

# Geometry of nutrition in field studies: an illustration using wild primates

David Raubenheimer · Gabriel E. Machovsky-Capuska ·  
Colin A. Chapman · Jessica M. Rothman

Received: 10 February 2014 / Accepted: 3 November 2014 / Published online: 30 November 2014  
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** Nutritional geometry has shown the benefits of viewing nutrition in a multidimensional context, in which foraging is viewed as a process of balancing the intake and use of multiple nutrients. New insights into nutrient regulation have been generated in studies performed in a laboratory context, where accurate measures of amounts (e.g. eaten, converted to body mass, excreted) can be made and analysed using amounts-based nutritional geometry. In most field situations, however, proportional compositions (e.g. of foods, diets, faeces) are the only measures readily available, and in some cases are more relevant to the problem at hand. For this reason, a complementary geometric method was recently introduced for analysing multi-dimensional data on proportional compositions in nutritional studies, called the right-angled mixture triangle

(RMT). We use literature data from field studies of primates to demonstrate how the RMT can provide insight into a variety of important concepts in nutritional ecology. We first compare the compositions of foods, using as an example primate milks collected in both the wild and the laboratory. We next compare the diets of different species of primates from the same habitat and of the same species (mountain gorillas) from two distinct forests. Subsequently, we model the relationships between the composition of gorilla diets in these two habitats and the foods that comprise these diets, showing how such analyses can provide evidence for active nutrient-specific regulation in a field context. We provide a framework to relate concepts developed in laboratory studies with field-based studies of nutrition.

---

Communicated by Joanna E. Lambert.

---

D. Raubenheimer (✉) · G. E. Machovsky-Capuska  
Faculty of Veterinary Science, The Charles Perkins Centre,  
School of Biological Sciences, University of Sydney, Sydney,  
Australia  
e-mail: david.raubenheimer@sydney.edu.au

C. A. Chapman  
Department of Anthropology McGill School of Environment,  
McGill University, Montreal, QC, Canada

C. A. Chapman  
Wildlife Conservation Society, Bronx, New York, USA

J. M. Rothman  
Department of Anthropology, Hunter College of the City  
University of New York, New York, USA

J. M. Rothman  
New York Consortium of Evolutionary Primatology,  
New York, USA

**Keywords** Nutritional ecology · Nutritional geometry ·  
Mixture triangles · Primates · Gorillas

## Introduction

Understanding the relationships between nutrition and behaviour, ecology, physiology, and demographic processes of animals is a central aim in nutritional ecology (Parker 2003; Barboza et al. 2009; Raubenheimer et al. 2009, 2012; Lambert 2010; DeGabriel et al. 2014). Many studies have shown that this can best be achieved by disentangling the discrete and interactive roles of different food components (Westoby 1974; Dearing and Schall 1992; Simpson and Raubenheimer 1993; Bowen et al. 1995; Robbins et al. 2007). A geometric framework was introduced for this purpose, called the geometric framework for nutrition (Raubenheimer and Simpson 1993; Simpson and Raubenheimer 1993). This framework defines the important facets

of animal nutrition (e.g. foods, nutrient requirements, body compositions, nutrient utilisation) in a cartesian space, where each dimension represents a food component. Modelling nutrition in this way enables the combined effects of different food components to be quantified, and the various levels of response by the animal (e.g. intake, growth, nutrient absorption, performance) to be integrated within this multi-dimensional context (Raubenheimer and Simpson 1997; Raubenheimer et al. 2009; Simpson and Raubenheimer 2012).

An important feature of this geometric framework is that the axes are scaled as amounts. Consequently, many of the factors described in a nutrient space are represented as time-integrated rates (e.g. intake over a given period, growth within the same period), while other factors can be represented either as amounts (e.g. nutrient content of a stipulated quantity of food) or as proportions (e.g. the balance of nutrients X and Y within the food, or the balance of nutrients required by the animal). Combining amounts and proportions in this way has proved a powerful approach for predicting an animal's behavioural and physiological responses to the nutritional environment (Simpson and Raubenheimer 2012).

There are, however, many situations where models of the proportional compositions of mixtures are preferable to models of the absolute amounts of the constituents (Raubenheimer 2011). First, in field work, the complex sets of interacting variables and the logistical challenges of collecting reliable data typically constrain the possibilities for nutritional studies. For example, in the field, it is challenging to measure the daily intake of nutrients by an animal, but an estimate of the proportional composition of the diet can be obtained using gut contents analysis (Hyslop 1980; Kamler and Pope 2001; Petry et al. 2007; Machovsky-Capuska et al. 2011; Tait et al. 2014), regurgitations (Schuckard et al. 2012; Tait et al. 2014), faecal analysis (Klare et al. 2011; Giri et al. 2011; Panthi et al. 2012), bite rates analysis (Shrader et al. 2006; Paddack et al. 2006) and related methods. Second, field-based questions often relate directly to proportions rather than absolute amounts, as is the case where the nutritional compositions of different foods or of foods versus non-foods are compared. Third, for some purposes, the inclusion of amounts in the model will introduce noise or surplus information, which is avoided in an analysis of compositions. For example, a comparison of the diets versus body composition of animals from different trophic levels can be made using proportional compositions (Fagan et al. 2002; Raubenheimer et al. 2007), whereas analysis of absolute amounts of nutrients in, say, a predator and its various prey species would introduce variance associated with body size, thus complicating the model for little benefit. Fourth, because proportional measures such as food compositions are easy to obtain compared to measures

of absolute amounts (e.g. daily intakes), there exists a wealth of data in the literature from which compositional data can be extracted for comparative and meta-analyses. For instance, Raubenheimer and Rothman (2013) were able to examine the nutritional correlates of insectivory in humans and other primates using published data on the compositions of prey insects, when very few measures of amounts of insects eaten were available.

Recently, a graphical approach, the right-angled mixture triangle (RMT), was recommended as a complementary geometric framework for problems in nutritional ecology that involve primarily proportional data (Raubenheimer 2011). Like amounts-based nutritional geometry, RMT provides a graphic model in which various facets of animal nutrition can be represented and interrelated within a multidimensional context, but the axes represent proportions of nutrients in mixtures (e.g. an animal's diet) rather than amounts. The exclusion of amounts in the model frees up a dimension in RMT plots, enabling the relationships among  $n$  components to be visualised in an  $n - 1$  dimensional space. This property is particularly useful for representing three components in a regular two-dimensional plot, because two-dimensional plots are intuitively accessible and many problems in nutritional ecology concern three-component mixtures. For example, numerous studies have demonstrated the importance of the macronutrients protein, carbohydrate, and fat in the nutritional responses of animals (Barboza et al. 2009; Simpson and Raubenheimer 2012; see also supplementary table in Raubenheimer et al. 2009), and the elements nitrogen, carbon, and phosphorus have been identified in the science of ecological stoichiometry as important drivers of ecosystem dynamics (Sterner and Elser 2002). There are, however, also ways to represent more than three components in RMTs (Raubenheimer 2011).

Although RMT is technically different from amounts-based nutritional geometry (henceforth ABNG), the two approaches are complementary means for addressing similar questions under different circumstances. In contrast with RMTs, however, the widespread application of ABNG in laboratory studies has yielded a substantial body of concepts around multidimensional analyses of nutritional problems, the utility of which has been demonstrated in a range of systems, questions and contexts (Simpson and Raubenheimer 2012). For example, using this approach Lee et al. (2008) and Solon-Biet et al. (2014) have demonstrated that the life-extending effects of mild dietary deprivation are not due to "caloric restriction" as widely assumed, but rather specific effects of macronutrient ratios. This has taken a number of years, partly because the data suitable for amounts-based geometric analyses are seldom found pre-existent in the literature, but require de-novo studies designed for the purpose (although exceptions do

exist: Simpson and Raubenheimer 1997; Raubenheimer and Simpson 1997; Lee et al. 2008).

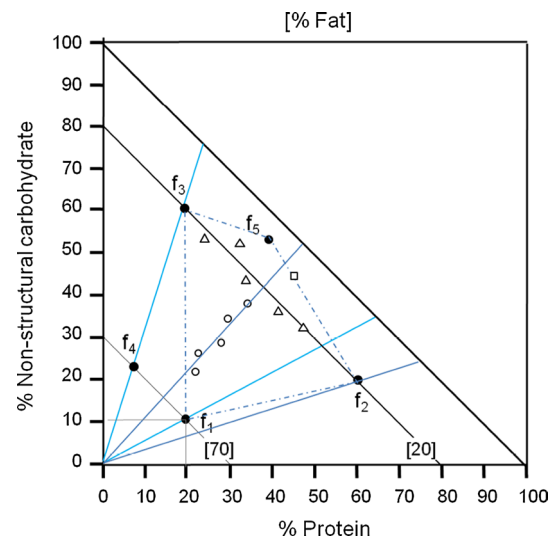
Here, we illustrate the use of RMTs for addressing important questions in field-based nutritional ecology, with the aim of contributing to the development of a conceptual framework for the study of animal nutrition in the wild. We are able to do so by drawing on the conceptual foundation already developed in ABNG, and capitalising on the abundant proportions-based literature data. Primates provide an excellent system for our analyses, because a long history of field studies with observational data of individuals has yielded abundant data enabling us to illustrate how RMTs may be used to address a range of significant questions in nutritional ecology. We also illustrate how RMTs can be used as a synthetic and comparative tool for integrating the wealth of published data on the nutritional ecology of animals. Such integration is a powerful means for developing new insights and hypotheses, as has recently been done in relation to the ways that appetite and regulatory physiology interact with economics and global change to generate obesity in humans and companion animals (Raubenheimer et al. 2014).

### The right-angled mixture triangle

Details of the history, derivation, and logic of the RMT are provided by Raubenheimer (2011). In brief, RMTs provide a means to represent mixtures (e.g. foods, diets, and animal nutrient requirements) as points on a graph, and to extract information from the geometric relationships among such points. For the present purposes, there are four categories of information that we wish to illustrate: compositional representations, compositional comparisons, combinatorial constraints, and patterns of scatter (Fig. 1). These categories of information provide the basis in the rest of the paper for examples illustrating the application of RMT to specific biological problems.

In RMTs, the composition of a mixture such as a food is represented as an  $n$ -dimensional point in a space of  $n - 1$  dimensions. For example, if the macronutrients protein, carbohydrate, and fat are the focus of the model, the mixture is depicted as a 3-coordinate point in a two-dimensional plot, where each coordinate gives the proportional contribution of one of these components to the macronutrient fraction of the mixture (Fig. 1). If a fourth component is added to the model, for example fibre, then a 3-dimensional plot can be used. Higher-dimensional mixtures can be represented in various ways (Raubenheimer 2011), but models involving such data can be intractably complex and might better be parsed into a series of three- or four-dimensional analyses.

Compositional differences between two mixtures (e.g. foods) can be geometrically defined in terms of discrete



**Fig. 1** Right-angled mixture triangle showing hypothetical data representing five foods ( $f1$ – $f5$ ) and the diets (i.e. combinations of foods, *hollow symbols*) eaten by various animals. Mixture composition: each point shows the protein (P), carbohydrate (C) and fat (F) composition of the mixture. In this model, P and C are represented on the X and Y axes, respectively. Since P, C and F sum to 100 %, stipulating values for P and C implicitly fixes the value for F. For example, since food  $f1$  contains 20 % P and 10 % C, the value for F is 100 % – (20 + 10) % = 70 %; point  $f1$  therefore has X:Y:Z coordinates of (20:10:70). By the same reasoning, the P:C:F coordinates for point  $f3$  are (20:60:20). The third axis label is given in *square brackets* above the plot, and the value for the third variable is given in *square brackets* on the respective isolines for that variable. Comparing mixtures: compositional relationships between mixtures are defined by discrete vectors, or combinations of vectors: (1) points that fall on the same vertical contain the same concentration of P (e.g.  $f1$  and  $f3$  both have 20 % P); equivalently, points aligning on a horizontal have the same C concentration; (2) the radials projecting from the origin represent P:C ratio (e.g.  $f3$  and  $f4$  have the same P:C ratio, which is lower than that of  $f1$  and  $f2$ ); and (3) fat concentration is represented by *diagonals* with a slope of negative 1. The fat concentration represented by each diagonal is obtained by subtracting from 100 % the value where the diagonal intersects the P and C axes. Thus, both  $f1$  and  $f4$  contain fat at a concentration of 100 % – 30 % = 70 %, and  $f2$  and  $f3$  have a fat concentration of 100 % – 80 % = 20 %. Combining mixtures: the diets that can be composed by combining foods are constrained by the spatial relationship between the component foods. By mixing its intake from two foods an animal can compose a diet with composition that falls anywhere on the line connecting the points representing these foods, but nowhere off this line. For example, the diet represented by the *square* could be assembled by combining  $f2$  and  $f5$ , but none of the diets represented by *triangles* or *circles* could be assembled in this way. Where three or more foods are eaten, the resulting diet is confined to the *polygon* formed by joining the component foods. Thus, all the circle diets could be achieved by combining foods  $f1$ – $f3$ , as can all but one of the triangular diets (the one with composition closest to  $f5$ ). To achieve this latter diet composition, the animal would need also to eat  $f5$ . Interpreting scatter of replicate points: the pattern of scatter of replicate points can contain significant biological information. For example, the scatter among the circle diets is tightly compressed around a P:C balance vector, but spread along this vector. This could indicate that the animals prioritize dietary P:C balance over fat content. Conversely, the triangular diets are aligned with a fat vector of 20 % but span a range of P:C balances, suggesting prioritization of fat

quantitative vectors, or combinations of these; conversely, similarities between mixtures can be recognized as shared parameters within mixture space (Fig. 1). When two foods are combined to form a diet, the set of possible diets is constrained to lie on the line connecting these foods. When more than two foods are combined, the set of possible diets falls within the area joining the points representing the component foods (Fig. 1). Finally, the scatter of replicate points in an RMT can provide important biological information. Thus, if the compositions of the selected diets of several replicate animals clustered more tightly along the vector representing the balance of protein:carbohydrate than the vector for dietary fat content, this might suggest that the mechanisms regulating nutrient intake prioritize protein to carbohydrate balance over fat intake (Fig. 1).

In the sections that follow, we analyse literature data to show how the above principles can be used in field-based primate studies to model key concepts in nutritional ecology. Since many of these concepts have been developed in ABNG, we also briefly explain how each concept is represented within that framework.

#### Foods: the composition of milk

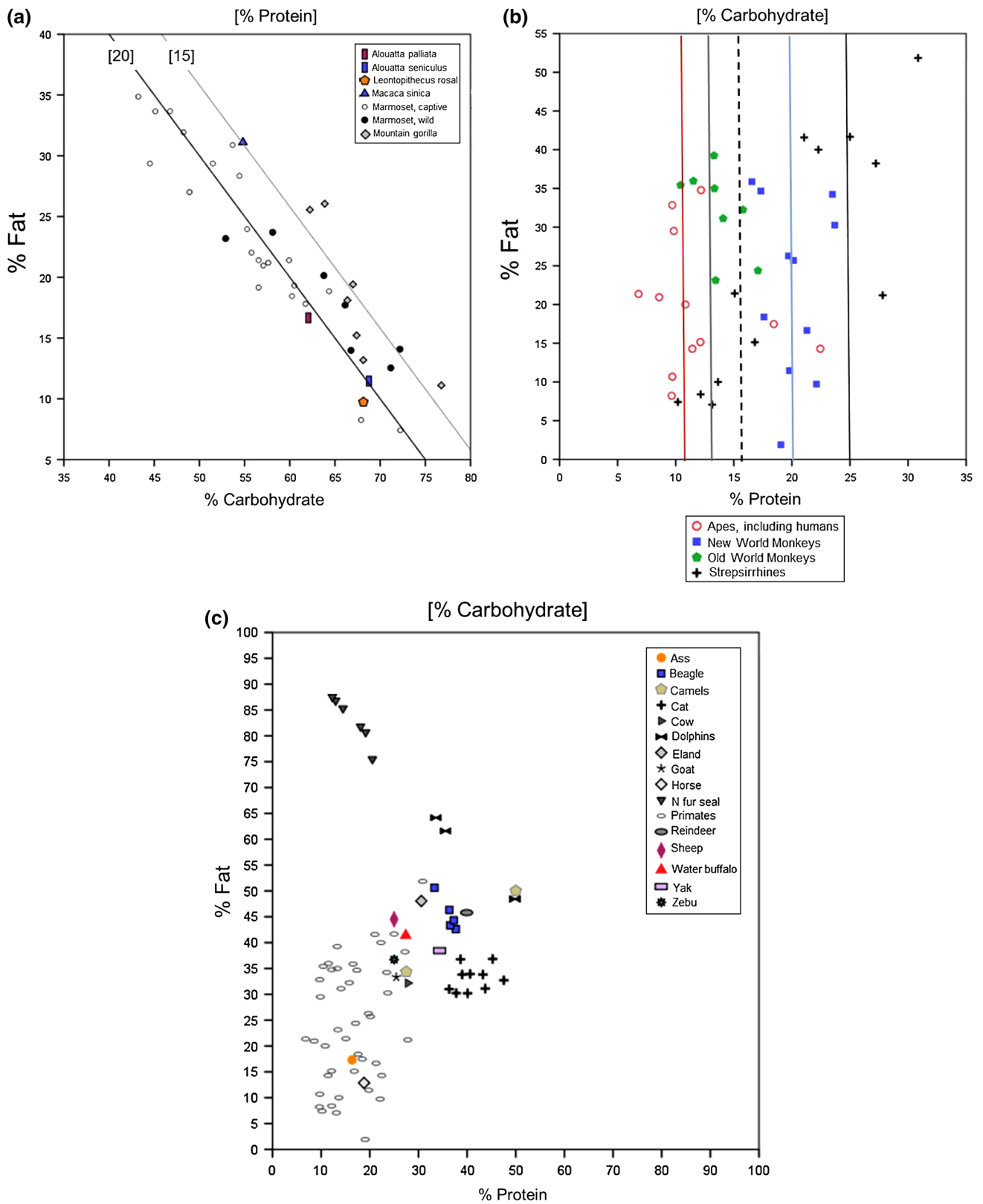
Our first example concerns the multi-component comparison of the composition of foods. In ABNG, foods are represented in two ways. First, a stipulated measure of a particular food is represented by a point with coordinates that give the amount of each of the focal nutrients. Second, the more general property that pertains to any quantity of the food, its nutrient balance, is given by the slope of the line that joins the above-mentioned point with the origin. Such lines representing the nutrient balance of a food are called “nutritional rails”, reflecting the fact that as an animal eats the food its nutritional state changes along a trajectory that is coincident with the rail for that food.

As explained above, in RMTs the composition of foods is depicted as an  $n$ -dimensional point in a space of  $n - 1$  dimensions. To illustrate the use of RMT in the analysis of food compositions, we will use as an example the macronutrient content of primate milk. In our first analysis, we plot the composition of field-collected samples of milk from six species of primates (Fig. 2a). For two of these species, common marmosets (*Callithrix jacchus*; Power et al. 2008) and mountain gorillas (*Gorilla beringei*; Whittier et al. 2010), replicate samples are plotted, thus providing information on the within-sample variability of the three nutrients. For both gorillas and marmosets, the replicate samples clustered more tightly along the negative-sloped diagonal (representing protein concentration) and were more widely spread along that vector suggesting that both species produce milk with a relatively fixed proportion of macronutrients contributed by protein, with higher intra-specific

**Fig. 2** Macronutrient composition of mammalian milk (protein, fat and carbohydrate, on a mass basis). **a** Replicate samples of milk from wild and captive common marmosets (*Callithrix jacchus*, Power et al. 2008) had a similar proportion of protein (clustered along a negative diagonal representing 20 % P), but varied in the fat:carbohydrate ratio (was spread along the diagonal). Replicate samples of milk collected from free-ranging mountain gorillas *Gorilla beringei* (Whittier et al. 2010) also had a relatively constant protein content, but this was lower (clustered along the diagonal representing 15 % P) than marmoset milk. Also plotted are single milk samples collected in the field from four other primate species, three of which had similar protein content to marmoset milk and the fourth had similar protein content to gorilla milk, but a higher fat:carbohydrate ratio. **b** Comparison of macronutrient content in the milks of apes, New World monkeys, Old World monkeys and Strepsirrhines. Mean protein content was lowest in apes (11.3 %, indicated by the red line), intermediate in Old World monkeys (13.6 %, grey line) and highest in New World monkeys (20.0 %, blue line). Strepsirrhines split into two clusters, one with intermediate protein (16 %, dashed black line) and low fat, and the other with higher protein (25 %, solid black line) and higher fat. The two clusters of Strepsirrhines represent different dietary groups: the former being herbivorous, and the latter including a substantial portion of insects in the diet. Data from Hinde and Milligan (2011). **c** Comparison of macronutrient content in the milks of primates with a range of non-primate mammals. Primate milks generally have low protein and fat, with high carbohydrate content compared with the other mammals (colour figure online)

variation in the fat:carbohydrate ratios. This has previously been noted for common marmosets (Power et al. 2008) and tufted capuchins (Milligan 2010; see also Raubenheimer 2011), and Fig. 2a shows that a similar pattern exists for mountain gorillas. Raubenheimer (2011) suggested that this pattern might reflect physiological regulation by the mother to ensure that the suckling infant obtains a diet that is balanced with respect to the protein:non-protein ratio, a parameter that is commonly achieved through food selection and complementary feeding in weaned animals (Simpson and Raubenheimer 2012). Relatively high variability in the carbohydrate:fat ratio likely reflects their substitutability as sources of non-protein energy, as has been demonstrated through the patterns of macronutrient selection in several species including fish (Ruohonen et al. 2007), domestic dogs (Hewson-Hughes et al. 2013), grizzly bears (Erlenbach et al. 2014) and humans (Simpson and Raubenheimer 2005).

Given the logistical challenges of collecting milk from primates in the field, an important question is to what extent the milk of captive animals resembles that of conspecifics in the wild. To address this, Power et al. (2008) considered samples from both wild common marmosets (plotted as filled circles in Fig. 2a) and captive conspecifics (hollow circles). The protein content of the milk from captive and wild marmosets was relatively constant with more variation in the balance of fat:carbohydrate. Further, the analysis of Power et al. (2008) showed that the protein content of the milk from the two groups did not differ statistically, as is suggested in Fig. 2a by the alignment



of the samples from the two groups along the same protein isoline (negative diagonal). On the other hand, the captive marmosets had a higher fat:carbohydrate ratio than wild

marmosets, as indicated by their displacement to the left along the protein isoline (Fig. 2a), although there was substantial overlap. Overall, this suggests that milk taken from

captive marmosets might be representative of wild samples with respect to the ratio of protein:non-protein energy, but the balance of fat to carbohydrate is more context specific.

Despite the fact that the concentration of protein was maintained relatively constant in the milk of both marmosets and gorillas, there was also a marked difference in the milk of these two species. The milk of gorillas clustered along an isoline representing a lower protein concentration (displaced further from the origin, mean 14 %) than marmosets (20 %) ( $t_{1,34} = 3.76$ ,  $P < 0.001$ , independent samples  $t$  test). Also plotted are single milk samples from four other primates. Three of these had similar protein content to marmoset milk (*Alouatta palliata*, *A. seniculus*, and *Leontopithecus rosalia*), and the fourth (*Macaca sinica*) had similar protein content to mountain gorilla milk but a higher fat:carbohydrate ratio.

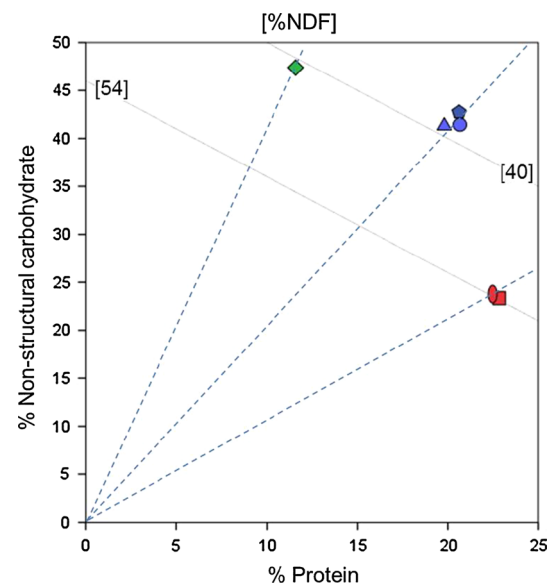
Is the proportional protein content more generally a dimension that distinguishes the milk of different primates? Hinde and Milligan (2011) presented data which suggest that this is the case. These data, plotted as an RMT in Fig. 2b, show that across several species of apes, Old World Monkeys and New World monkeys, protein was relatively constant within groups compared with fat and carbohydrate, but differed between primate groups. Apes had the lowest protein content (mean  $\pm$  SE =  $11.3 \pm 1.27$  %), followed by Old World monkeys ( $13.6 \pm 0.75$  %) and New World Monkeys ( $20.0 \pm 0.72$  %) ( $P < 0.0001$ , independent samples Kruskal–Wallis test). A fourth group, the Strepsirrhines, separated into two sub-groups, which corresponded with dietary differences. Milk from the herbivorous Strepsirrhines had lower protein ( $16 \pm 2.19$  %) and fat ( $13 \pm 2.39$  %) than that from species that include a substantial proportion of insects (at least 27 %, National Research Council 2003) in the diet (protein =  $25 \pm 1.76$  %, fat =  $43 \pm 2.38$  %). These differences did not, however, stand up to a more conservative phylogenetic analysis (mean logit difference  $\pm$ CI, protein =  $-0.454$ ,  $-1.577$  to  $0.702$ ; fat =  $-1.591$ ,  $-3.090$  to  $0.140$ ; phylogenetic mixed model approach, as described by Hadfield and Nakagawa 2010). It would be worth exploring this question using a larger sample size.

Finally, Fig. 2c compares the data for primate milk with equivalent data for other mammals. The plot shows that only the horse and the ass fell within the range for primates, whereas most other milks had higher proportional protein and/or fat content than primates, clearly showing that the milk of primates differs markedly from other mammals in terms of its protein concentration. In addition, primates produce relatively dilute milks with lower energy density than other mammals (Hinde and Milligan 2011); although not illustrated here, this can readily be modelled using RMT (Raubenheimer 2011). Comparative analysis suggests that such variation in the composition of

mammalian milk is due to a combination of phylogeny and specific adaptations such as diet and life histories (Skibieli et al. 2013).

#### Diets: Comparative nutrient intakes

RMTs also provide a means to visualise and compare the relationships between the mixtures of foods eaten by animals and the resulting nutrient gains (i.e. animal diets). Figure 3, for example, presents the estimated annual intakes of protein, non-structural carbohydrate and fibre in the plant-derived component of the diets of six wild primates, representing five species. These are chimpanzees (*Pan troglodytes*), blue monkeys (*Cercopithecus mitis*), red-tailed monkeys (*Cercopithecus ascanius*), and grey-cheeked mangabey (*Lophocebus albigena*) in Kibale National Park, Uganda, and mountain gorillas in Bwindi National Park, Uganda, and Virunga National Park, Rwanda. Plotting the diets of these populations in this way clearly illustrates



**Fig. 3** Protein, non-structural carbohydrate (NSC) and neutral-detergent fibre composition of the plant-derived component of the diets of chimpanzees and three species of monkeys from Kibale National Park, Uganda, compared with mountain gorillas from Bwindi and Virunga (chimpanzees *Pan troglodytes*, green diamond; blue monkey *Cercopithecus mitis*, blue circle; red-tailed monkey *Cercopithecus ascanius*, blue pentagon; mangabey *Lophocebus albigena*, blue triangle; Virunga gorillas, red ellipse; Bwindi gorillas, red square). Radials show the protein:NSC ratio, and the negative diagonals the %NDF. The three different species of monkeys living in overlapping home ranges had very similar dietary composition, as did the two populations of mountain gorillas living in different habitats. Chimpanzees, which overlap in habitat with the monkeys, had a lower protein:carbohydrate ratio than the other species, but similar proportional NDF intake as the monkeys (40 %). The diet of gorillas had the highest protein:carbohydrate ratio, and also the highest concentration of NDF (54 %) (colour figure online)

several interesting patterns in a single plot. First, the balance of protein, non-structural carbohydrates, and fibre in the plant tissues eaten by the three monkey species was remarkably similar (Conklin-Brittain et al. 1998). It is interesting that the plant component of the diet of red-tailed monkeys did not differ from the other two monkey species, even though, in addition to plants, red-tailed monkeys also include a significant proportion of high-protein insects in their diet (Rode et al. 2006; Bryer et al. 2013). This suggests that omnivory in this species is associated with a higher protein target than the other monkey species, rather than complementary feeding to achieve a similar nutritional target (Raubenheimer and Jones 2006). Second, the fibre content of the diets of chimpanzees and the three monkey species was similar, but the proportion of fibre in the diets of gorillas was higher. Third, the protein:non-structural carbohydrate ratio in the diets of these primates increased from chimpanzees to gorillas, with the diets of monkeys being intermediate. Finally, the intakes of the two gorilla populations converged in the nutrient space, despite the fact that they lived in two geographically separate and botanically very distinct forests (Rothman et al. 2007). This is significant, for reasons that we explain next.

#### Role of nutritional regulation in diet selection

Amounts-based nutritional geometry has been used in laboratory experiments to demonstrate that many animals actively regulate their intake of different nutrients separately to track an intake target. Known instances include herbivores, omnivores, and predators, spanning invertebrates and vertebrates (Simpson and Raubenheimer 2012). It is important in investigating this issue to determine the extent to which the composition of the selected diet results from active, homeostatic regulation of intake, or is simply a passive consequence of the composition of available foods (Raubenheimer et al. 2012).

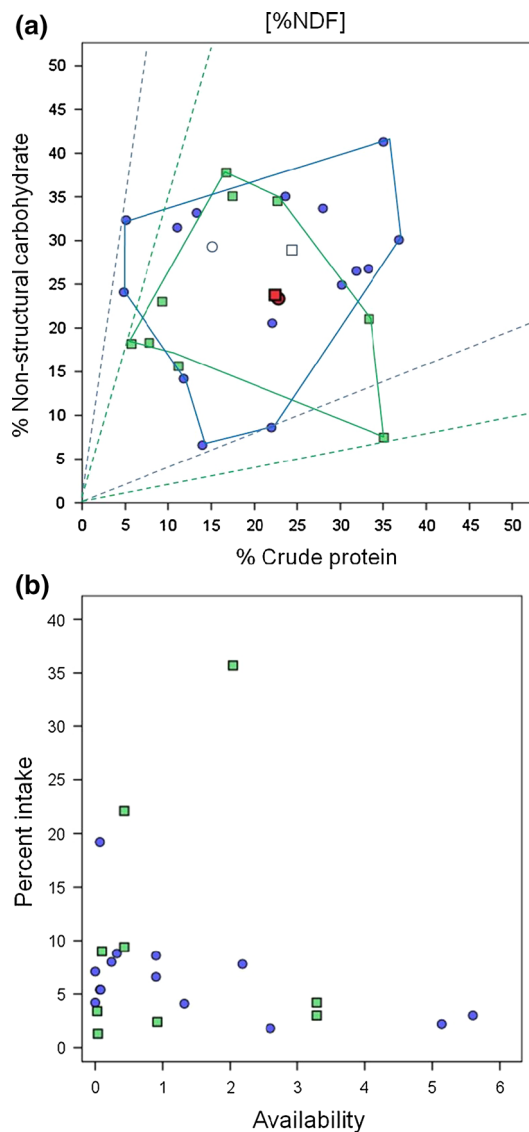
There are several ways to do this. One approach is to compare the intakes of two or more groups of similar animals that are provided with different nutritionally complementary food combinations. In this design, the animals in the different experimental groups have to spread their feeding among the foods differently to achieve the same nutrient gain, because combining the foods in similar proportions will result in different nutrient gains. Chambers et al. (1995) took this approach in experiments on the African migratory locusts (*Locusta migratoria*). There were four groups of locusts, each of which was given a pair of synthetic foods: one containing a protein:carbohydrate (P:C) ratio of 1:2 and the other of 2:1. The treatments differed, however, in the extent to which the foods were diluted using indigestible cellulose: the macronutrient mixture comprised either 42 % (dry weight) of both foods, 21 % of

both foods, or 21 % of one food and 42 % of the other. If the locusts in the different experimental groups ate similar amounts of the respective food pairings, then they would end up with very different nutrient intakes. This was not the case: the locusts spread their feeding across their respective food pairings in such a way that the nutrient intake points of the four groups converged tightly in the nutrient space. These results demonstrate that locusts faced with variation in the composition of available foods alter their feeding behaviour to maintain a target macronutrient intake.

Demonstrating macronutrient regulation to a target intake by free-ranging animals in the wild is more challenging. However, the core principle of testing for constant nutrient intake in the face of variation in food composition applies equally in the laboratory and field. Using RMT, this would mean comparing the nutrient gains of different groups of the animals when feeding on disparate food combinations. If the foods are combined in different proportions that result in a diet of similar nutrient balance, then this suggests that diet selection is driven by nutrient-specific regulation; i.e. the animals in different environments are regulating food intake so as to gain the required balance of nutrients. It is, however, also possible that the distribution of food compositions in the respective environments is, by coincidence, such that diet selection using criteria other than nutrient requirements (e.g. frequency-dependent selection of foods) results in similar nutrient gain across environments. This possibility can be addressed by comparing the frequency of different foods in the diet and environment.

An example of such an analysis to test for nutrient-based food selection in the wild is given in Fig. 4a. The plot shows the estimated annual intake of protein, non-structural carbohydrate, and fibre in the diets of mountain gorillas in Virunga and Bwindi National Parks (the same data as in Fig. 3). Also shown are the compositions of all the foods that contributed 1 % or more of the diets by weight (these cumulatively amounted to 90 and 96 % of the diets of the Virunga and Bwindi populations, respectively; Rothman et al. 2007). This figure shows that the similar nutrient intakes of the two populations were compiled from different combinations of foods, an outcome which suggests that the diet of these gorillas is determined by active nutrient regulation.

As noted above, it remains possible, however, that the similar nutrient intakes of Bwindi and Virunga gorillas were a passive consequence of the relative availabilities of different foods in the two habitats. If this were the case, then observed diet compositions of the two populations would correspond with the hollow square (Virunga) and circle (Bwindi) in Fig. 4a. Visually, it appears that this is not the case. To evaluate this statistically, we tested for relationships between percentage contribution to the diet



**Fig. 4** **a** Protein, non-structural carbohydrate (NSC) and neutral-detergent fibre ratios of the principal foods (those contributing >1 % to the diet) and diet composition of two allopatric populations of mountain gorillas, in Virunga and Bwindi National Parks, Uganda. Circles represent the foods (blue) and diet composition (red) of Bwindi gorillas, and squares represent the foods (green) and diet (red) of Virunga gorillas. The hollow circle and square represent the expected diet composition of Bwindi and Virunga gorillas, respectively, if foods were eaten in proportion to their availability. The line joining the outermost foods from each site delineates the accessible space available to each gorilla population given its choice of foods. Despite the foods differing between the sites, the composition of the diet ingested by the two populations of gorillas was closely similar, but different from the expected diet if feeding was proportional to availability. **b** Scatterplot of the relationship between availability and percentage contribution of foods to the diets of Bwindi (blue circles) and Virunga (green squares) gorillas. The lack of positive correlation suggests that foods were not eaten in proportion to their availability (Virunga: Spearman's  $\rho = -0.465$ ,  $P = 0.094$ ; Bwindi: Spearman's  $\rho = 0.160$ ,  $P = 0.682$ ). Food availability within the home ranges of Bwindi and Virunga gorillas was estimated by Plumptre (1995) and by Ganas et al. (2004), respectively. Data from Rothman et al. (2007) (colour figure online)

of the foods and their relative availability in the respective habitats (Fig. 4b). There was no significant relationship, suggesting that the similar dietary compositions of gorillas in Bwindi and Virunga were not a passive consequence of food availability, but involved selection of foods in a pattern that was disproportionate in relation to availability.

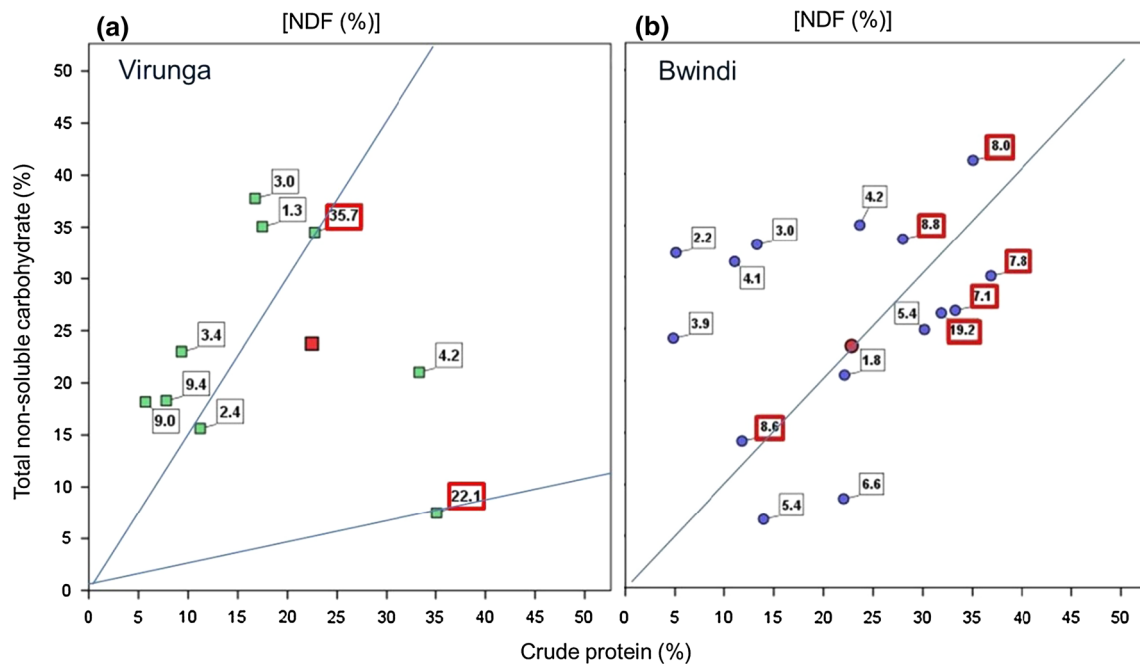
Further, Fig. 5a, b shows that the mechanism for achieving the observed nutrient gains differed between the populations. In the Virunga gorillas, 36 and 22 % of the diet were contributed from the first and second highest-ranking foods in the diet, respectively. The top contributing food had a protein:carbohydrate ratio that was lower than the overall diet, while the second had protein:carbohydrate ratio that was appreciably higher than the diet. This shows that 58 % of the diet of the Virunga gorillas was constituted by mixing two nutritionally complementary foods. In contrast, the relationships among the top-ranking foods that comprised 58 % of the diet of Bwindi gorillas were very different. In this case, six foods were involved, all of which had a protein:carbohydrate ratio similar to the diet overall. The diet of Bwindi gorillas was therefore composed largely from foods that had a similar balance to the selected intake point, with complementary mixing of disparate foods playing a lesser role than for the Virunga gorillas.

#### Digestive efficiencies

The functional significance of nutrition derives from the interaction of ingestion and post-ingestive processing of foods. Amounts-based geometric analysis can investigate this issue, by constructing multi-component nutrient budgets in which the amounts of the focal nutrients ingested, used, and excreted are plotted separately in the same nutrient space (Raubenheimer et al. 2009). Measuring post-ingestive processing of dietary components in this way is more challenging for free-ranging wild animals, because of the difficulties of estimating for an individual the amounts of a food eaten and amounts of faeces produced from that food.

It is, however, possible using RMTs to estimate the relative digestive priorities of wild animals by comparing the compositions of their foods and faeces (Raubenheimer 2011). To illustrate, Fig. 6 shows an example concerning the fibre components (cellulose, hemicelluloses, and lignin) in fruit and leaves eaten by juvenile, female and silverback gorillas from Bwindi, and in the faeces associated with fruit- and leaf-eating periods. The plot shows, firstly, that there was no distinct separation of fruit and leaves in the composition space, indicating that the fibre composition of these two foods did not differ (as noted previously by Rothman et al. 2006). Secondly, the ratio of lignin:hemicellulose was higher in the faeces than the foods, reflecting the fact that lignin is undigestible for gorillas whereas





**Fig. 5** Food and diet composition of Virunga (a) and Bwindi (b) gorillas plotted separately (symbols and data as in Fig. 4a). Also shown is the % contribution of each food to the diet, with the top-ranking foods that jointly contributed approximately 60 % of the diet highlighted in red boxes. The comparison shows that 58 % of the Virunga diet was comprised by two foods, one with a protein:carbohydrate ratio that was considerably greater than, and the other smaller than, that of the diet composition. This dem-

onstrates that the diet of Virunga gorillas was assembled to a large extent through complementary feeding. By contrast, 60 % of the diet of Bwindi gorillas was composed from 6 foods, all of which had a protein:carbohydrate ratio that closely resembled the diet composition. This suggests a stronger role in the selection by gorillas in Bwindi of foods that are balanced with respect to protein:carbohydrate, with a minimal role for complementary feeding (colour figure online)

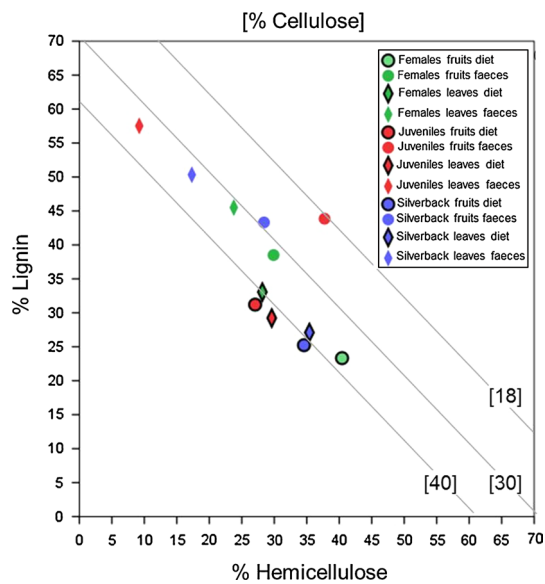
hemicellulose is partly digested (Van Soest 1994; Remis 2000; Remis and Dierenfeld 2004). Thirdly, hemicellulose was extracted from leaves to a greater extent than fruits, as shown by the higher lignin:hemicellulose ratio in leaf-derived than fruit-derived faeces. Finally, the points for foods aligned on a diagonal that is closer to the origin than the points for faeces, showing that the faeces were depleted of cellulose relative to the foods. Overall, this analysis shows that hemicellulose is depleted in the faeces of gorillas relative to lignin, and this depletion is more pronounced when eating leaves than fruit, reflecting the fact that leaf diets are more digestible than fruit diets, due to the large seeds in fruits that are not digested (Rothman et al. 2008). Cellulose, too, is depleted in the faeces compared with the foods, but in this case there was no apparent difference between fruits and leaves.

## Conclusions

We have used published data on primates to illustrate how RMTs can be used to address a range of questions in nutritional ecology. These span from basic questions concerning, for example, the variation in the composition of

primate milk, to questions of practical importance in the conservation of biological diversity. For example, by better understanding the ways in which animals balance their nutrient intake needs, we are better informed about their habitat needs. Bears on salmon streams are a good example: while it had previously been thought that salmon intake maximisation is the best strategy for bears, it has become clear in recent studies that bears can minimise energetic requirements by appropriately balancing their protein to non-protein energy ratio (Erlenbach et al. 2014). Similarly, a recent study showed that giant pandas migrate between two habitats to balance their intake of calcium, phosphorus and protein (Nie et al. 2014). In both cases, conservation decisions would need to take into account the non-substitutability of habitats on which these species rely to balance their nutrition.

There are several reasons why nutritional geometry in general, including RMT and ABNG, is a powerful tool for addressing such questions. First, it provides a means of conceptualising nutrition in more than one dimension, thereby capturing both the independent and interactive effects of nutrients on animals. Numerous studies have shown that these interactive effects play a substantial role in influencing animals—their behaviour, physiology, life



**Fig. 6** Use of RMT to investigate relative digestive efficiencies of fibre components of dietary fruits (*circles*) and leaves (*triangles*) by comparing the foods (*symbols with black outline*) with faeces (*symbols without black outline*). Colours distinguish juveniles (*red*), adult females (*green*) and silverback (*blue*) mountain gorillas. The data show that, for adult female and silverback gorillas and both food types, faeces were lower in hemicellulose (shift to the left) and cellulose and higher in lignin relative to matched foods. The data also suggest that the faeces derived from leaves (comparison of *triangles with and without black outline*) were reduced in hemicellulose relative to lignin to a greater extent than faeces derived from fruits (comparison of *circles with and without black outline*). The same pattern applies for leaves eaten by juveniles (comparison of *red triangles with and without black outline*), whereas faeces derived from fruits eaten by juveniles were enriched in both lignin and hemicellulose, and depleted to a greater extent in cellulose (18 vs. 30 % for other faecal samples) (comparison of *red circles with and without black outline*) (colour figure online)

history, ecology and evolution (Despland and Noseworthy 2006; Behmer and Joern 2008; Hawlena and Schmitz 2010; Simpson and Raubenheimer 2012; Saravanan et al. 2012). Second, the geometric space provides a device in which salient components of the interaction of animal and environment can be conceptually and quantitatively interrelated in common, multi-dimensional, terms. Examples presented here include foods, diets, and faecal composition, and others have been discussed elsewhere (Raubenheimer et al. 2009; Simpson and Raubenheimer 2012). Third, nutritional geometry is versatile, because different combinations of axes (e.g. nutrients) and model components (e.g. foods, diets) can be selected to address specific problems. Finally, although not illustrated in the present paper, non-nutritional variables (e.g. life-history responses to nutritional state) can be incorporated into geometric models using response surface methodology (Lee et al. 2008; Jensen et al. 2012; Blumfield et al. 2012).

Amounts-based nutritional geometry has been applied extensively in laboratory studies, yielding advances in, among other fields, foraging theory (Raubenheimer et al. 2007, 2009), life-history theory (Lee et al. 2008; Maklakov et al. 2009; Simpson and Raubenheimer 2010; Jensen et al. 2012), conservation (Raubenheimer and Simpson 2006), causes of human obesity (Simpson et al. 2003; Simpson and Raubenheimer 2005; Gosby et al. 2011; Raubenheimer et al. 2014), and the design of feeds for agriculture (Ruohonen et al. 2007) and companion animals (Hewson-Hughes et al. 2011, 2012). The potential of nutritional geometry for field studies with ecological applications is receiving increasing attention (Raubenheimer et al. 2009, 2012; Simpson et al. 2010; Kearney et al. 2010, 2012; Tait et al. 2014). A limitation, however, is that accurate amounts-based data on animal foraging can be challenging or impossible to collect in the field. To date, only three field projects have succeeded in this respect: Peruvian spider monkeys (*Ateles chamek*, Felton et al. 2009a, b), mountain gorillas (Rothman et al. 2011) and chacma baboons (*Papio hamadryas ursinus*; Johnson et al. 2013). For this reason, Raubenheimer (2011) introduced the RMT as a proportions-based modelling platform that is less demanding of data and can be applied broadly in field studies. The examples presented here are intended to illustrate how concepts developed in ABNG can be represented in RMT, including foods, diets, nutritional regulation, and digestive efficiencies. Primates provide a fitting system, because the extent to which they have been studied in the wild provides abundant published data for our illustration.

This highlights a further strength of RMT, namely that they can readily be applied to re-analyses of the substantial proportions-based published data (e.g. of food compositions), whereas there are fewer amounts-based data available in the literature (but see Simpson and Raubenheimer 1997 for rats, Raubenheimer and Simpson 1997 for chickens, and Lee et al. 2008 for flies). This enables RMT to be used in literature-based studies, as demonstrated by Raubenheimer and Rothman (2013) in their investigation of the nutritional drivers of insectivory in humans and other primates. It is hoped that the present paper will both stimulate synthetic studies of published data on animal foraging and diet choice, and help to frame new studies that will contribute to the understanding of comparative nutritional ecology.

**Acknowledgments** We are grateful to Dr Alistair Senior for assistance with the comparative analysis of primate milk compositions. This research was partially funded by Faculty of Veterinary Science Research Fund, The University of Sydney. D.R. is part-funded by Gravidia, The National Research Centre for Growth and Development, New Zealand.

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Barboza PS, Parker KL, Hume ID (2009) Integrative wildlife nutrition. Springer, Berlin
- Behmer ST, Joern A (2008) Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proc Natl Acad Sci USA* 105:1977–1982
- Blumfield M, Hure A, Macdonald-Wicks LK, Smith R, Simpson SJ, Raubenheimer D, Collins C (2012) The association between the macronutrient content of maternal diet, adequacy of micronutrients during pregnancy. *Nutrients* 4:1958–1976
- Bowen SH, Lutz EV, Ahlgren MO (1995) Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* 76:899–907
- Bryer MAH, Chapman CA, Rothman JM (2013) Diet and polyspecific associations affect spatial patterns among redtail monkeys (*Cercopithecus ascanius*). *Behaviour* 150:277–293
- Chambers PG, Simpson SJ, Raubenheimer D (1995) Behavioural mechanisms of nutrient balancing in *Locusta migratoria*. *Anim Behav* 50:1513–1523
- Conklin-Brittain NL, Wrangham RW, Hunt KD (1998) Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II: macronutrients. *Int J Primatol* 19:971–998
- Dearing MD, Schall JJ (1992) Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. *Ecology* 73:845–858
- DeGabriel JL, Moore BD, Felton AM, Ganzhorn JU, Stolter C, Wallis IR, Johnson CN, Foley WJ (2014) Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. *Oikos* 123:298–308. doi:10.1111/j.1600-0706.2013.00727.x
- Despland E, Noseworthy M (2006) How well do specialist feeders regulate nutrient intake? Evidence from a gregarious tree-feeding caterpillar. *J Exp Biol* 209:1301–1309
- Erlenbach JA, Rode KD, Raubenheimer D, Robbins CT (2014) Macronutrient optimization and energy maximization determine diets of brown bears. *J Mammal* 95:160–168
- Fagan WF, Siemann E, Denno RF, Mitter C, Huberty AF, Woods HA, Elser JJ (2002) Nitrogen in insects: implications for trophic complexity and species diversification. *Am Nat* 160:784–802
- Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, Lindenmayer DB (2009a) Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behav Ecol* 20:685–690
- Felton AM, Felton A, Wood JT, Foley WJ, Raubenheimer D, Wallis IR, Lindenmayer DB (2009b) Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choices. *Int J Primatol* 30:675–696
- Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, Mcneilage A (2004) Dietary variability of mountain gorillas in Bwindi impenetrable national park, Uganda. *Int J Primatol* 25:1043–1072
- Giri S, Aryal A, Koirala RK, Adhikari B, Raubenheimer D (2011) Feeding ecology and distribution of Himalayan serow (*Capricornis thar*) in Annapurna conservation area. *Nepal World J Zool* 6:80–85
- Gosby AK, Conigrave AD, Lau NS, Iglesias MA, Hall RM, Jebb SA, Brand-Miller JI, Caterson D, Raubenheimer D, Simpson SJ (2011) Testing protein leverage in lean humans: a randomised controlled experimental study. *PLoS ONE* 6:e25929
- Hadfield JD, Nakagawa S (2010) General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J Evol Biol* 23:494–508
- Hawlena D, Schmitz OJ (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *Am Nat* 176:537–556
- Hewson-Hughes AK, Hewson-Hughes VL, Miller AT, Hall SR, Simpson SJ, Raubenheimer D (2011) Geometric analysis of macronutrient selection in the adult domestic cat, *Felis catus*. *J Exp Biol* 214:1039–1051
- Hewson-Hughes AK, Hewson-Hughes VL, Colyer A, Miller AT, Hall SR, Raubenheimer D, Simpson SJ (2012) Consistent proportional macronutrient intake selected by adult domestic cats (*Felis catus*), despite variations in dietary macronutrient and moisture content of foods offered. *J Comp Physiol B*, pp 1–12
- Hewson-Hughes AK, Hewson-Hughes VL, Colyer A, Miller AT, McGrane SJ, Hall SR, Butterwick RF, Simpson S (2013) Geometric analysis of macronutrient selection in breeds of the domestic dog, *Canis lupus familiaris*. *Behav Ecol* 24:293–304
- Hinde K, Milligan LA (2011) Primate milk: proximate mechanisms and ultimate perspectives. *Evol Anthr* 20:9–23
- Hyslop EJ (1980) Stomach contents analysis—a review of methods and their application. *J Fish Biol* 17:411–429
- Jensen K, Mayntz D, Toft S, Clissold FJ, Hunt J, Raubenheimer D, Simpson SJ (2012) Optimal foraging for specific nutrients in predatory beetles. *Proc R Soc Lond B* 279:2212–2218
- Johnson CA, Raubenheimer D, Rothman JM, Clarke D, Swedell L (2013) 30 Days in the life: daily nutrient balancing in a wild chacma baboon. *PLoS ONE* 8:e70383. doi:10.1371/journal.pone.0070383
- Kamler JF, Pope KL (2001) nonlethal methods of examining fish stomach contents. *Rev Fish Sci* 9:1–11
- Kearney M, Simpson SJ, Raubenheimer D, Helmuth B (2010) Modelling the ecological niche from functional traits. *Philos Trans R Soc Lond B* 365:3469–3483
- Kearney MR, Simpson SJ, Raubenheimer D, Kooijman SALM (2012) Balancing heat, water and nutrients under environmental change: a thermodynamic niche framework. *Funct Ecol* 4:950–966
- Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Rev* 41:294–312
- Lambert, JE (2010) Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campbell C, Fuentes A, MacKinnon KC, Panger M, Bearder S (eds) *Primates in Perspective*, 2nd edn. Oxford University Press, Oxford
- Lee KP, Simpson SJ, Clissold FJ, Brooks R, Ballard JWO, Taylor PW, Soran N, Raubenheimer D (2008) Lifespan and reproduction in drosophila: new insights from nutritional geometry. *Proc Natl Acad Sci USA* 105:2498–2503
- Machovsky-Capuska GE, Dwyer SL, Alley MR, Stockin KA, Raubenheimer D (2011) Evidence for fatal collisions and kleptoparasitism while plunge diving in Gannets. *Ibis* 153:631–635
- Maklakov AA, Hall MD, Simpson SJ, Dessmann J, Clissold FJ, Zajitschek F, Lailvaux SP, Raubenheimer D, Bonduriansky R, Brooks RC (2009) Sex differences in nutrient-dependent reproductive ageing. *Aging Cell* 8:324–330
- Milligan LA (2010) Milk composition of captive tufted capuchins (*Cebus apella*). *Am J Primatol* 72:81–86
- National Research Council (2003) Nutrient requirements of nonhuman primates, 2nd edn. National Academic Press, Washington
- Nie Y, Zhang Z, Raubenheimer D, Elser JJ, Wei W, Wei F (2014) Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. *Funct Ecol*. doi:10.1111/1365-2435.12302
- Paddack MJ, Cowen RK, Sponaugle S (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25:461–472
- Panthi S, Aryal A, Lord J, Adhikari B, Raubenheimer D (2012) Summer diet and habitat ecology of red panda (*Ailurus fulgens fulgens*) in Dhopatan hunting reserve. *Nepal Zool Stud* 51:701–709
- Parker KL (2003) Advances in the nutritional ecology of cervids at different scales. *Ecoscience* 10:395–411

- Petry MV, Fonseca VSD, Scherer AL (2007) Analysis of stomach contents from the black-browed albatross, *Thalassarche melanophris*, on the coast of Rio grande do sul, southern Brazil. *Polar Biol* 30:321–325
- Plumptre AJ (1995) The chemical composition of montane plants and its influence on the diet of large mammalian herbivores in the Parc National des Volcans, Rwanda. *J Zool* 235:323–337
- Power ML, Verona C, Ruiz-Miranda CE, Oftedal OT (2008) The composition of milk from free-living common marmosets (*Callithrix jacchus*) in Brazil. *Am J Primatol* 70:78–83
- Raubenheimer D (2011) Toward a quantitative nutritional ecology: the right-angled mixture triangle. *Ecol Monogr* 81:407–427
- Raubenheimer D, Jones SA (2006) Nutritional imbalance in an extreme generalist omnivore: tolerance and recovery through complementary food selection. *Anim Behav* 71:1253–1262
- Raubenheimer D, Rothman JM (2013) The nutritional ecology of entomophagy in humans and other primates. *Annu Rev Entomol* 58:141–160
- Raubenheimer D, Simpson SJ (1993) The geometry of compensatory feeding in the locust. *Anim Behav* 45:953–964
- Raubenheimer D, Simpson SJ (1997) Integrative models of nutrient balancing: application to insects and vertebrates. *Nutr Res Rev* 10:151–179
- Raubenheimer D, Simpson SJ (2006) The challenge of supplementary feeding: can geometric analysis help save the kakapo? *Notornis* 53:100–111
- Raubenheimer D, Mayntz D, Simpson SJ, Toft S (2007) Nutrient-specific compensation following overwintering diapause in a generalist predatory invertebrate: implications for intraguild predation. *Ecology* 88:2598–2608
- Raubenheimer D, Simpson SJ, Mayntz D (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework. *Funct Ecol* 23:4–16
- Raubenheimer D, Simpson SJ, Tait AH (2012) Match and mismatch: conservation physiology, nutritional ecology and the timescales of biological adaptation. *Philos Trans R Soc Lond B* 367:1628–1646
- Raubenheimer D, Machovsky-Capuska GE, Gosby AK, Simpson S (2014) The nutritional ecology of obesity: from humans to companion animals. *Br J Nutr*. doi:10.1017/S0007114514002323
- Remis MJ (2000) Initial studies on the contributions of body size and gastrointestinal passage rates to dietary flexibility among gorillas. *Am J Phys Anthropol* 112:171–180
- Remis MJ, Dierenfeld ES (2004) Digesta passage, digestibility and behavior in captive gorillas under two dietary regimens. *Int J Primatol* 25:825–845
- Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA (2007) Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos* 116:1675–1682
- Rode KD, Chapman CA, McDowell LR, Stickler C (2006) Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica* 38:625–634
- Rothman JM, Dierenfeld ES, Molina DO, Shaw AV, Hintz HF, Pell AN (2006) Nutritional chemistry of foods eaten by gorillas in Bwindi impenetrable national park, Uganda. *Am J Primatol* 68:675–691
- Rothman JM, Plumptre AJ, Dierenfeld ES, Pell AN (2007) Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. *J Trop Ecol* 23:673–682
- Rothman JM, Dierenfeld ES, Hintz HF, Pell AN (2008) Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia* 155:111–122
- Rothman JM, Raubenheimer D, Chapman CA (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biol Lett* 7:847–849
- Ruohonen K, Simpson SJ, Raubenheimer D (2007) A new approach to diet optimisation: a re-analysis using European whitefish (*Coregonus lavaretus*). *Aquaculture* 267:147–156
- Saravanan S, Schrama JW, Figueiredo-Silva AC, Kaushik SJ, Verreth JAJ, Geurden I (2012) Constraints on Energy Intake in Fish: the Link between Diet Composition, Energy Metabolism, and Energy Intake in Rainbow Trout. *PLoS ONE* 7:e34743
- Schuckard R, Melville D, Cook W, Machovsky-Capuska GE (2012) Diet of the Australasian gannet (*Morus serrator*) at Farewell Spit, New Zealand. *Notornis* 59:66–70
- Shrader AM, Owen-Smith N, Ogutu JO (2006) How a mega-grazer copes with the dry season: food, nutrient intake rates by white rhinoceros in the wild. *Funct Ecol* 20:376–384
- Simpson SJ, Raubenheimer D (1993) A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. *Philos Trans R Soc Lond B* 342:381–402
- Simpson SJ, Raubenheimer D (1997) The geometric analysis of macronutrient selection in the rat. *Appetite* 28:201–213
- Simpson SJ, Raubenheimer D (2005) Obesity: the protein leverage hypothesis. *Obes Rev* 6:133–142
- Simpson SJ, Raubenheimer D (2010) The nutritional geometry of aging. Springer, Berlin
- Simpson SJ, Raubenheimer D (2012) The nature of nutrition: a unifying framework from animal adaptation to human obesity. Princeton University Press, Princeton
- Simpson SJ, Batley R, Raubenheimer D (2003) Geometric analysis of macronutrient intake in humans: the power of protein? *Appetite* 41:123–140
- Simpson SJ, Raubenheimer D, Charleston MA, Clissold FJ (2010) Modelling nutritional interactions: from individuals to communities. *Trends Ecol Evol* 25:53–60
- Skibił AL, Downing LM, Orr TJ, Hood WR (2013) The evolution of the nutrient composition of mammalian milks. *J Anim Ecol* 82:1254–1264
- Solon-Biet SM, Aisling CM, Ballard JWO, Ruohonen K, Wu LE, Cogger VC, Warren A (2014) The ratio of macronutrients, not caloric intake, dictates cardiometabolic health, aging, and longevity in ad libitum-fed mice. *Cell Metab* 19:418–430
- Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton
- Tait A, Raubenheimer D, Stockin KA, Merriman M, Machovsky-Capuska GE (2014) Nutritional geometry of gannets and the challenges in field studies. *Mar Biol* 12:2791–2801. doi:10.1007/s00227-014-2544-1
- Van Soest PJ (1994) Nutritional ecology of the ruminant. Cornell University Press, Ithaca
- Westoby M (1974) An analysis of diet selection by large generalist herbivores. *Am Nat* 108:290–304
- Whittier CA, Milligan LA, Nutter FB, Cranfield MR, Power ML (2010) Proximate composition of milk from free-ranging mountain gorillas (*Gorilla beringei beringei*). *Zool Biol* 29:1–10