost of diet selection (γ) is small, then the proportion of clover in the diet is independent of the proportion of clover in the environment. As the costs of diet selection increase, then the proportion of clover in the diet approaches the proportion of clover in the environment. These results are also in line with observations which suggest that sheep prefer a mixed diet of grass and clover (Illius *et al*. 1992; Newman *et al*. 1993; Parsons *et al*. 1994), despite the fact that clover only diets are optimal for growth and lactation (Gibb & Treacher, 1983).

Ketelaars & Tolkamp (1992*a,b*, 1996) and Tolkamp & Ketelaars (1992) have proposed that the metabolic costs of food intake, such as the free radical by-products from metabolism, may play a role in regulating food intake. Their conceptual model predicts that food intake maximises the energy intake per unit O_2 consumption. The model has been parameterised from independent studies (Blaxter & Boyne, 1978), and its predictions of food intake by sheep consuming a number of different forages have been compared with independent observations. On average the predictions and observations were in good agreement, with the model overestimating food intake by 1 % (Tolkamp & Ketelaars, 1992). However, no further quantitative tests of the model have been performed, and the idea remains contentious (Emmans & Kyriazakis, 1995).

Further costs associated with food intake have been incorporated into ecological models, perhaps most notably the costs of predation (Lima & Dill; 1990; Houston *et al*. 1993; Lima, 1998; Brown, 1999; Lima & Bednekoff, 1999; Ward *et al*. 2000). These models have been concerned less with predicting food intake and more with general feeding behaviour. The general conclusion from the studies of predation risk is that an optimal food intake strategy should maximise energy intake:risk of mortality (Houston & McNamara, 1999).

Stochastic dynamic programming

Cost–benefit models are static, in that they predict a time-invariant optimal behaviour. Stochastic dynamic programming models, on the other hand, are non-static, since an animal's optimal behaviour can change with an animal's state, such as age, or body weight (Mangel & Clark, 1988; McNamara & Houston, 1996; Houston & McNamara, 1999). Moreover, dynamic programming models can incorporate the stochastic nature of both the feeding environment and the outcome of a behavioural strategy. They are, therefore, well suited to modelling adaptive animal behaviour.

Stochastic dynamic programming calculates the optimal behaviour of an individual over a finite period of time. The timescale may be short, e.g. hours or days, or it may be an evolutionary timescale over several lifetimes. 'Optimal' refers to the maximisation of some quantity, which on an evolutionary timescale is Darwinian fitness, whilst on a shorter timescale energy intake may be an appropriate measure of fitness. Intrinsic to the method is the idea that food intake behaviour early on in an animal's life will not only have an immediate effect on fitness, but will also have implications for the rest of the animal's lifetime. These models are therefore state-dependent, since future behaviour can depend on an animal's current state (e.g. body weight, age, reproductive status, fat reserves, gut fill, body temperature, nutritional status). Uncertainty in the outcome of an animal's behaviour can be included by calculating an animal's best average strategy (Mangel & Clark, 1988), whilst fluctuating environments are more complicated and require the fitness measure to be carefully defined (McNamara *et al*. 1995; McNamara & Houston, 1996; Houston & McNamara, 1999). These models are therefore well suited for exploring many of the factors faced by a wild animal during its foraging lifetime.

Owen-Smith (1994) has suggested that static optimisation models may be a misleading tool for studying food intake, and points to dynamic optimisation models as a possible way forward. However, the only stochastic dynamic programming model to make predictions of food intake is a model of diet selection by herbivores (Newman *et al*. 1995). This model predicts the behaviour that maximises a herbivore's survival during the non-breeding season. An animal is described by three state variables: digestible gut contents; indigestible gut contents; stored energy. Each animal can choose between three behaviours: grazing; ruminating; resting. Each activity carries with it a predation risk (where grazing is assumed to be more hazardous than ruminating or resting) and a rule for updating each state variable. The model was used to demonstrate that total daily intake under the optimal survival strategy is not constrained, but is a payoff between the energy benefits of feeding and the risk of predation. Predictions could also be made of how the daily food intake of lactating and non-lactating animals varies as a function of instantaneous intake.

As with most applications of stochastic dynamic programming, verification of the model is the greatest problem, since models are often complex, highly parameterised and able to generate a large amount of data. Often, authors point towards qualitative agreements between model predictions and observational data, but this approach is rarely a satisfactory method of validation. Hutchinson & McNamara (2000) have suggested that verification must rely on several independent qualitative tests rather than a quantitative test. An example of the proposed validation method of Hutchinson & McNamara (2000) has been published for the well-developed model of a bird's daily singing routine (McNamara *et al*. 1987; Hutchinson *et al*. 1993). A number of qualitative predictions made by the model, such as a positive correlation between song output and ambient temperature or song output and foraging success, have been compared with real data on song bird behaviour (Thomas, 1999*a,b*, 2000). The results show that dynamic programming models can produce testable results that can be verified or refuted by comparison with real data.

Further examples of dynamic programming models of food intake behaviour have looked at the consequences of a specific food intake, instead of calculating an optimal food intake (Chan & Godfray, 1993; Anderson & Roitberg, 2000; Burrows *et al.* 2000). Burrows *et al.* (2000) developed a stochastic dynamic programming model for the food intake behaviour of limpets (*Patella vulgata*) on an inter-tidal coastline, where the environment was time varying due to the tidal changes and food intake was limited by gut volume. They were able to predict how a limpet's feeding behaviour should change with tidal phase if the energy intake were to be maximised.

In contrast to the model of Burrows *et al.* (2000), which predicted behaviour on a timescale much shorter than animal's lifespan, other models have looked at behaviour over an animal's entire lifetime. The lifetime reproductive benefits of reproducing in the immediate future *v.* the benefits of delaying reproduction in favour of feeding have been addressed by Chan & Godfray (1993) and Anderson & Roitberg (2000). Anderson & Roitberg (2000) studied the feeding behaviour of mosquitoes (*Culex nigripalpus*) to determine if persistent feeding on defensive hosts gave a higher lifetime reproductive effort relative to non-persistent mosquitoes, despite the increased risk of mortality from persistent feeding. Chan & Godfray (1993) investigated the feeding behaviour of parasitoid wasps (*Hymenoptera parasitica*), to compare the immediate fitness benefits of laying eggs on a host *v.* the delayed benefits of feeding on the host and reproducing at a later date. Both models consider the lifetime fitness as the relevant quantity in determining food intake behaviour. The parasitoid wasp model was used to investigate the optimal feeding strategy for different rules of food allocation. The predicted strategies could then be compared with observations to give some indication of the likely food allocation rules being used by the parasitoid wasps. The mosquito model showed that persistent feeding on a defensive host could be advantageous, despite the increased risk of mortality. It could also be shown that the threshold meal size for a feeding mosquito, after which it is advantageous to seek another host, increased with age. The mosquito model therefore predicts that the lifetime fitness-maximising strategy is to take more risks with increasing age, which is supported by observations that older female mosquitoes (*Aedes aegypti*) are more likely to feed more than once (Xue *et al.* 1995). Increased risk taking with age has also been derived in a more general feeding scenario using a lifetime-optimal foraging model (Engen & Stenseth, 1989).

Conclusions

For intensive agricultural systems, empirical models are the most widely used and predict food intake with the greatest precision. It is perhaps indicative of our current understanding of feeding behaviour that the most precise models of food intake also contain the least details of regulation mechanisms. Of the models which include regulation mechanisms, the requirements model (Emmans, 1997) is unique in giving accurate predictions of food intake for growing and reproducing animals in controlled environments. In this sense, the requirements model seems to be capturing a

general rule of feeding behaviour. However, extending the requirements model to general limiting and uncertain environments is more problematic, since it is not clear whether an animal's requirements can always be clearly defined. In summary, for intensive agricultural systems prediction of food intake, for growing and reproducing animals, has been able to make significant headway with the concept of eating to requirements. Its extension to more extensive systems is a challenge that has yet to be developed, but has the potential of shedding new light on the current ideas of food intake for wild and open-pasture animals.

In open-pasture or wild environments the general assumption has been that animals tend towards maximising their food intake, and emphasis has therefore been placed on finding possible constraints that limit food intake. Ingestion constraints suggest that, for a wide range of wild herbivores, the variability in food intake rate can be well described by a type II functional response of bite size (Spalinger & Hobbs, 1992; Laca & Demment, 1992). This finding indicates that the competing ingestion processes of cropping *v.* chewing are important determinants of a wild herbivore's food intake. However, this is not the complete picture, because these ingestion constraints assume that food intake rate is ultimately bounded by some other mechanism, and leave open the question of what this other mechanism may be. Digestion constraints have had some success in explaining the observed variation in food intake for unlimiting poor-quality forages (Hyer *et al.* 1991*a,b*; Illius & Gordon, 1991), but attempts to improve these models by including more detailed dynamics have met problems of parameter estimation and have not been as successful (Bannick *et al.* 1997). Gut-reactor and cost–benefit models of food intake have not been rigorously tested. Models which integrate a number of mechanisms (Poppi *et al.* 1994; Illius *et al.* 2000) show that it is possible for more than one mechanism to be limiting, and suggest that metabolic mechanisms may be more important for food regulation than previously thought. The overall impression is of several possible mechanisms, where each mechanism plays some part in regulating food intake. This approach has inspired conceptual models that describe the integration of many regulatory responses in the central nervous system (Forbes, 1996, 1999; Berthoud, 2000). These models are likely to be difficult to falsify, and as a tool for predicting food intake they have been criticised as having no value (Emmans & Kyriazakis, 2001).

There is no commonly-accepted model of food intake regulation in open-pasture and wild environments, although some mechanisms certainly apply in limited situations (e.g. digestion constraints when food is bulky and unlimited). Furthermore, the mechanisms that have been proposed do not fully address complications, such as environmental variability, and the response to infections. Novel regulation mechanisms are still being sought. The only universal principal, that is common to almost all ideas on food intake, is the adaptation of feeding behaviour by evolutionary forces in cases where human breeding programmes have not disrupted food intake. Although this principle remains hypothetical, the relevance of evolutionary adaptation is supported by observed links between reproductive strategies and feeding behaviour (Sæther & Gordon, 1994). Food intake adaptation usually amounts to assuming that food

intake is maximised, subject to genetic and physical constraints. Maximising food intake allows models to look at short-term behavioural strategies, over several feeding bouts. Few models look at feeding behaviour on timescales as long as lifetimes, which is the fundamental timescale for evolutionary theory. If food intake has no cost to an animal, then intake maximisation in the short term will be equivalent to fitness maximisation in the long term, and a lifetime view is unnecessarily complex. The question of which timescale to use amounts to whether food intake carries with it costs as well as benefits. We are only just beginning to seriously consider the possibility that food intake may carry a cost which impacts on behaviour, with the realisation that factors such as toxins, or parasites have a detectable influence on an animal's feeding behaviour (Hutchings *et al*. 1999). Lifetime reproductive effort provides a common currency for integrating diverse factors such as predation risk and food supply uncertainty. If food intake costs are important to feeding behaviour, then a lifetime view will provide an important modelling approach which allows the investigation of how an animal balances the costs of food intake against the other requirements of its life history.

There is a need for future research on food intake mechanisms in extensive systems to continue testing existing ideas against reliable data. However, in view of the lack of any generic ideas on food intake regulation in this area, perhaps the time is ripe for the development of new ideas. The knowledge from intensive agricultural systems could be used to a larger degree than it is at present in helping to resolve the important mechanisms. First, intensive systems can generate highly-controlled data for the much needed testing of hypothetical mechanisms. Second, requirement models could have a useful role to play in investigating food intake mechanisms for extensive systems, and may help to answer questions such as, are fat reserves adaptive, or are they a consequence of an animal meeting its protein requirements? Is a genetic potential meaningful for wild animals, and if so, can they ever attain their genetic potential? If nothing else, application of eating to requirements will clarify the similarities and differences between extensive and intensive systems. Feeding behaviour in intensive systems also has challenges for the future. Understanding the effects of infections and disease on food intake appears to require new ideas for which the broad-scale evolutionary models may play a fruitful role in developing understanding, whilst issues of animal welfare may require an understanding of the important factors in an animal's evolutionary past (Deag, 1996). Closer collaboration between the fields of ecology and animal science can only further our understanding of food intake, and highlight not only the differences but also the important similarities between the food intake behaviour of domestic and wild animals.

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