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Nutritional contributions of insects to primate diets: Implications for primate evolution

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ABSTRACT

Insects and other invertebrates form a portion of many living and extinct primate diets. We review the nutritional profiles of insects in comparison with other dietary items, and discuss insect nutrients in relation to the nutritional needs of living primates. We find that insects are incorporated into some primate diets as staple foods whereby they are the majority of food intake. They can also be incorporated as complements to other foods in the diet, providing protein in a diet otherwise dominated by gums and/or fruits, or be incorporated as supplements to likely provide an essential nutrient that is not available in the typical diet. During times when they are very abundant, such as in insect outbreaks, insects can serve as replacements to the usual foods eaten by primates. Nutritionally, insects are high in protein and fat compared with typical dietary items like fruit and vegetation. However, insects are small in size and for larger primates (>1 kg) it is usually nutritionally profitable only to consume insects when they are available in large quantities. In small quantities, they may serve to provide important vitamins and fatty acids typically unavailable in primate diets. In a brief analysis, we found that soft-bodied insects are higher in fat though similar in chitin and protein than hard-bodied insects. In the fossil record, primates can be defined as soft- or hard-bodied insect feeders based on dental morphology. The differences in the nutritional composition of insects may have implications for understanding early primate evolution and ecology.

Introduction

A diverse number of invertebrate taxa are eaten across the Order Primates. Although invertebrates are usually small in size, they provide larger amounts of energy, protein and fat per unit of mass than most other foods eaten by primates, such as fruit and vegetation. While the nutritional properties of the plant-based diets of primates have been characterized in many instances (Altmann et al., 1987; Barton et al., 1993; Conklin-Brittain et al., 1998; Norconk and Conklin-Brittain, 2004; Rothman et al., 2006a; Doran-Sheehy et al., 2009; Johnson et al., 2012, 2013; Ryan et al., 2013), little is known about the nutritional aspects of insectivory by non-human primates (but see Deblauwe and Janssens, 2008; O'Malley and Power, 2012; Isbell et al., 2013). Here, we provide an overview of the nutritional properties of insects eaten by primates. We begin by describing the different types of primate insectivory, as defined by McGrew (2001). We then review the different macro- and micronutrients that insects provide in comparison with the fruits and leaves that are typically eaten by primates. We discuss the ways that insects are incorporated into primate diets as staple, complementary, supplementary, or replacement foods. Finally we discuss the mechanical properties of insects, and the nutritional implications of eating soft-bodied insect diets compared with hard-bodied insect diets, with implications for understanding the dietary strategies of the earliest fossil euprimates. We provide a detailed resource base of nutrient compositions of insects in a Supplementary Online Materials (SOM) appendix.

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Types of primate insectivory

In a review of primate insectivory and its potential role in early human dietary habits, McGrew (2001) classifies primates into four categories based on different grades of insectivory. The first two categories of insectivory are related to the amounts of insects in primate diets. The final two categories are related to the mode of acquisition. First, the obligate insectivores are small in body mass, and usually weigh less than 1 kg. Only small primates are able to rely heavily on insects as a food source because it is energetically expensive to capture insects and they are not usually widely available in large amounts (Kay, 1975; Kay and Hylander, 1978; Terborgh, 1983). These smaller primates include tarsiers (MacKinnon and MacKinnon, 1980; Gursky, 2010), bushbabies (Nekaris and Bearder, 2007), lorises (Nekaris and Rasmussen, 2003; Nekaris, 2005), mouse lemurs (Atsalis, 1999), and some of the smaller New World monkeys such as the callitrichines (Terborgh, 1983; Garber, 1992) and squirrel monkeys (Lima and Ferrari, 2003; Stone, 2007). A variety of sensory methods for the detection and capture of prey are used (Dominy et al., 2001; Siemers, 2013). Bushbabies (*Galago* spp.) and tarsiers (*Tarsius* spp.) detect prey by listening to rustling by insects and the fluttering of their wings (Charles-Dominique, 1977; MacKinnon and MacKinnon, 1980), while mouse lemurs (*Microcebus murinus*) may rely more on visual than auditory cues for successful prey detection (Piep et al., 2008, but see; Siemers et al., 2007). The aye–aye (*Daubentonia madagascariensis*), which consumes a large portion of its diet from insects (Sterling et al., 1994), uses a percussive foraging technique whereby it taps logs to see where larvae are located (Erikson, 1991, 1994).

The second category of insect feeding is occasional insectivory, which generally applies to primates that are over 1 kg in body mass (McGrew, 2001), such as the African guenons (Chapman et al., 2002). The blue monkey (*Cercopithecus mitis*) and red-tailed monkey (*Cercopithecus ascanius*) spend 50% and 66% of their feeding time, respectively, capturing, searching for and consuming insects in Uganda (Tashiro, 2006), and this is generally applicable to guenons in at least two other East African forests (Cords, 1986; Bryer et al., 2013). In a study of sympatric guenons, Cords (1986) noted that red-tails used fast action patterns of movement to capture insects compared with blue monkeys, who tended to focus on less mobile prey. These fast action motions consisted of picks, swipes and pounces (Cords, 1986). Though it is not known if searching and processing time was considered, studies in Guyana and Brazil have demonstrated that saki monkeys (*Chiropotes* spp.) spend 30–40% of their feeding time eating insects in some seasons when insect availability is high (Veiga and Ferrari, 2006; Shaffer, 2013). Shaffer (2013) notes that the sakis in Guyana traveled in a directed manner towards caterpillar host trees during the caterpillar breeding season, and suggests that the monkeys tracked and exploited this predictable annual resource. In contrast to some sensory modes used by the smaller obligate insectivores, larger primates typically find insects visually, either by grasping flying insect prey, or uncovering wingless insects within leaves, dead trees or nests (Terborgh, 1983; Cords, 1986; Melin et al., 2007). Melin et al. (2007) found that the dichromatic capuchins (*Cebus capucinus*) were better at detecting surface-dwelling insects, while trichromats of the same species were more successful at obtaining non-camouflaged, embedded insects. Dichromatic vision could thus help some primates more efficiently find camouflaged insects (Melin et al., 2007), particularly those that forage in shaded areas (Caine et al., 2010).

The third category of insectivory that McGrew (2001) describes is elementary technology insectivory, which is confined to primates that use tools to facilitate the consumption of social insects of Isoptera and Hymenoptera. A variety of tools are used by chimpanzees (*Pan troglodytes*) to capture and consume insects (McGrew, 1974, 1992, 2010; Sanz, 2009; Sanz et al., 2009). For example, ant-dipping or ant-fishing tools are used at several study sites (McGrew, 1974; Hulme and Matsuzawa, 2002; McGrew et al., 2005; O'Malley et al., 2012). There is a lot of variability in insectivory across chimpanzee study sites. In Gabon, 31% of chimpanzee feces contained insect fragments during a seven-year period (Tutin and Fernandez, 1992), and in Senegal male chimpanzees spent an average of 24% of their foraging and feeding time on termites (*Macrotermes* spp.) (Bogart and Pruetz, 2011). However, in Uganda insects are rarely or never consumed by chimpanzees (Wrangham et al., 1991; Sherrow, 2005). Orangutans (*Pongo* spp.) also use tools to obtain insects (Galdikas, 1989; van Schaik et al., 1996). Gorillas (*Gorilla* spp.) do not use tools, though like chimpanzees they consume insects in large quantities in some forests (Tutin and Fernandez, 1992; Deblauwe et al., 2003), but not in others (Harcourt and Harcourt, 1984; Watts, 1989). Capuchin monkeys (*Cebus* spp.) use sticks and twigs to dig for social insects (Moura and Lee, 2004; Ottoni and Izar, 2008). Insects are a regular part of the capuchin diet and at different study sites they may spend 50% of their foraging time searching for them (Chapman, 1987; Janson and Boinski, 1992; Fragaszy et al., 2004).

The final grade of insectivory described by McGrew (2001) concerns the human consumption of insects. Humans use a wide variety of insects and preparation styles (cooking, tool use) and consume insects in variable quantities. Several reviews exist on insect eating by humans (DeFoliart, 1995; Bukkens, 2005; Raubenheimer and Rothman, 2013).

The insects

Members of the Class Insecta are extremely diverse and there are currently 28–30 orders of insects recognized depending on taxonomic viewpoints (Gullen and Cranston, 2010). This does not include other joint-legged invertebrates such as the spiders, scorpions, ticks and mites in Class Arachnida, or the earthworms that are in the Phylum Annelid and the Class Oligochaetes. For the purpose of this review, we consider feeding on arachnids, oligochaetes and insects as 'insectivory' and we refer to them collectively as 'insects'. We do not consider marine or aquatic invertebrates eaten by primates in this review, but some primates eat substantial amounts of marine invertebrates (Carpenter, 1887; Fernandes, 1991; Gumert and Malaivijitnond, 2012). All insects have chitin in their cuticle and exoskeleton, which is a structural polysaccharide that contains carbon, nitrogen and oxygen, and is mainly indigestible to insectivores. Insect life cycles are divided into several stages depending on the developmental pattern and we outline them here based on Gullen and Cranston (2010). The primitive developmental pattern is termed ametaboly, whereby the insect emerges from its egg in a form that is almost identical to the adult but is not reproductively mature. This primitive pattern is found in the wingless Orders Archaeognatha and Zygentoma. The majority of insects have a more derived developmental pattern, whereby they undergo some form of metamorphosis from an immature form to a mature form. In hemimetaboly, or incomplete metamorphosis, the insect hatches as a nymph, goes through several immature nymph stages or instars, and eventually becomes an adult. Hemimetaboly is seen in cockroaches, grasshoppers, bugs and mantids (Blattodea, Orthoptera, Mantodea and Hemiptera). Nymphs are typically smaller but similar in form to adults. In holometaboly, or complete metamorphosis, the insect hatches as a larva and goes through several larval instars before it becomes a pupa and then an adult. A larva is very different phenotypically from the adult form. At some point, usually at a specific body mass,

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the larvae will molt into an inactive, non-feeding pupa, sometimes in a cocoon where it develops into the adult form. Holometaboly is seen in many insects including beetles, flies, butterflies, moths, ants, wasps, and fleas (Coleoptera, Diptera, Hymenoptera, Siphonaptera). The adults of eusocial insects such as the ants, wasps, bees and termites from the Orders Hymenoptera and Isoptera (also called Order Blattodea, Epifamily Termitoidae) have a caste system whereby the adult forms can be queens, kings, workers, and in many ants, soldiers. The winged reproductive adult termites are called alate adults. For some species there are further subdivisions into major and minor workers. The immature stages of eusocial insects are called brood. The arachnids have similar life stages and they are variable. Some spiders are born live; however, in the majority of species a larva hatches from an egg and this larva molts into a nymph that eventually becomes an adult.

This variation in different forms of insects during their life stages can translate into specific preferences and nutritional differences for insectivorous primates, particularly with respect to mature versus immature forms (Table 1). For example, captive slender lorises (*Loris tardigradus*) preferred the larval stage to the adult stage when given choices between adults or larvae of mealworms (Coleoptera), waxworms (Coleoptera) and superworms (Lepidoptera) (Clayton and Glander, 2011). Chimpanzees in Gombe, Tanzania, apparently prefer ant soldiers to workers (O'Malley and Power, 2012). One of the major theories of euprimate origins (i.e., the Visual Predation Theory; Cartmill, 1972, 1974, 1992) identifies insect predation as the driving force behind the evolution of a number of distinct euprimate morphological features, making a deeper understanding of insectivory and insect nutritional quality critical for understanding primate morphological and behavioral evolution.

Nutrients in insects

To understand the role of insects in living and fossil primate diets, a review of their nutritional properties is paramount. There is evidence that insects are not only selected on the basis of their environmental availability, but also their nutrient composition. For example, O'Malley and Power (2012) found that insect prey consumed by Gombe chimpanzees had a higher fat and lower ash content than prey they did not eat, suggesting that energy was a consideration. Similarly, chimpanzees in Cameroon selected available and palatable prey that were higher in some minerals such as iron and manganese (Deblauwe and Janssens, 2008; O'Malley and Power, 2012). At both sites, nutritional compositions of the fruit and vegetation were not available for comparison, but there may be limitations in some minerals in their plant-based diets (Deblauwe and Janssens, 2008; O'Malley and Power, 2012).

It is important to note that insects are 'small packages' of nutrients and so nutritional payoffs from eating insects are limited unless primates are small, or they can consume sufficient quantities. Based on fecal analysis, western gorillas (*Gorilla gorilla*) in Cameroon ate an estimated 8 g of insects per day in fresh weight, but this is very small in relation to the rest of their diet (Deblauwe and Janssens, 2008). Although estimates are not available from the gorillas in Cameroon, Rothman et al. (2008) estimated that, on a dry matter basis, silverback gorillas in Uganda ate ~4 kg of food per day in dry mass, and on a wet weight basis ~20 kg, thus insects are

Table 1
Mean nutrient concentrations of different orders of insects and other invertebrates consumed by primates from the published literature.

Insect order	Nutritional Composition[a] (% dry matter aside from moisture)					N
	% Moisture	% Protein	% Lipid	% Chitin	% Ash	
	Mean ± Std Dev	Mean ± Std Dev	Mean ± Std Dev	Mean ± Std Dev	Mean ± Std Dev	
Araneae (spiders)						
Adult	62.7	65.2	7.9	13.1	4.2	1
Blattodea (cockroaches)						
Adult	64.5 ± 8.3	57.5 ± 16.9	25.5 ± 13.9	9.8 ± 4.2	4.5 ± 2.3	11
Coleoptera (beetles)						
Adult	51.1 ± 23.9	42.2 ± 20.2	13.4 ± 11.1	8.7 ± 8.3	3.8 ± 2.2	23
Immature	59.6 ± 17.7	37.3 ± 13.3	38.7 ± 15.9	8.2 ± 5.9	4.6 ± 3.5	36
Diptera (flies)						
Adult	58.8 ± 25.9	53.5 ± 23.4	12.9 ± 7.8	6.1 ± 3.7	4.7 ± 2.3	6
Immature	74.4 ± 12.7	48.1 ± 14.0	17.1 ± 7.7	6.7 ± 4.2	8.9 ± 3.4	12
Haplotaxida (worms)						
Adult	77.3 ± 18.0	49.9 ± 21.6	7.3 ± 5.8	2.6 ± 2.5	12.6 ± 12.7	22
Hemiptera (bugs)						
Adult	51.0 ± 25.8	46.8 ± 18.4	27.5 ± 18.2	12.2 ± 5.8	4.4 ± 5.1	17
Immature	n/a	62.0	7.0	3.0	19.0	1
Hymenoptera (sawflies, wasps, bees, ants)						
Adult	67.1 ± 8.3	50.3 ± 21.1	13.3 ± 11.8	17.9 ± 11.0	6.8 ± 9.4	34
Immature	62.5 ± 26.7	52.5 ± 18.7	22.6 ± 13.4	3.0 ± 1.9	3.9 ± 3.4	28
Isoptera (termites)						
Adult	59.1 ± 25.6	44.0 ± 18.4	13.3 ± 16.5	18.5 ± 12.6	16.0 ± 20.5	52
Immature	n/a	61.5 ± 6.4	14.5 ± 9.2	11.5 ± 4.9	5.5 ± 3.5	2
Lepidoptera (moths, butterflies)						
Adult	61.9	42.5 ± 1.8	51.4	17.8	3.3	1–3
Immature	47.1 ± 30.7	45.4 ± 19.8	24.5 ± 17.1	6.1 ± 5.3	4.7 ± 3.3	60
Megaloptera (fishflies)						
Adult	73.5	63.9	19.5	5.9	5.8	1
Neuroptera (dobsonflies)						
Adult	10.8	57.0	11.3	n/a	4.9	1
Odonata (dragonflies)						
Adult	77.9	76.2	58.5	n/a	9.2	1
Orthoptera (grasshoppers, crickets, locusts)						
Adult	57.5 ± 24.6	49.0 ± 23.0	12.5 ± 11.9	7.4 ± 4.8	5.2 ± 3.3	61

[a] Data were obtained from SOM Appendix 1 where references are listed.

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likely a minute portion of the gorilla diet. O'Malley and Power (2012) report that the average weight of a single honeybee (*Apis mellifera*) eaten by Gombe chimpanzees is 0.099 g. This honeybee is actually heavier than other Hymenoptera prey (weights vary from 0.015 to 0.099 g; O'Malley and Power, 2012). A single *A. mellifera* of this size provides 11.6 mg of protein. If we estimate that, like human males, male primates need about 1.8 g of protein per kg of metabolic body mass on a daily basis (Food and Nutrition Board, 2005) then a 50.0 kg male chimpanzee would need to eat about 38.8 g of protein per day. If the chimpanzee was solely eating these honeybees to meet his protein needs, he would need to eat 3344 honeybees to meet this protein requirement, if we assume 100% assimilation (which is unlikely). O'Malley and Power (2012) estimated that a chimpanzee in Gombe gains only about 2.36 g of protein, and just 19 calories from eating a meal of *Macrotermes subhyalinus*. As O'Malley and Power (2012) suggest, the impetus for insectivory in apes may also be related to the acquisition of important minerals and vitamins, similar to the meat-scrap hypothesis, which suggests motivation for chimpanzee vertebrate hunts is related to micronutrient gain (Tennie et al., 2009; O'Malley and Power, 2012). However, at some study sites, chimpanzees eat large numbers of social insects so nutritional yields are indeed significant. In Nigeria, it is roughly estimated that 11,217 army ants (*Dorylus rubellus*) are harvested during ant dipping sessions by chimpanzees (Allon et al., 2012). The authors suggest that the aggressive nature of the army ants may contribute to this greater yield than at other sites (Allon et al., 2012).

Nutritional analysis

Various studies describe the observation, collection and preservation methods for primate foods, including insects (Ozanne et al., 2011; Rothman et al., 2012). Additionally, new molecular methods are being used to identify insects in the feces of primates where insect ingestion is difficult or impossible to observe (Pickett et al., 2012). The nutritional analyses used to measure macro- and micronutrients in insects are similar to those used in estimating the nutrients in plants (Rothman et al., 2012), and estimating the chitinous exoskeleton in insects is typically based on the acid detergent fiber assay, with adjustments for the ash and the nitrogen that is bound to the chitin (Finke, 2007, 2013; O'Malley and Power, 2012; Isbell et al., 2013). Like plant material (Chapman et al., 2003; Rothman et al., 2012), it should be noted that there is likely to be intraspecific variability in the nutritional composition of insects within a locale, particularly with respect to the micronutrients based on the insect's food source (Finke, 2002, 2003; Finke and Winn, 2004).

Because nutrients are typically reported in terms of their concentration or percentage of dry mass, it is important to recognize that the weight of an insect is very small compared with the weight of a leaf or fruit. This is not typically considered because, for analyses, nutrients are compared on a standard weight or concentration basis (g of a nutrient per 100 g, or concentration such as 100% dry matter). Thus, if a fruit contains 50 kcal per 100 g of dry weight, and an ant contain 588 kcal per 100 g of dry weight (as in Isbell et al., 2013), it would seem that the ant has a lot more energy and is thus more beneficial nutritionally. While this is true on a concentration basis, the mass of the individual ant must be considered. In this scenario, to consume a total of 200 kcal, a primate only has to consume eight 50 g fruits that each have 50 kcal/100 g, whereas considerably more ants need to be eaten at 588 kcal/100 g, as, for example, individual *Crematogaster mimosae* ants eaten by patas monkeys (*Erythrocebus patas*) have a mass of 0.00078 g each (Isbell et al., 2013). In order to gain 200 kcal of energy from these ants, a primate would have to consume over 43,000 ants. This difference in size of the food item illustrates why the availability of insects is important.

The following section reviews what is known about the nutritional content of insects, particularly those commonly included in non-human primate diets.

Protein

Although they are small, insects are protein-rich (McGrew, 2001; Verkerk et al., 2007). Across adult insect orders there is a mean protein concentration of ~55% on a dry matter basis (DM), and this protein concentration varies from ~20 to 80% (Table 1). This protein concentration is comparable with vertebrate meat (McGrew, 2001; O'Malley and Power, 2012; but see; Raubenheimer et al., 2014). Protein quality of insects is typically excellent; essential amino acids provide 46–96% of insect protein composition (Verkerk et al., 2007; Finke, 2013). On average, the insects consumed by non-human primates are typically higher in protein than the insects eaten by humans (Raubenheimer and Rothman, 2013), which is perhaps a reflection of high-protein insects in primate environments.

If they can be eaten in sufficient quantities, insects are far more protein-rich compared with high-protein young leaves (which usually vary from 10 to 30% DM; Milton, 1979; Dierenfeld and McCann, 1999; Ryan et al., 2013). For some primate diets that are limited in protein (Milton, 1979; Altmann, 1991; Ganzhorn et al., 2009), the ingestion of insects for their protein becomes especially important if insects can be eaten in sufficient quantities. Indeed, it has been suggested that the nutritional yields from insect abundance might affect reproductive seasonality in night monkeys (*Aotus azarai*) in Argentina and saddle-back tamarins (*Saguinus fuscicollis*) in Peru, where the time of lactation is when insect abundance is highest (Goldizen et al., 1988; Fernandez-Duque et al., 2002).

Fat

With 9 kcal/g, fats are higher in energy than other macronutrients, and consequently, each unit of mass of fat leads to more energy intake than an equally sized unit of mass of carbohydrate (4 kcal/g) or protein (4 kcal/g) (National Research Council, 2003). Aside from the seed-eating primates such as saki monkeys (*Pithecia pithecia*) (Norconk and Conklin-Brittain, 2004), most primate diets contain very little fat because leaves usually do not contain fat and only some fruits are high in fats (Milton, 2000, 2008). Folivore diets are usually quite low in fat; mountain gorillas (*Gorilla beringei*) eat a diet of about 3% DM fat annually based on measurements of food intake (Reiner et al., 2014), and the plant-based diets of frugivorous chimpanzees and the plant-based portion of cercopithecine diets was under 4% DM based on time spent feeding (Conklin-Brittain et al., 1998), though the fat from insects was not included in this estimate.

Compared with plant material, the concentrations of some insects are high in fat, but span a wide range (Table 1). Across orders, the mean fat concentration in adult insects is 20.7 ± 8.7% DM. Some insects are particularly high in fat, as for example, damselflies and dragonflies in Odonata (Pennino et al., 1991). Some larval Lepidoptera that are as high as 60–80% fat DM, as are some termites (Isoptera), for which concentrations over 50% have been recorded (Redford and Dorea, 1984). The concentrations of essential fatty acids (omega-3 and omega-6) can be quite high in insects and are comparable with those in fish and chicken. For example, over 50% of the fat in the larvae of *Cirina forda* (Lepidoptera), which are consumed by humans in Nigeria, is linolenic acid (Akinnawo and Ketiku, 2000). Across a sample of 35 species from many

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terrestrial insect orders, linoleic acid comprised 26.0% of the total fat, and linolenic acid was 17.5% (Fontaneto et al., 2011), though concentrations of their long-chained polyunsaturated derivatives, arachidonic and docosahexaenoic acid, are low compared with meat (Fontaneto et al., 2011). Fatty acid profiles for chimpanzee foods are not yet available, but data from mountain gorilla foods suggest that the balance and amounts of fatty acids in their plant-based diets are adequate to meet nutritional needs (Reiner et al., 2014). However, chimpanzee tool use could be an impetus to obtaining essential fatty acids that are not available in their plant-based diet (Hladik, 1977; Collins and McGrew, 1985).

Carbohydrates

Non-structural carbohydrates (NSC) are a good energy source at 4 kcal/g, and include the sugars, starches and other monosaccharides/oligosaccharides. Primates usually obtain these NSC from the fruits and young leaves in their diets (Chapman et al., 2012). Insects are not expected to be high in non-structural carbohydrates because their bodies are comprised of mainly fats, chitin and protein, but they may contain carbohydrates from their food sources (Raubenheimer and Rothman, 2013). For example, in a study of the invertebrates fed to captive mammals, mealworms were 3% soluble carbohydrate DM and crickets were 6% DM (Donoghue and Langernberg, 2008). By contrast, the honey ant (*Myrmecocystus melliger*) is 81% carbohydrate because it is gorged with food for its workers. This is far higher than the digestible carbohydrate concentrations of most primate foods excluding, perhaps, some gums (Power, 2010).

Chitin

Most insect-feeding primates use their high shearing molar crests to masticate the insect exoskeleton before swallowing it (Kay, 1975; Strait, 1993a), or they manually remove it (Janson and Boinski, 1992; Rode et al., 2006; Melin et al., 2010). The majority of the exoskeleton of insects is composed of chitin, a structural polysaccharide that contains carbon, nitrogen and oxygen, which is usually found in a matrix with other compounds such as minerals and protein (Finke, 2007). Chitin composes about 2–20% of insects on a DM basis, and is variable within and between insect orders (Table 1). Chitin is considered a feeding deterrent because it adds bulk to the diet but is not digestible by primates unless they possess chitinases. Chitinases may partially digest chitin to usable energy and protein, though chitin digestibility is likely less than 20% (Hirano et al., 1990; Finke, 2013). Chitinases have been identified in the digestive tracts of the following primates: pottos (*Perodicticus potto*) (Cornelius and Dandrifosse, 1976), two species of macaques (Krykbaev et al., 2010), capuchins (National Research Council, 2003), and humans (Paoletti et al., 2007). There is also some evidence that insectivorous galagos are able to reduce the particle size of chitin (Kay and Sheine, 1979). However, for the most part, chitin should be viewed as an antifeedant that increases bulk and dilutes the portion of macronutrients in eaten insects.

Energy

Per unit of mass, insects provide a superior source of energy than fruits and vegetation (DeFoliart, 1995). This is because insects are rich in fat, which supplies high amounts of calories (DeFoliart, 1995). The mean energy content of leaves and fruits eaten by primates in Ugandan forests is 50–370 kcal/100 g, assuming some fiber fermentation (Unpublished data; Johnson et al., 2012). Insects eaten are much higher in energy. For example, ants eaten by patas monkeys were ~330–588 kcal/100 g assuming no chitin could be used as an energy source (Isbell et al., 2013). Of course, as discussed earlier, many insects must be eaten in order to gain substantial energetic benefits because insects are smaller in size than fruit and vegetation, and energy must be expended to search for and capture these mobile food items.

Vitamins

Little is known about the vitamins in primate diets, but the vitamins in wild leaves and fruits eaten by humans are usually plentiful (Grivetti and Ogle, 2000; Nesamuvuni et al., 2001; Milton, 2003).The most significant vitamin gained from insects is likely vitamin B_{12}, because it is only found in animal products and microorganisms (National Research Council, 2003). Indeed, the acquisition of vitamin B_{12} has been suggested as an impetus of insectivory in chimpanzees, gorillas and langurs (Srivastava, 1991; McGrew, 2001; Deblauwe and Janssens, 2008; Bogart and Pruetz, 2011). Signs of vitamin B_{12} deficiency include anemia and nervous system disorders (National Research Council, 2003). Some lemurs practice coprophagy (Gemmill and Gould, 2008), and the bacteria ingested are thought to provide vitamin B_{12}, but most wild primates probably rely on the intentional or accidental consumption of insects to meet their needs. Vitamin B_{12} is apparently variable among insects (Wakayama et al., 1984), and only some insects supply it in sufficient quantities to meet primate requirements (Finke, 2002). However, the few studies that have been conducted on the vitamin composition of insects have been performed on insects that were commercially raised (Barker et al., 1998).

Minerals

Minerals may be limiting in primate diets because many of them, including sodium, copper and iron, are not found in abundance in wild herbs, tree leaves and fruits (Rode et al., 2003, 2006; Rothman et al., 2006b; Rothman et al., 2012). For example, copper deficiency was implicated in wild savannah baboons (*Papio cynocephalus*) that consumed low levels of copper and high levels of zinc. They had impaired mobility and stiffening of the hindlimbs, which affected their survivorship (Markham et al., 2011).

Insects are quite variable in their mineral compositions, but a few generalities exist. Insects are generally low in calcium, magnesium, and manganese compared with plants eaten by primates, but higher in sodium, phosphorous, iron, zinc and copper, as evidenced by a comparison of the nutrient content of insect prey of gorillas with that of their plant foods (Deblauwe and Janssens, 2008). In particular, like vertebrate meat, insects are usually much higher in sodium than the plant portions in primate diets (Rode et al., 2003). Unless primates are eating particular plant foods specifically for their sodium (Oates, 1978; Rothman et al., 2006b), insects probably contribute substantially towards the sodium needs of primates. For example, insects across orders varied from 125 to 3000 ppm in sodium (Studier and Sevick, 1992), which is far higher than forest vegetation and fruit analyzed at several primate field sites (Rode et al., 2003; Rothman et al., 2006b; Behie and Pavelka, 2012).

Insects as a dietary component

We provide examples of how insects are incorporated into primate diets as staple foods, complementary foods, supplementary foods and replacement foods. However, it should be noted that these dietary strategies are not mutually exclusive.

Insects as staples

For the purpose of this review, we define a staple food as one that is eaten daily in sufficient quantities such that it represents the

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primary portion of the diet by mass and provides most of the major macronutrients and energy in the diet. Most insects provide a consistently good source of protein and fat, but there is wide variation in nutritional composition (Fig. 1). The obligate insectivores (McGrew, 2001) are included this category, because the majority of mass consumed is insects. Examples of the small primates (<1 kg) that use invertebrates as staple foods include the tarsiers (about 58–141 g in body mass; Gursky, 2011) that are almost exclusively faunivorous. Lepidoptera and Blattodea compose 50% of the diet of *Tarsius spectrum* (Gursky, 2011), and they ate other insects when these taxa were not available. Tarsiers also consume vertebrate prey (11%; Niemitz cited in Gursky, 2011). The golden angwantibo, *Arctocebus calabarensis* (body mass:150-–270; Nekaris and Bearder, 2007), in Gabon consumes a diet of about 85% insects based on stomach contents, and it also eats some fruit or gums (Charles-Dominique, 1977). Some mouse lemurs (*Microcebus* spp., body mass: 50–90 g; Nekaris and Bearder, 2007) use insects as staples, as the majority of their diets are mainly insect secretions, supplemented by other animal matter, and small amounts of gums, fruits and flowers (Dammhahn and Kappeler, 2008). In addition, *Loris lydekkerianus* (body mass: 227–322 g; Nekaris and Bearder, 2007), and *L. tardigradus* (body mass: 103–172 g; Nekaris and Bearder, 2007) consume a mainly insect-based diet as calculated using all-occurrence sampling, where acquisition of insects was considered a feeding event (Nekaris, 2005; Nekaris and Bearder, 2007).

Insects as complements

A food complement is one that supplies a suite of nutrients that is not available in sufficient quantities in the other portions of the diet. In this respect, insects used as complements provide significant nutritional benefits by providing more than one nutrient, or a crucial macronutrient. Examples of primates that use insects as complements include marmosets and tamarins (*Sanguinus* spp.), which eat insects 10–60% of their feeding time including time spent foraging and searching for insects (Nickle and Heymann, 1996; Garber, 1998), along with their fruit or gum-based diet. Patas monkeys (*E. patas*) consume the majority of their diets as gums and ants (Isbell, 1998). The ants in the diet provide a protein source, while the gums provide energy (Isbell et al., 2013). Based on time spent feeding, reaching for and manipulating insects, the blue monkey (*C. mitis*) dietary component of insects is up to 36% in Kenya and Uganda (Chapman et al., 2002). These insects complement the fruit-based portion of the diet in that they provide protein, whereas the fruit provides energy (Hladik, 1975). Lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Ecuador eat more insects when fruit is abundant (DiFiore, 2003), possibly to balance the protein and energy in their diets.

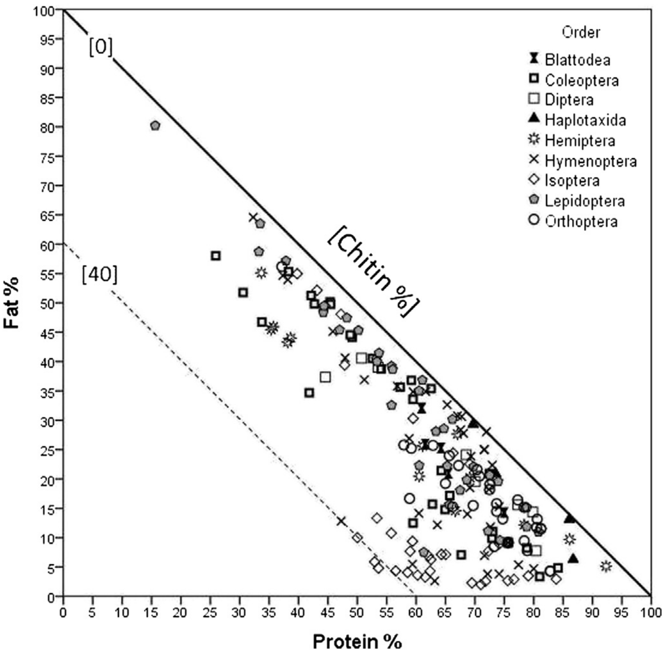

Figure 1. A right angle mixture triangle (RMT) plot illustrating the diversity of insect nutrient concentrations (protein, fat and chitin) across the different orders of insects eaten. The 0% and 40% chitin isolines are added for reference. Data are from SOM Table 1, but only samples with all three analyses (protein, fat and chitin) are included. See Raubenheimer (2011) and Raubenheimer et al. (2014) for more information about the RMT.

Insects as supplements

Supplemental foods typically provide a single nutrient that is deficient in the staple diet. Supplemental foods are typically eaten irregularly or in small quantities. For example, Vitamin B_{12} is deficient in plant-based diets, but is required by mammals in small amounts. In this respect, the accidental or intentional consumption of insects provides a supplemental source of vitamin B_{12} (Hamilton and Busse, 1978; Milton, 1993, 1999). For red colobus monkeys (*Procolobus rufomitratus*) that eat insects infrequently (Struhsaker, 2010), and perhaps for diademed sifakas (*Propithecus diadema*) where very few feeding records indicate insectivory (Irwin, 2008), the accidental or very rare consumption of insects suggests that they might serve as supplements in the diet, providing an essential micronutrient that is not widely available in the staple diet. In addition, mountain gorillas (*G. beringei*) eat insects inadvertently and intentionally in low quantities. This consumption has been suggested to be related to trace element requirements (Harcourt and Harcourt, 1984; Watts, 1989). Insects may also be used as protein supplements for pregnant or lactating females. For example, lactating female capuchins (*C. capucinus*) in Costa Rica increase their food intake rate to consume more protein per hour than other females (McCabe and Fedigan, 2007; Melin et al., 2010), and lactating female titi monkeys (*Callicebus cupreus*) in Peru eat more insects or young leaves as a portion of their diet than cycling females and males (Herrera and Heymann, 2004). Western gorilla females ate more termites as fallback foods than males, and insect protein concentrations were higher (27% DM) than most vegetation in the diet (Doran-Sheehy et al., 2009). Orangutan females (lactating and pregnant) spent more time feeding on insects using extractive tools than did males (Fox et al., 2004). In these cases, insects are supplements to support the increased demands for protein during lactation and pregnancy (Clutton-Brock et al., 1989).

Insects as replacements

When insect availability is high, opportunistic consumption of large quantities of insects serves as a replacement in primate diets where they are not normally included. The most notable examples come from geladas (*Theropithecus gelada*) and Hanuman langurs (*Presbytis entellus*). Geladas eat large amounts of locusts during outbreaks and replace much of their typical staple diet of grasses, corms and fruits with locusts (Fashing et al., 2010). Hanuman langurs seasonally include scale insects (Hemiptera) in up to 20% of their diets during insect outbreaks in India (Srivastava, 1991), and across sites this species consumes high amounts of insects during outbreaks, including caterpillars (Koenig and Borries, 2001). Normally, their diets are almost entirely devoid of invertebrates and include mainly leaves (Srivastava, 1991; Koenig and Borries, 2001).

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In addition to langurs and geladas, in a study using fecal analysis, Deblauwe (2009) found that when alates are available, they may replace the plant-based diet of gorillas and chimpanzees. In these cases, it appears that primates opportunistically take advantage of these insect outbreaks and since insect availability is high at these times, primates exploit them to gain substantial nutritional profits.

Mechanical properties of insects

To access the nutrients within insects, primates must be able to bite into the insect and crush the exoskeleton if it is present. There are typically three measures to assess the mechanical properties of potential primate foods: fracture toughness (the energy consumed to propagate a crack), Young's Modulus (ability to resist elastic deformation under strain), and hardness (yield stress) (Lucas et al., 2000; Lucas, 2004; Rothman et al., 2013). Strait (1993b) noted that extant insectivorous mammals, including primates, can be classified as 'soft-object' specialists, or 'hard-object' generalists, according to the different types of insects that are eaten. In primates, Strait gave the examples of the angwantibos (*A. calabarensis*), which eats soft-bodied insects including adult moths and immature larvae, and Demidoff's galago (*Galagoides demidovii*), which eats hard-bodied beetles (Strait and Vincent, 1998). Several other primates have these feeding distinctions as well (Table 2). The physical properties of hard-bodied versus soft-bodied insects were confirmed using a fracture toughness test, and investigating the strength or 'ultimate stress' of samples of caterpillars (larval lepidopteran) and beetles (adult coleopterans). The beetles were substantially tougher, with a mean of 2770 Jm^{-2} than caterpillars, which had a mean of 390 Jm^{-2} (Strait and Vincent, 1998). The authors suggested that these findings may be indicative of the harder outer cuticle of beetles than caterpillars. Few studies have compared other primate foods with insects. Based on fracture toughness tests of a number of cultivated foods including apple pulp, almonds, carrots, pears, apple skin, popcorn kernels, and prune and cherry pits, the cuticle of crickets was tougher than all of the fruits and their skins at a mean of 1030 Jm^{-2}. In comparison, apple skin is 663 Jm^{-2}, apple pulp is 57.0 Jm^{-2} and almonds are 309 Jm^{-2} (Williams et al., 2005), and leaves in Costa Rica varied from 252 to 868 Jm^{-2} (Teaford et al., 2006).

Implications for early primate evolution

Not only are insects an important dietary component for extant primates, they are also recognized as significant food items in the reconstructed diets of fossil primates (Szalay and Delson, 1979; Kay and Covert, 1984; Covert, 1986; Fleagle, 1999; Strait, 2001). One of the major theories of euprimate origins, the Visual Predation Hypothesis, asserts that the crucial ecological adaptation selecting for many unique euprimate anatomical features (particularly those associated with the visual system) was a shift to some form of insect predation in the most recent common ancestor of all living primates (Cartmill, 1972, 1974, 1992). Supporters of this hypothesis note that many of the earliest and most dentally primitive euprimates known in the fossil record, namely *Altanius*, *Teilhardina*, *Steinius*, *Donrussellia*, and now *Archicebus*, all display features consistent with insectivory (e.g., Szalay and Delson, 1979; Kay and Covert, 1984; Covert, 1986, 2002; Williams and Covert, 1994; Rose, 1994; Ni et al., 2004, 2013; Gilbert, 2005).

As noted above, insectivorous primates do not eat all insects indiscriminately, but specialize on different types, selecting a small portion of those available. Based on the living primates for which both diets and dental measurements are available, significant differences in soft- versus hard-bodied insect feeders are correlated

Table 2
Insectivorous primates that specialize on hard-bodied and soft-bodied insects.

Strepsirrhine insectivores (body mass: 40 g–3 kg)	Majority hard-bodied insect eaters	Majority soft-bodied insect eaters	% of diet animal Prey[a]	Taxa commonly eaten			References
				1st	2nd	3rd	
Allen's bush baby (*Galago alleni*)	X		25 (i)	Coleoptera	Lepidoptera	Hymenoptera	Charles-Dominique, 1977
Thick tailed greater bush baby (*Galago crassicaudatus*)	X		5–59 (a)	Hymenoptera	Orthoptera	Coleoptera	Harcourt, 1985 Bearder, 1986
Demidoff's bush baby (*Galago demidovii*)		X	70 (i)	Coleoptera	Lepidoptera		Charles-Dominique, 1977; Strait, 1993b
Garnett's greater bush baby (*Galago garnettii*)	X		50 (a)	Coleoptera	Orthoptera	Araneae	Harcourt and Nash, 1986; Rowe, 1996
Northern lesser bush baby (*Galago senegalensis*)	X		52 (i)	Coleoptera	Orthoptera	Hymenoptera	Harcourt, 1985; Rowe, 1996
Southern needle-clawed bush baby (*Euoticus elegantulus*)	X		20 (a)	Orthoptera	Coleoptera	Lepidoptera	Charles-Dominique, 1977
Potto (*Perodicticus potto*)	X		10 (a)	Hymenoptera	Coleoptera	Lepidoptera	Charles-Dominique, 1977
Calabar angwantibo (*Arctocebus calabarensis*)		X	85 (i)	Lepidoptera	Coleoptera		Charles-Dominique, 1977; Strait, 1993b
Golden angwantibo (*Arctocebus aureus*)		X	85 (i)	Lepidoptera	Hymenoptera/ Coleop-tera/ Orthoptera		Rowe, 1996
Grey slender loris (*Loris lydekkerianus lydekkerianus*)	X		96 (a)	Isoptera	Coleoptera	Orthoptera	Nekaris and Rasmussen, 2003
Gray mouse lemur (*Microcebus murinus*)		X	12 (i)	Lepidoptera	Coleoptera		Dammhahn and Kappeler, 2008
Brown mouse lemur (*Microcebus rufus*)	X		54 (i)	Coleoptera	Hymenoptera	Orthoptera	Atsalis, 1999
Berthae's mouse lemur (*Microcebus berthae*)	X		13 (i)	Coleoptera	Lepidoptera		Dammhahn and Kappeler, 2008
Aye aye (*Daubentonia madagascariensis*)		X	38 (i)	n/a	n/a	n/a	Sterling et al., 1994
Zanzibar Bush Baby (*Galago zanzibaricus*)	X		70 (a)	Coleoptera	Orthoptera	Diplopoda	Harcourt and Nash, 1986; Rowe, 1996
Haplorhine insectivores (body mass: 100–132 g)							
Spectral tarsier (*Tarsius spectrum*)	X		100 (i)	Orthoptera	Lepidoptera	Hymenoptera	Gursky, 2000
Western tarsier (*Tarsius bancanus*)		X	100 (a)	Coleoptera	Hymenoptera	Orthoptera	Strait, 1991; Rowe, 1996

[a] (i) Indicates only invertebrates in percentage, (a) indicates animal prey is included in percentage; note that these percentages may reflect foraging and capture time as well as feeding time in some cases. See references for details.

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with morphological and anatomical adaptations in their feeding apparatus, particularly in tooth morphology. Hard-bodied feeders have less molar shearing crest development than soft-bodied feeders, which have longer molar shearing crests to facilitate the complex task of fracturing their foods (Strait, 1993a; Evans and Sanson, 1998, 2005). In addition, microwear patterns are different between hard-object feeders and soft-object feeders, suggesting that it is possible to decipher these patterns in the fossil record and infer potential diets of ancestral primates (Strait, 1993a,b,c, 2001).

Given the review of insect nutritional properties above, we hypothesize that, in addition to differences in the physical properties between hard and soft-bodied insects, there may be nutritional differences as well. To examine this hypothesis, we surveyed the published literature on the nutritional properties of adult coleopterans and the larval lepidoterans to determine whether soft-bodied insects differed in chitin, protein and fat from hard-bodied insects (Supplementary Online Material [SOM]) using an independent samples *t*-test with unequal variances (PASW Statistics Release 18.0.2, 2010). We chose these Orders because they were used in Strait and Vincent (1998)'s analysis to represent the chosen items of soft-bodied insect feeders and hard-bodied insect feeders. In this assessment, the soft-bodied larval insects were higher in fat, and similar in chitin and protein to the hard-bodied adult insects, (fat: $t = -4.52$, df $= 65.34$, $p < 0.001$; chitin: $t = 1.34$, df $= 15.50$, $p = 0.10$; protein: $t = 0.343$, df $= 27.98$, $p = 0.734$; Fig. 2). Because fat is higher in energy than protein and carbohydrates, the soft-bodied insects provide more energy per gram of dry weight, or more energy per bite of insect. Thus, this difference in dietary ecology and nutritional strategy may have implications for primate behavioral ecology and evolution.

Since many of the earliest fossil euprimates are considered insectivorous based on dental morphology (Szalay and Delson, 1979; Kay and Covert, 1984; Covert, 1986, 2002; Rose, 1994; Ni et al., 2004; Gilbert, 2005), it is interesting to consider the nutritional implications of early fossil primate diets. Based on data for *Donrussellia* and *Teilhardina*, it would appear that these earliest insectivorous euprimates did not have the extremely long shearing crests associated with the consumption of soft-bodied food items (Williams and Covert, 1994; Strait, 1997, 2001; Gilbert, 2005; Gilbert, Unpublished data), indicating a more generalized insect diet focusing on hard-bodied insects. Since these hard-bodied insects are of lower energy per unit of mass, this observation suggests that similarly sized early primates either had to catch more of these insects to satisfy their basic nutritional requirements, supplement their diet with a significant portion of other dietary items, or some combination of both. Another logical extension is that, as hard-bodied insects are usually quicker and more agile than soft-bodied ones, perhaps the earliest euprimates were relatively quick-moving animals as well, an adaptation perhaps selected to increase the efficiency of insect predation. Indeed, the majority of extant prosimian hard-bodied insect feeders are small, fast-moving animals (e.g., *Galago*, *Microcebus*, and *Tarsius*, see Table 2). The earliest fossil euprimates were tiny (<150 g), also consistent with a high metabolism and fast-moving locomotor pattern. Postcrania from *Teilhardina belgica* and *Archicebus achilles* indicate frequent leaping behavior in these taxa, also consistent with high metabolisms and fast moving locomotor patterns (no postcrania exist for *Donrussellia*, *Steinius*, or *Altanius*). Thus, it is quite possible that preying upon and including certain hard-bodied insects as a significant portion of the diet also required a locomotor shift in the earliest euprimate ancestors. Such an adaptive scenario for euprimate origins is consistent with both the Visual Predation Hypothesis (Cartmill, 1972, 1974, 1992) as well as some version of the Grasp-Leaping Hypothesis (Crompton, 1995; Szalay, 1980, 1988) and suggests that multiple selective factors may have been acting at the same time or in quick succession (e.g., see also Dagosto, 2007; Gilbert, 2008). However, there are also slow-moving, hard-bodied insect specialists among the living primates, so without additional fossil evidence to more accurately assess the ancestral euprimate locomotor mode, we must consider the current evidence for a quick, grasp-leaping euprimate ancestor as currently equivocal.

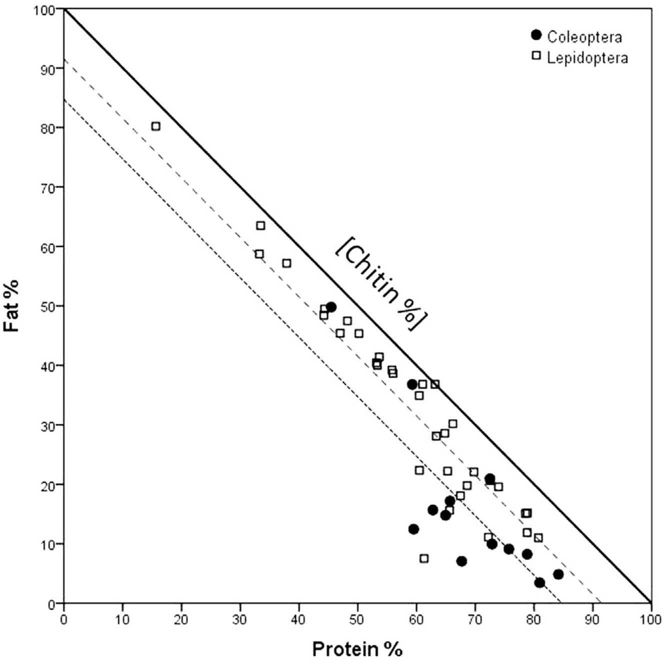

Figure 2. A right angle mixture triangle plot illustrating the differences in fat (*y*-axis), protein (*x*-axis), and chitin (*z*-axis) between the adult hard-bodied Coleoptera and immature soft-bodied Lepidoptera. The solid diagonal represents 0% chitin, and the broken diagonals show the mean chitin concentrations in Lepidoptera (large dashes) and Coleoptera (small dashes). Fat was significantly higher in the Lepidoptera than Coleoptera, while chitin and protein were similar.

Conclusions

Most primates include insects in their diets to varying extents. As a dietary component, insects are incorporated as staples, complements, supplements and replacements. Overall, it is apparent that insects are a good source of protein and fat, and a micronutrient source, when they are available in sufficient quantities. Since the earliest primates were likely insectivorous, understanding insect nutritional properties is important for reconstructing ancestral primate feeding strategies and behavioral ecology. On the basis of dental morphology, the earliest fossil primates can be classified into soft-bodied or hard-bodied insectivores. Hard-bodied insects, apparently preferred by the earliest euprimates, are typically fast-moving and of lower nutritional value compared with soft-bodied insects, which may have implications for early primate evolution and theories of euprimate origins.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2014.02.016.

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