NUTRITIONAL ECOLOGY

Nutritional goals of wild primates

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Summary

1. Primates meet their nutritional goals by prioritizing certain nutritional parameters when choosing the types and quantities of different foods.

2. There are five major models applied in primate nutritional ecology, each of which proposes that diet selection subserves a different primary nutritional goal: (i) energy maximization; (ii) nitrogen (protein) maximization; (iii) avoidance or regulation of intake of plant secondary metabolites; (iv) limitations on the intake of dietary fibre; and (v) nutrient balancing.

3. Here, we review the evidence in support of each of these nutritional goals as drivers of primate diet selection. We discuss some of the costs and benefits associated with different methodological approaches used in primate nutritional ecology.

4. New approaches developed outside of primatology have provided better frameworks for understanding the nutritional goals of some primate species. We suggest that the field of primate nutritional ecology needs to take greater advantage of the techniques developed by nutritional ecologists working in other fields.

5. Specifically, we recommend (i) the increased application of the Geometric Framework for nutrition, (ii) the application of methodological approaches that enable the estimation of nutrient and energy availability from food sources, and (iii) continuous follows of individual primates in the wild for determining primary nutritional goals.

Key-words: non-human primates, energy, plant secondary metabolites, protein, nutrient balancing

Introduction

Primate nutritional ecology involves the interactions between the environment and a primate's nutrient intake, and the individual's resultant physiological state. It is a diverse field that includes physiology (Ross 1992), morphology (Vinyard *et al*. 2003), ontogeny, growth, development (Leigh 1994), and ecology (e.g. Oates *et al*. 1990). Underpinning all aspects of nutritional ecology is the need for individuals to procure appropriate quantities of certain macro- and micro-nutrients from their habitat. This requirement is not uniform among different species or individuals but may vary depending on factors such as body size, metabolic requirements, lifestyle, and digestive system (Parra 1978; Milton 1993). Thus, different species may prioritize different nutritional parameters when choosing the types and quantities of foods they consume. We refer to this prioritization as the primates' nutritional goals.

There are five major models in nutritional ecology that have been applied in primatology. Each of these models proposes that diet selection subserves a different primary nutritional goal: (i) energy maximization (Schoener 1971); (ii) nitrogen (protein) maximization (Mattson 1980); (iii) avoidance or regulation of plant secondary metabolites (PSMs) (Freeland & Janzen 1974); (iv) limitations of dietary fibre (Milton 1979); and (v) nutrient balancing (Raubenheimer & Simpson 2004). These different views partly reflect the diversity of species and systems that have been studied, but are also influenced by different approaches to studying nutritional goals.

There are several approaches to the study of primates' nutritional goals (Table 1). We place these approaches into three broad 'levels of inquiry' based on the core question asked: Level (1) Which properties of foods determine whether or not they are included as part of the normal diet? Level (2) Which properties determine the preference ranking among foods that are part of the normal diet? Level (3) What are the nutritional goals that underlie the choice and ranking of foods? These three levels of inquiry incur various costs in terms of time and effort, and provide different insights into a species' nutritional goals (Table 1). Determining which nutritional goal governs diet selection in a primate species can be valuable in zoo husbandry, comparative physiology, maintenance of primate populations in managed ecosystems,

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Table 1. Three major levels of inquiry on which a primate's nutritional ecology can be studied and analysed

Level of inquiry and associated question(s)	Approach	Knowledge gained	Weaknesses/costs
(1) Which properties of foods determine whether or not they are included as part of the normal diet?	Comparison between the chemical compositions of selected and rejected food items	The nutritional factors that influence overall diet selection	Results influenced by differences in food availability. Sensitive to subjective choice of 'rejected' foods. Does not necessarily explain the underlying nutritional goal†.
(2) Which properties determine the preference ranking among foods that are part of the normal diet?	(a) Comparisons between preference indices‡ and the nutritional composition of each food item; (b) Compositional description of foods eaten which are ranked in terms of relative feeding time and/or mass ingested (preference indices not calculated)	The composition of food items that are (a) highly preferred versus less preferred‡, or (b) frequently selected versus rarely selected	Results influenced by differences in food availability and estimates of plant abundances (as a basis for preference indices‡). Uncertainties associated with preference indices‡. Does not necessarily explain the underlying nutritional goal†.
(3) What are the nutritional goals that underlie the choice and ranking of foods?	(a) Estimation of daily nutrient intake by extrapolating from scan sampling protocols§. (b) Detailed analysis of daily nutrient intake per individual per day, recorded continuously all day including all feeding events	Which chemical aspect of the food is prioritized and therefore governs nutrient intake; how the composition of preferred food items fit into the greater picture of the animal's nutritional goal (b) provides a more accurate view than (a)	Labour intensive: Requires detailed data of nutrient intake of the same individual for at least one day (all feeding events included, feeding rates measured for each item etc), and relevant analyses of all food items consumed.

†See text for an explanation.

‡Preference indices (or selection ratios) normally contrast the relative time spent feeding on a food item with the relative abundance of this food item in the home range of the animal (Krebs 1989). Such indices are rough estimations of relative selectivity, as it is difficult to quantify the actual density and abundance of leaves, fruits etc. Even when selectivity is accurately measured, it may not reflect 'preference' (McKey *et al*. 1981). For example, with some behavioural sampling methods (e.g., continuous follows) some rarely eaten items that are found at a low density can be ranked as preferred when they contribute little to the diet.

§Researchers observe one or several group members during each sampling period (e.g. 5 min periods conducted every 20 min), often alternating between different visible focal individuals during the day or part of the day (Altmann 1974).

and for increasing our understanding of primate behaviour, ecology and also human evolution.

In this review, we assess each of the five major models in the study of animal nutritional goals and their influence on primate nutritional ecology. We also assess studies in relation to the level of inquiry employed by the researchers. We discuss new advances in nutritional ecology of potential interest to primatologists. We do not review the influence of mechanical aspects of food items (e.g. fruit hardness or pulp adhesiveness), although we readily acknowledge their importance in the wider framework of diet selection (see review by Lambert 2007). In this review, we concentrate on leaf- and fruit eating primates as more information is available for these taxa, compared to seed-, insect- or exudate-eating primates (Lambert 1998).

Diverse nutritional goals of wild primates

ENERGY MAXIMIZATION

The idea that an animal's nutritional goal may revolve around maximizing energy intake originated with optimal foraging theory (Emlen 1966; Schoener 1971; Pyke *et al.* 1977). This framework hypothesizes that individuals maximize their energy yield per unit time feeding, with this behaviour presumed to be commensurate with an individual's fitness. Energy maximization models often acknowledge that an animal may consume some foods to obtain rare nutrients, rather than for their energy content. Further constraints on nutrient intake built into these models include feeding time and an animal's digestive capacity (Belovsky & Schmidt 1991).

Empirical studies support the view that energy maximization guides foraging behaviour in hundreds of herbivore species, predominantly grazers (Belovsky & Schmidt 1991). Primates are, however, rarely used as subjects for testing energy maximization theory (but see Robinson 1986; Grether *et al.* 1992; Barton & Whiten 1994; Altmann 2006). This is partly because their diets and the constraints under which they forage are considered to be too complex for simple rate-maximizing models to apply (Milton 1979; Post 1984). Nevertheless, the view that a high energy intake equates with a high quality diet has influenced the work of numerous primate ecologists (Leighton 1993; Cowlishaw & Dunbar 2000; Lambert 2007; Strier 2007).

Comparative analyses of anatomical, behavioural and ecological data has led researchers to conclude that some primate species are 'energy maximizers' (e.g. Rosenberger & Strier 1989; Strier 1992). For example, spider monkeys (*Ateles* spp.) are suggested to be energy maximizers (Rosenberger & Strier 1989; Strier 1992), because of their short food retention times (Milton 1981), large territories and fluid social structure (Strier 1992), and their preference for consuming fruit rich in sugars and lipids (Castellanos 1995; Dew 2005; Di Fiore *et al.* 2008). These conclusions were reached using inquiry levels 1 and 2 (Table 1). However, more recent research, using inquiry level 3, indicates that the underlying nutritional goal of *Ateles chamek* is to ingest a set amount of protein each day, not to maximize daily energy intake (Felton *et al.*, in press). Hence, what may

appear as a diet with a goal of maximizing energy intake, may in fact be secondary to the underlying nutritional goal of protein-dominated macronutrient balancing (Felton *et al.* in press).

Notably, few studies quantify digestible or metabolizable energy, that is, the fraction of the ingested energy that is available for the animal to use (but see Conklin-Brittain *et al.* 2006). Instead, researchers normally multiply each macronutrient fraction with a standard caloric factor and thus obtain gross energy content of the food (as per National Research Council 2003 and earlier editions). Because gross energy does not represent the energy available to an animal (Robbins 1983), it is preferable to estimate the digestible and/or metabolizable energy concentrations of different foods.

NITROGEN (PROTEIN) MAXIMIZATION

Nitrogen (N), in the form of amino acids, is the fundamental building block of protein and plays a central role in metabolic processes, cellular structure, and genetic coding (Mattson 1980). For this reason, nitrogen has been proposed as a limiting factor for the growth, health, reproduction, and survival in many organisms (Mattson 1980).

The majority of primate studies that assess the importance of protein do so in the context of food selection (inquiry level 1, Table 1) or food preference (inquiry level 2). It has been suggested that some primates prefer foods high in protein, as they often select protein-rich plant parts or supplement their herbivorous diets with insects (Milton 1979; Oftedal 1991). For instance, gorillas are observed to prefer foods with high protein content (Calvert 1985; Rogers *et al.* 1990; Rothman *et al.* 2008b), but it is unclear whether this is merely a consequence of the high amounts of protein in the plants available (Rothman *et al.* 2008b). Another example of a behaviour that increases protein intake is the ingestion of special faeces (a behaviour known as 'caecotrophy') by sportive lemurs (*Lepilemur leucopus*, Hladik 1978).

Although some researchers have suggested that primates aim to maximize protein intake by careful selection of food items (various colobine species, McKey *et al.* 1981; Waterman *et al.* 1988; *Papio anubis*, Barton & Whiten 1994), rarely there is a conclusive pattern suggestive of protein maximization. For instance, high concentrations of protein do not consistently characterize the plants eaten even by highly folivorous primates (Oates *et al.* 1980; Gaulin & Gaulin 1982; Kool 1992). Furthermore, although total N may be an important influence on food choice in some primate species, other drivers also appear to be strongly influencing food selection, such as dietary fibre and digestion-inhibitors (Milton 1979; McKey *et al.* 1981). There are very few studies that have tested protein maximization, using detailed information on daily nutrient intake by individuals (inquiry level 3). While attempting to do so, Felton *et al.* (in press) found that protein maximization did not explain the pattern of daily nutrient intake of spider monkeys.

AVOIDANCE OF PSMS

PSMs occur widely and can influence which plants and plant parts that are eaten (Palo & Robbins 1991). Thousands of

PSMs have been identified, but relatively little is known about their effects on consumers (Lambert 1998; see also Torregrossa & Dearing 2009). What is known is that PSMs can have toxic effects on the animal's physiology and/or influence digestion (Cork & Foley 1991; Foley & McArthur 1994). A PSM is not inherently toxic or harmful. Rather, its effect depends on its chemistry, the amount ingested, and the consumer in question (Foley & McArthur 1994). For example, leaves containing cyanogenic glycosides form the staple food for the golden bamboo lemur (*Hapalemur aureus*). These lemurs are capable of consuming 12 times the lethal dose of cyanide for other similarly sized mammals (Glander *et al*. 1989).

Polyphenolic compounds, especially condensed or hydrolyzable tannins, are one of the most frequently studied classes of PSM (Lambert 1998; Milton 1998). Tannins have long been considered to have widespread negative effects on digestion and nutrient uptake, due to the capacity of some specific types of tannins to bind with some plant proteins or digestive enzymes and form insoluble complexes (Rhoades & Cates 1976). Several studies have suggested that the presence of condensed tannins in plant foods is negatively related to primate food selection (inquiry level 1, Table 1) (*Colobus guereza*, Oates *et al.* 1977; *Alouatta palliata*, Glander 1981), or food preference (inquiry level 2) (*Cercopithecus aethiops*, Wrangham & Waterman 1981). However, most studies have found conflicting or unclear relationships between food selection, food preferences, and the concentration of tannins and other PSMs (Milton 1979; Davies *et al*. 1988; Marks *et al*. 1988; Waterman *et al*. 1988; Ganzhorn 1989; Kool 1992; Maisels *et al.* 1994; Mowry *et al*. 1996; Chapman & Chapman 2002; Fashing *et al*. 2007). Studies that have conducted parallel analyses on inquiry levels 1 and 2 indicate that while concentrations of PSMs may influence some primates' overall food selection, PSMs may not satisfactorily explain the species' relative preferences for different food items (e.g. in colobines, Maisels *et al*. 1994; Fashing *et al*. 2007).

Ambiguities of this sort are not surprising considering the complex roles PSMs have on diet selection and food intake (Foley & McArthur 1994; Moore & Foley 2005). First, recent research suggests that the effect of PSMs on an animals' physiology is intricately linked to the relative balance of nutrients and energy in the food, and that these factors cannot be assessed in isolation (Simpson & Raubenheimer 2001; Villalba & Provenza 2005). This is because although some PSMs restrict the availability of certain nutrients, large quantities of nutrients also can ameliorate the negative effects of PSMs (Villalba & Provenza 2005). A further complication is the fact that some PSMs (such as condensed tannins) also can have positive effects on the consumer, including protection against intestinal parasites (Min *et al*. 2003), and reduction of the negative physiological effects of other ingested PSMs (Cork & Foley 1991). To accurately study the effects of PSMs on diet selection, researchers need to perform careful chemical analyses, consider intra-specific variation in PSMs, and examine large numbers of potential food items. When analysing large numbers of food items, the use of near

infrared reflectance spectroscopy has proven particularly useful (McIlwee *et al*. 2001; Ortman *et al*. 2006).

A second problem in regards to tannin assays is that the materials used as standards vary greatly, making comparisons between different studies difficult or impossible (Rautio *et al*. 2007). Although there are approaches to avoid these problems, we recommend that initial studies be conducted with an approach that does not require external standards. This could include the *in vitro* approach described by De Gabriele *et al*. (2008). Alternatively, if *in vivo* experiments are possible, primate ecologists could also consider some of the advances that have been made in the agricultural sciences, especially the use of tannin-blocking agents to quantify the effect of tannins on diet selection and nutrient digestibility (Silanikove *et al*. 2001). More detailed chemical studies of tannins may be worth pursuing once broad patterns have been identified (Marsh *et al*. 2003).

REGULATION OF FIBRE INTAKE

Milton (1979) suggested that to understand the food preferences of herbivorous primates, the relative amount of plant cell wall material in diets should be considered. Plant cell wall material is often referred to as 'dietary fibre' and is composed primarily of cellulose, hemicellulose and lignin (Cork & Foley 1991). Because most animals lack the appropriate enzymes to digest cell walls, they must rely on gut micro-organisms to hydrolyze components of dietary fibre for the production of short-chain fatty acids and microbial protein (Cork & Foley 1991; Clements *et al*. 2009). The digestive tract of some primate species is expanded to facilitate more effective fermentative digestion, for example, colobine monkeys (Bauchop & Martucci 1968) and howler monkeys (Milton 1981; 1982). While some studies of captive primates have reported high fibre digestibility of compounded synthetic diets (e.g. Edwards & Ullrey 1999; Campbell *et al*. 2004), it is uncertain how well these diets reflect the lignified cellulose found in natural diets. In the only study that has attempted to quantify the contribution of fermentation to energy intake in free-ranging primates, it was found that fermentation contributed 31% of daily energy requirements (*Alouatta palliata*, Milton & McBee 1983). However, these results should be treated cautiously because the fermentation rates and molar proportions of individual short-chain fatty acids were very unusual (see Cork & Foley 1991). Thus, given the small body size of most primates, it remains unclear whether fermentative digestion of plant cell walls can be a major source of energy intake (Cork & Foley 1991).

It has been proposed that folivorous primates deal with digestive limitations by selecting leaves that are rich in protein but relatively low in dietary fibre (Davies *et al*. 1988; Waterman *et al*. 1988). Diet quality is thus defined as the ratio between protein and dietary fibre. This ratio has been found to be a useful indicator of whether or not certain folivorous primate species choose to consume a particular leaf (inquiry level 1, Table 1). For instance, this pattern has been found in *Alouatta palliata* (Milton 1979, 1998), *Presbytis rubicunda* (Davies

et al. 1988), *Colobus satanas* (McKey *et al.* 1981), *Nasalis larvatus* (Yeager *et al.* 1997), *Gorilla g. gorilla* (Rogers *et al.* 1990) and several lemur species (Ganzhorn 1992). Sometimes the ratio can also explain relative preferences of certain leaves included in diets (inquiry level 2): *Procolobus badius* (Chapman & Chapman 2002), *Colobus guareza* (Chapman *et al.* 2004; Fashing *et al.* 2007), and *Papio* spp. (Whiten *et al.* 1991).

Although these studies indicate that leaf choice by some primates is positively related to a high ratio of protein to fibre, many exceptions occur. Leaf types with low protein : fibre ratios may be preferred under some circumstances (Oates *et al.* 1990; Mowry *et al.* 1996), and rejected leaf types can have high protein : fibre ratios (McKey *et al.* 1981). Furthermore, the protein : to fibre ratio may explain leaf choice for some study groups but not others (Chapman & Chapman 2002; Chapman *et al.* 2004), or only for some closely related taxa (Ganzhorn 1992; Kool 1992; Dasilva 1994). It has been suggested that these inconsistencies may be explained by differences in competitive pressures affecting the feeding behaviour of study subjects (Ganzhorn 1992; Mowry *et al.* 1996; Chapman & Chapman 2002).

We suggest that there are several additional reasons which may account for inconsistent findings arising from assessments of the protein : fibre ratio. First, studies often use different measures of fibre (neutral detergent fibre (NDF) or acid detergent fibre (ADF)). This makes inter-study comparisons difficult. Second, what often is measured as fibre in tree leaves (either NDF or ADF) is actually a complex mixture of fibre, tannins and protein (Makkar *et al.* 1995). A substantial proportion of the crude protein found in plant material may be unavailable because it is bound to tannins and fibre (De Gabriel *et al.* 2008; Rothman *et al.* 2008a). Finally, although the protein : fibre ratio is primarily used to explain preferences for some leaves over others, the physiological underpinnings of such food choices are likely to be obscured by chemical aspects of other foods eaten. For instance, the leaf-based diet of colobine primates is often mixed with fruits and seeds (Dasilva 1994). Because the ingestion of one diet item can affect the digestion of another item (Bjorndal 1991; Villalba & Provenza 2005), the value of one food type cannot be assessed in isolation of other food items eaten. In summary, although correlations have been found between the protein : fibre ratio and the types of foods selected or preferred, the value of the approach needs careful evaluation in conjunction with complementary analytical procedures.

NUTRIENT BALANCING

Researchers have suggested for several decades that herbivores balance their nutrient intake by mixing food items of varying nutritional composition, rather than trying to maximize the capture rate of a particular nutrient (Westoby 1974; Milton 1982; Whiten *et al.* 1991). In the concept of nutrient balancing, both digestible foliage and fruits rich in ready energy constitute high-quality food items when eaten in combination (Milton 1982). Several studies indicate that nutrient balancing

may be a fundamental aim of wild primates. For example, Davies *et al.* (1988) found that two colobine species selected leaves if they had high protein : fibre ratios, but selected seeds on the basis of high lipid concentrations and high digestibility (see also Whiten *et al.* 1991). Such different selection criteria for two different food groups suggest that the monkeys may be aiming for a balance in their nutrient intake. However, a complete picture does not emerge from assessing food selection criteria alone (inquiry level 1, Table 1).

Not until recently has the field of primate nutritional ecology had access to an analytical framework appropriate for empirically demonstrating nutrient balancing. The Geometric Framework for nutrition (GF) is a multidimensional approach designed to assess nutritional priorities of animals (Simpson & Raubenheimer 1993; Raubenheimer & Simpson 2004; Raubenheimer *et al.* 2009). This framework unifies several nutritionally relevant measures within simple geometrical models, thus allowing for a comparison between observed patterns, and predicted reference patterns (Fig. 1a). The GF allows the analysis of observed patterns of nutrient intake without the need for *a priori* assumptions as to what may be guiding diet selection, and can thus assess all nutritional parameters and the five models discussed above. This framework has successfully been applied to a range of vertebrate and invertebrate taxa (e.g. Chambers *et al.* 1995; Raubenheimer *et al.* 2005; Simpson & Raubenheimer 2005; Raubenheimer & Simpson 2006; Robbins *et al.* 2007).

By applying the GF, and using inquiry level 3b (Table 1), Felton *et al.* (in press), concluded that the nutrient intake of *Ateles chamek* was governed by protein-dominated macronutrient balancing, rather than energy- or protein maximization, or avoidance of dietary tannins. Felton *et al.* (in press) found that the daily intake of available protein (when effects of tannins and cell walls had been taken into account) was regulated more tightly than either carbohydrates or fats (Fig. 1b). Because regulation of protein intake in this case was prioritized, only slight changes in diet composition had substantial consequences for non-protein energy intake and thus energy balance. Hence, large variation occurred in the daily intake of non-protein energy, which was significantly related to the availability of ripe fruit within the spider monkeys' territory (Felton *et al.* in press). In contrast, daily protein intake remained relatively stable, regardless of season, sex of the individual, availability of fruit, relative proportion of leaves or the amount of dietary tannins in their diet.

Most applications of GF to date have involved laboratory studies, using tightly controlled experimental designs. Additional challenges are posed in observational field studies. First, it is difficult to determine which of two co-varying nutritional factors may be prioritized in a non-experimental setting. For example, in the above study, ash (crude mineral) and protein concentrations were moderately correlated in food items, resulting in a corresponding relationship between mineral and protein intake by focal animals (Felton *et al.* in press). More data are needed to establish the relative influence of minerals on spider monkey diet selection. Second, it is important to assess the potential influence of a number of
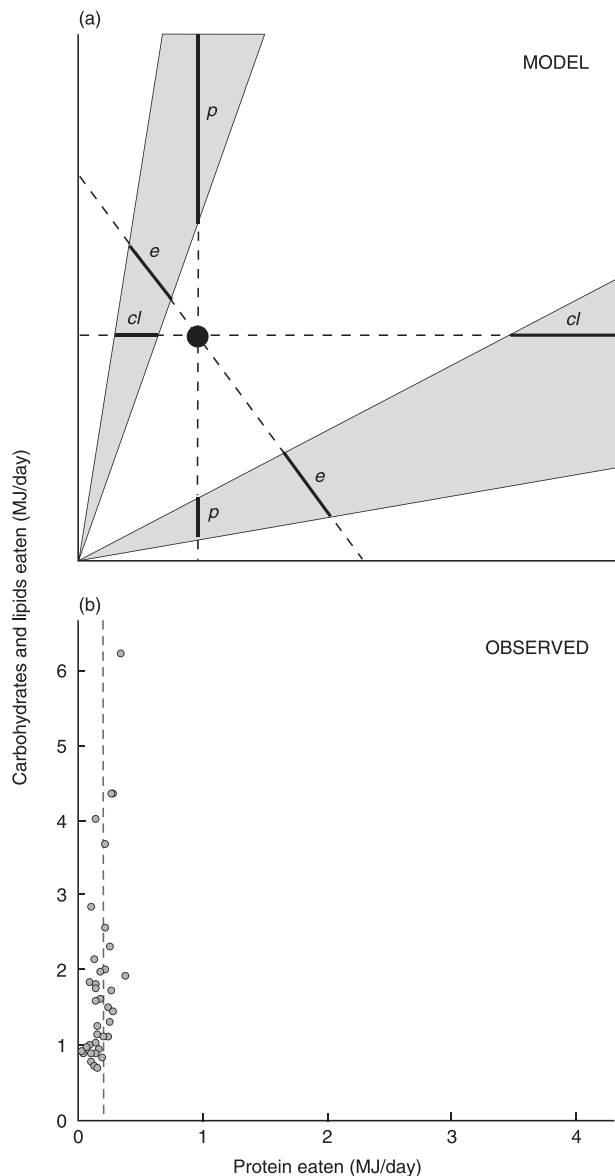
Fig. 1. Predicted and observed outcomes of diet selection. (a) A model using the Geometric Framework to represent potential outcomes when animals are fed diets containing different ratios of protein (P) versus carbohydrates (C) and lipids (L) (Simpson *et al.* 2003). When animals are free to choose foods representing the entire spectrum of P : (C+L) ratios, two outcomes are plausible: (i) daily nutritional intakes fall along line *e* due to energy maximization subject to constraints, or (ii) daily intakes converge around a point in nutritional space (dot) due to target regulation through nutrient balancing. Lines emanating from the origin represent 'food rails' which indicate the food's ratio of P : (C+L). When animals are restricted to diets containing limited amounts of either P or C+L (shading), three outcomes are plausible: (i) total energy intake is prioritized (intake points fall along line segments *e*); (ii) C+L intake is prioritized (segments *cl*) or (iii) protein intake is prioritized (segments *p*). (b) Each point represents the daily endpoint in nutritional space of a focal individual of *Ateles chamek* (38 daily follows included, Felton *et al.*, in press). The vertical line, which represents mean protein intake, fits protein prioritization in Fig. 1a. Protein intake data indicate available protein and account for any protein bound by tannins. For uniformity, protein was plotted in energy units, although mass units could also have been used. The exact placement of the physiological target point (dot in Fig. 1a) is

constraining factors on food intake such as gut limitations, time spent feeding, and intake of indigestible cell wall material (Mattson 1980). These analyses can be conducted in parallel with the GF, given access to detailed observational data (see Raubenheimer & Simpson 2006; Felton *et al.*, in press). We note that the above challenges apply equally to any field-based approach to nutritional ecology. Indeed, these issues call for a multi-dimensional approach, as these provide greater opportunities for revealing (and analytically resolving) potential confounds.

THE ROLE OF MINERALS

It is well known that minerals are fundamental to the health of individuals (Robbins 1983), and some primates travel long distances to reach rare items rich in particular minerals (Fashing *et al.* 2007). Mineral availability has also been a proposed limitation to population growth of frugivorous primates in Ugandan rainforests (Rode *et al.* 2006). However, the intake of most minerals by primates eating natural, balanced diets in the wild often exceeds established requirements of humans, and dietary deficiencies in minerals are suggested to be unlikely (Milton 2003; Rothman *et al.* 2006). Because minerals can be obtained from non-food sources (e.g. salt licks, soil, egg shells), they may not influence food choice in general. Few authors propose that minerals govern diet selection by primates, and no general theories have been put forward. Remarkably little is known about micronutrient content of wild primate foods and their corresponding intake by individuals (Milton 2003). Until further data are available regarding daily mineral intake by focal individuals, little can be concluded regarding the role of minerals in primate diet selection.

FURTHER CONSIDERATIONS

An individual's primary nutritional goal, or the strategy by which it attempts to reach this goal, may change as an individual moves between different life stages. This has been shown to be the case for taxa as evolutionarily distinct as insects (Raubenheimer *et al.* 2007; Boggs 2009) and brown bears (Robbins *et al.* 2007). Adult female primates often have higher energy intakes than adult males (Strier 2007), and lactation in particular demands females to ingest more energy and protein every day than at other times in their lives (e.g. McCabe & Fedigan 2007). Likewise, infant primates have higher relative protein requirements than adults due to their rapid growth and development (Oftedal 1991). It is unknown whether these differences in relative nutrient requirements are indicative of corresponding changes in the underlying nutritional goals of an individual. This may be a fruitful area for future research.

not essential for the interpretation of the pattern. This point can, however, be estimated in a field-based study by analysing the observed pattern of intake, if it is assumed that a free-ranging animal, when given the opportunity, will achieve its intake target (Raubenheimer & Simpson 2006). Figure modified from Felton *et al.* (in press).

Future directions

There are a number of methodological approaches that can be used more extensively than at present by primate nutritional ecologists attempting to answer questions regarding nutritional goals. First, analyses of underlying nutritional goals depend on the accuracy of the estimates of daily nutrient intake. Because of the practical difficulties (or legal/ethical restrictions, Rothman *et al.* 2008b) involved in conducting continuous follows of individual primates in the wild, the vast majority of field studies conduct focal animal scan sampling (as per Altmann 1974). Using this methodology, researchers observe one or several group members during short sampling periods, alternating between different visible focal individuals (level 3a, Table 1). Researchers then estimate relative feeding time on different food items and the nutrient contributions of these items, without direct assessment of the actual weights of food ingested.

Scan sampling is an appropriate method for answering various research questions (Altmann 1974). However, if the aim is to assess underlying nutritional goals (inquiry level 3, Table 1), we suggest that it is preferable (whenever possible) to conduct continuous behavioural observations of the same focal individual over the course of a day. Whereas continuous data collection involves some limitations compared to scan sampling (e.g. a smaller number of focal animals can be followed, and high sensitivity to quality of data collection), this method has several advantages. First, nutrient regulation appears to occur over the period of approximately one day (de Castro 2000; Robbins *et al.* 2007), and what an individual consumes during the morning is likely to influence what it consumes in the afternoon (Booth & Thibault 2000). The use of an average daily nutrient intake based on the activities of several individuals can obscure such patterns of daily nutrient intake. Second, by not recording every feeding event of the day, the relative contribution of some nutrients may be underestimated. A single unrecorded meal may significantly alter the nutrient intake pattern of a day. Third, any quantification of nutrient intake that is based on feeding time rather than weight of ingested food is problematic (Kurland & Gaulin 1987). The use of feeding time as a measure may underestimate the nutritional contribution of fruits by a factor of five, and overestimate the contribution of insects by a factor of 15 (Chivers & Hladik 1980). It is therefore recommended that weight-based data of food intake are documented and intake rates established for each type of food ingested (Oftedal 1991; Chivers 1998; Rothman *et al.* 2008b). Because preference indices (or selection ratios) are usually based on relative feeding times of certain foods (Krebs 1989), quantitative analyses attempting to relate such indices with the food's nutrient composition (inquiry level 2a) should be treated with caution.

As a second recommendation, we wish to draw attention to the use of approaches that enable the estimation of nutrient and energy availability (see above regarding the importance of estimating digestible or metabolizable energy). For instance, protein intake is often a core interest of researchers, but only rarely do researchers attempt to determine 'available' protein (but see Rothman *et al.* 2008a). Not all of the nitrogen in plant foods is available to the consumer, due to the effects of fibre and tannins (Foley & McArthur 1994). Quantifying the effect of dietary tannins on nitrogen digestibility is one approach that is relatively simple to apply to a wide range of different plants (De Gabriel *et al.* 2008).

The importance of taking availability into account when assessing nutrient intake cannot be overemphasized (Rothman *et al.* 2008a). For example, total protein intake by *Ateles chamek* varies dramatically between seasons (A.M. Felton, unpublished data), potentially giving the impression that individuals obtain insufficient protein during certain times of the year. In contrast, intake of available protein remains relatively stable throughout the year, regardless of diet composition and food availability (Felton *et al.*, in press). Large variations in daily intake of total protein (in relation to seasons and diet composition) have been reported for other primate species (*Presbytis rubicunda* and *P. melalophos*, Davies *et al.* 1988; *Papio* spp., Whiten *et al.* 1991; *Gorilla berengei*, Rothman *et al.* 2007; Rothman *et al.* 2008b). It is possible that patterns of total protein intake are providing potentially misleading impressions of the actual nutritional intake and goals of these primates.

Finally, to understand a primate's nutritional goal, researchers may need to collect detailed feeding data at several different levels of inquiry, as all levels have strengths and weaknesses (Table 1). Food choice and associated preferences (levels 1 and 2 respectively) may not be reliable if used as indicators of underlying nutritional goals. This is because animals have several other means by which to attain their nutritional goals, such as mixing foods ('high' and 'low'-ranking alike), or selectively utilizing nutrients post-ingestion (Booth & Thibault 2000). One means by which all three levels of inquiry can be assessed, and hypotheses tested without *a priori* assumptions, is the Geometric Framework for nutrition (Raubenheimer & Simpson 2004; Simpson *et al.* 2004; Simpson & Raubenheimer 2005; Raubenheimer *et al.* 2009). Because of its inherent advantages, we foresee the increased use of this framework by primatologists trying to gain an insight into the nutritional goals of wild primates.

Acknowledgement

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