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

Jessica M. Rothman [a,b,c,d,*,1], David Raubenheimer [e], Margaret A.H. Bryer [b,c], Maressa Takahashi [b,f], Christopher C. Gilbert [a,b,c,d]

[a] Department of Anthropology, Hunter College of the City University of New York, New York, USA
[b] New York Consortium in Evolutionary Primatology, New York, USA
[c] Department of Anthropology, Graduate Center of the City University of New York, New York, USA
[d] Department of Biology, Graduate Center of the City University of New York, New York, USA
[e] Charles Perkins Centre, University of Sydney, Sydney, Australia
[f] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, USA

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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.

* Corresponding author.
E-mail address: jessica.rothman@hunter.cuny.edu (J.M. Rothman).
[1] 695 Park Avenue, Room 724, Hunter College of the City University of New York, USA.

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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,