



Nutritional Ecology of Entomophagy in Humans and Other Primates

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Abstract

Entomophagy is widespread among nonhuman primates and is common among many human communities. However, the extent and patterns of entomophagy vary substantially both in humans and nonhuman primates. Here we synthesize the literature to examine why humans and other primates eat insects and what accounts for the variation in the extent to which they do so. Variation in the availability of insects is clearly important, but less understood is the role of nutrients in entomophagy. We apply a multidimensional analytical approach, the right-angled mixture triangle, to published data on the macronutrient compositions of insects to address this. Results showed that insects eaten by humans spanned a wide range of protein-to-fat ratios but were generally nutrient dense, whereas insects with high protein-to-fat ratios were eaten by nonhuman primates. Although suggestive, our survey exposes a need for additional, standardized, data.

INTRODUCTION

Insects are in many respects an ideal staple component to the diets of humans and other primates. They are highly nutritious (8), compose a substantial proportion of terrestrial metazoan biomass, have higher reproduction rates and food conversion efficiencies than mammals do (78), and in many cases are relatively easy to gather (8). Yet there exists substantial variation in the extent to which insects actually are incorporated into the diets of humans and other primates, and a dearth of syntheses that attempt to explain this variation.

Primates probably evolved from a common ancestor shared with insectivorous tree shrews, and the earliest primates were likely insectivorous (31). Virtually all extant nonhuman primates include insects in their diet to some extent. Many small nocturnal primates are almost solely insectivorous, whereas for other primates, insects contribute a minor component of dietary intake. Although insects individually provide relatively small packets of nutrients, they are often highly sought after even by large-bodied apes. For example, some apes invest a substantial effort, including the use of purpose-built tools, to capture them (57, 110). Insects are thus clearly important in the diets of nonhuman primates, but not uniformly so (58).

The dietary use of insects by humans is even more variable. Evidence suggests that entomophagy featured significantly in the evolution, prehistory, and history of the human diet. Today, over 1,600 species of insects are eaten deliberately by humans, but cultures are highly variable, spanning the spectrum from active avoidance to occasional and substantial consumption.

Why does this diversity in the dietary utilization of insects by humans and other primates exist? Here we synthesize the literature to examine this question, and apply an analytical tool from nutritional ecology, the right-angled mixture triangle (85), to consider the influence of insect nutritional composition on the diversity of entomophagy among humans and nonhuman primates.

PATTERNS OF ENTOMOPHAGY IN PRIMATES

Nonhuman Primates

Given the diversity and abundance of insects across a range of tropical and temperate habitats, it is not surprising that almost every record of wild primate diet contains insects to some extent, but the dietary contribution of insects varies widely.

Body size and digestive ecology exert a strong influence on entomophagy. In general, insects compose a major portion of the diets of only smaller primates (<1,000 g) (49, 50), because small animals have higher metabolic needs per unit of body mass. Also, although they are energy dense (90), most insects are typically hard to catch, and it is more likely that the requisite biomass of insects is available to sustain only small-bodied animals. Primates that eat large portions of insects also have gut adaptations for insectivory. These include a simple, unspecialized gut, with smaller stomach-to-small intestine ratios (using metrics associated with mass, area, and length) than primates that are mainly frugivores and folivores (14). Stevens & Hume (105) note that the colon of the insectivorous tarsier (*Tarsius* spp.) was 20% the length of their small intestine, whereas this ratio was much larger in the folivorous-frugivorous monkeys. Many predators of arthropods possess chitinases; among the few primates that have been sampled, the same was true of the insectivorous potto (*Perodicticus potto*) and partially insectivorous white-headed capuchin monkey (*Cebus capucinus*), suggesting that they can at least partially digest insect exoskeletons (105).

The influence of accessibility on the patterns of entomophagy by primates is illustrated by the small-bodied titi monkey (*Callicebus oenanthe*), which apparently preferred feeding on easily

harvested insects found in rolled leaves and ate other more mobile species opportunistically (24). Likewise, larger primates typically eat insects only if they occur in swarms, such as during insect migrations (29) and in social colonies [e.g., apes feeding on ants and termites (57)]. Otherwise, they might eat insects in combination with other parts of their diet [e.g., *Colobus* spp. feeding on insects intentionally from the undersides of leaves (106)], or accidentally [e.g., black howler monkeys (*Alouatta caraya*), which consume invertebrates with their fig-based diet (6)].

Although primates eat insects from a diversity of orders (40), the insects eaten most often are from “the Big Five”: Coleoptera, Hymenoptera, Isoptera, Lepidoptera, and Orthoptera (58). As discussed below, the reason for this is likely the comparatively high accessibility of these insects, many of which are periodically abundant, wingless, or slow moving (58).

Humans

Undoubtedly, the primate with the most diverse entomophagy is our own species, with the dietary contribution of insects ranging from none (by intention) to substantial. Most humans in developed countries regard the consumption of insects with some revulsion, and where exceptions occur, these are sufficiently unusual that they are newsworthy (113). In such countries, insects are generally considered food more for their novelty than their nutrients, for example, embedded in chocolates or ice cream (48), or as a means of survival when wilderness adventures go wrong (122).

There are, however, also instances of regular entomophagy in developed countries. In Japan insects are eaten as part of the traditional diet (68), and in some parts of Italy (74) and Croatia (62) the cheese maggot (*Piophilidae casei* L.) is regarded as a delicacy. The feeding habits of the cheese maggot make it a particularly interesting food choice for humans that are otherwise not entomophagous. Most edible insects are herbivorous and are thus considered relatively clean feeders (7), whereas the diet of *P. casei* extends beyond maturing cheeses to decaying human corpses (10). This species is a vector of human pathogens (54) and is associated with myiasis (maggots feeding on living tissues), including the intestines of humans (80). Also in Europe, the mite *Trophagus casei*, which can cause dermatitis, is added to German Altenburger cheese to create a flavorful powdery gray coating, which consists of the mites, their exuviae, and their feces (74).

The Western abhorrence of eating insects is unusual on a global scale, with entomophagy being the norm rather than the exception in many human populations. The global center of human entomophagy is the Americas, where 679 species are reported to be eaten across 23 countries (48, 84). An interesting possibility is that this high incidence could be influenced by the fact that pre-Hispanic Mesoamerica was unusual among ancient civilizations in achieving organizational complexity and a high population density without a domesticated herbivore and was thus reliant on alternative protein sources (109). In Africa 524 species are eaten across 36 countries, in Asia 349 species across 29 countries, in the Pacific region 152 species across 14 countries, and in Europe 41 insect species are eaten across 11 countries (48, 84). The above figures are derived from the total number of insect species eaten globally, which is estimated to be 1,681, but the actual number might be 2,000 or higher (78).

Among these populations the proportional contribution of insects to the diet ranges from substantial to minor. In recent times in parts of central Africa, more than 50% of animal protein eaten was derived from insects (78), and this figure might reach 64% in parts of the Democratic Republic of Congo (23). Seasonally, insects provided up to 26% of animal protein (approximately 16% of total protein), and up to 23% of animal fat, eaten by Tukanoan Indians of Northwest Amazon (26). In other cases insects are eaten in small amounts, often regarded as a delicacy (78). There may also be appreciable variation in the dietary contribution of insects to different groups within communities. Typically, men rely to a greater extent on hunted meat and women and

children on small animals such as insects, which can be collected with minimal risk and effort (26, 78).

Considering the insect orders, Coleoptera contribute the greatest number of species to the human diet (468 species), followed by Hymenoptera (351 species), Orthoptera (267 species), Lepidoptera (253 species), Hemiptera (180 species), and Isoptera (61 species). Other orders eaten include Diptera, Odonata, Ephemeroptera, Trichoptera, Neuroptera, Anoplura, and Thysanura (48). The highest-ranking four orders, which jointly contribute 80% of the insect species known to be eaten by humans, are also represented among the Big Five orders eaten by nonhuman primates (58).

In general, there is a tendency for humans to eat insects at the largest stage in the life cycle, and those with the lowest proportion of exoskeleton (7). Larvae and pupae are commonly targeted, although adults are also eaten (48). In some societies insects are eaten only when edible vertebrates are scarce (61), whereas in other societies insects are continuously sought-after resources (77).

It is not always the insect itself that is eaten by humans, but sometimes food products produced by insects. The most widespread among these, which is the closest that many Westerners get to deliberate entomophagy, is honey, the regurgitated, concentrated nectar collected by honey bees (*Apis mellifera*), and the associated products royal jelly and propolis (112). Another example is the consumption by Italian children of the sugar-rich crops of *Zygaena* moths, while avoiding the cyanogenic body tissues (123).

ENTOMOPHAGY AND THE AVAILABILITY OF INSECTS

What explains the diversity of patterns of entomophagy in humans and other primates? It is widely believed that faunivores choose their prey based on availability, rather than specific nutrient content (22, 33, 90). We now consider the influence of insect availability on entomophagy in primates and address the role of nutrients below.

Nonhuman Primates

McGrew (58) presents a useful classification of entomophagy by nonhuman primates based partly on body size (hence the absolute energy requirement) and partly on the capacity to use extractive technology in foraging to improve harvest rates. The first type, obligate insectivory, applies to small primates (<1 kg) that are constrained to include insects and other fauna in their diet because of their small, unspecialized guts. These primates eat solitary prey frequently, typically flying insects, and do not use tool technology. Included in this group are small-sized lemurs, galagos, pottos, and tarsiers. For example, the diet of the spectral tarsier (*T. spectrum*) consists of over 50% Lepidoptera and Orthoptera (38). The diversity of insects eaten by smaller primates is illustrated in an examination of niche separation in sympatric bushbabies (*Galago crassicaudatus* and *Galago senegalensis*) in South Africa, where seven orders of insects were recorded in the diets of just these two species (40). In addition, the nocturnal pottos (*Perodicticus potto*) eat a mixture of tree gums and flying insects, ants (*Crematogaster* spp.), caterpillars, snails, and slugs (70). Pottos are also one of the few primates with confirmed chitinase activity in their gastric mucosa to assist in the digestion of exoskeletons (16). Sympatric tamarins (*Saguinus* spp.) form mixed-species associations whereby a 'beating effect' of one species' movement in the upper canopy increases the prey capture rate of the other species in the lower canopy (81). Although most obligate insectivores are small, the 10-kg patas monkey (*Erythrocebus patas pyrrhonotus*) eats predominantly gums and *Crematogaster* and *Tetraponera* found inside the swollen thorns of *Acacia* spp. trees in its savannah habitat in Kenya (44). Patas have long limbs relative to their body size and can travel short distances at high

speeds, which provides a unique adaptation to feeding on widely dispersed, high-quality foods such as insects (44, 45).

The second type is occasional insectivory, which applies to most medium-bodied monkeys and lemurs (1–15 kg) (58), in which the frequency of insectivory is low, insect prey are typically solitary, and only a few use extractive tools [e.g., *Cebus* spp. (73)]. For example, red colobus monkeys (*Procolobus tephrosceles*) are primarily folivorous, but they regularly consume invertebrates, particularly inside rolled leaves, as a minor portion of the diet (106). Guenons such as the blue monkey (*Cercopithecus mitis*), L'Hoest's monkey (*Cercopithecus lhoesti*), and redbellied monkey (*Cercopithecus ascanius*) consume insects regularly, and depending on their locations across Africa insects make up <1% to 36% of their diets (13). Occasional insectivory is often opportunistic and seasonal. Black-bearded sakis (*Chiropotes satanas*) in the Brazilian Amazon are usually seed predators, but seasonally they spend 14% to 26% of their feeding time eating insects when caterpillars and winged termites are abundant (111). In Yasuni National Park, Ecuador, the ranging patterns of woolly monkeys (*Lagothrix lagotricha poeppigii*) were apparently driven by insect prey availability (25). Although their diet consists almost entirely of grasses, geladas (*Theropithecus gelada*) in Ethiopia intensively consume desert locusts during outbreaks (29). Another example of occasional insectivory is the feasting of scale insects by langurs (*Presbytis entellus*) in India, which spend >15% of their time on insects during monsoons when the insects are abundant. During monsoons, langurs moved to areas where insects were plentiful, and they still had access to their normal foods, suggesting that insects were preferred (103). This is unexpected because langurs are foregut fermenters that eat mainly leaves. These observations suggest that when they are abundant, insects can act as replacements in the diets of some primates.

The third type of entomophagy by nonhuman primates, social insect feeding, is confined primarily as a supplement or complement to the diets of the great apes (58). For example, in savanna-woodland habitats chimpanzees (*Pan troglodytes*) spend up to 60% of their foraging time eating termites (*Macrotermes* and *Cubitermes* spp.) (4). In addition, chimpanzees ate weaver ants (*Oecophylla longinoda*), army ants (*Dorylus burmeisteri*), honey bees (*Apis mellifera*), and ponerine ants (*Pachycondyla analis*) (4). At other sites, different species are consumed, including *Dorylus molestus* in Uganda (41). In Gabon, gorillas (*Gorilla gorilla*) and chimpanzees eat weaver ants and chimpanzees also eat *Apis* bees and their honey (108). White-headed capuchin monkeys (*Cebus capucinus*) apparently closely follow and consume the foraging columns of army ants (75).

Humans

Body size is a factor that influences the extent to which a given biomass of insects is profitably harvested by humans, but we are unaware of any model that uses variation in body size to explain variation in entomophagy among human groups. Nonetheless, there is abundant evidence that the availability of insects per se influences the pattern of entomophagy among humans, and some authors have concluded that this is the primary determining factor (22, 90).

At the most general level, the strong representation of Coleoptera, Hymenoptera, Orthoptera, and Lepidoptera in the diets of humans and other primates is related to their availability. Insects from these orders are often abundant (for example, many Hymenoptera, Orthoptera, and Lepidoptera form large permanent or seasonal aggregations), large-bodied, or slow moving at some stage in the life cycle (65). Humans exploit these characteristics, often with the use of technology (see below). Geographic and seasonal availability of insects is also reflected in their contribution to the human diet. For example, in Thailand some insects are eaten only in specific regions, whereas other insects, such as the giant water bug (*Lethocerus indicus*), are eaten throughout the country (39). In Arunachal Pradesh, northeast India, edible insects that are perennially available are eaten

throughout the year, whereas the consumption of other insects is restricted by seasonal availability of the edible stage in the life cycle (12). Insect consumption can also vary with fluctuations in availability caused by interannual weather patterns (120, 121).

Compared with other primate insectivores, insects compose a highly variable proportion of dietary animal foods for humans, the remainder coming from a diverse range of other invertebrates and vertebrates (58). Therefore, the availability of alternative animal foods is likely to exert a strong influence on entomophagy by humans. Some studies demonstrate that insects are eaten by humans more frequently when other animal foods are scarce or not available (26, 61, 64). In the extreme, insects have been advocated as a survival diet in cultures that are not normally entomophagous (122). Conversely, there are cases in which insects are preferred over conventional meats (26) and can displace conventional meats from the diet (21). One survey, conducted in Thailand, indicated their pleasant taste as the most frequently cited reason for eating insects (120).

As stated above, some insectivorous nonhuman primates have chitinase enzymes that increase the availability of insect-derived nutrients. Chitinase activity has been demonstrated in the gastric juices of humans (79). There was, however, considerable variation among the subjects tested, which the authors speculate might relate to genetic diversity associated with between-population variation in the consumption of insects and other chitin-producing invertebrates.

TECHNOLOGY AND CULTURAL PRACTICES FOR OBTAINING EDIBLE INSECTS

The previous section suggests that availability is an important factor influencing the consumption of insects by primates. Both humans and nonhuman primates have developed technology to increase the rate at which insects can be harvested.

Nonhuman Primates

Of all primates, chimpanzees exploit social insects most frequently and often use a sophisticated array of tools to do so. The first reports of chimpanzee tool use were made by Jane Goodall's pioneering observations that chimpanzees use grass stalks to extract Isoptera (36). We now know from many long-term research sites that chimpanzee tool use for entomophagy is common and widespread across Africa (3, 57, 59, 63, 96, 107) and that other primates (and other animals; 2) use tools to capture a variety of insects. For example, chimpanzees use dipping sticks to extract *Dorylus* spp. from ground nests (3, 37) and fishing sticks to obtain *Camponotus* sp. in trees (67, 118). Some chimpanzee populations use complex tool kits, involving up to 20 different types of tools, some of which are used in sequence, to obtain and process insect prey (59). Chimpanzees in other areas do not eat insects frequently and consequently do not use extractive tools as readily (59, 116).

In addition to hypotheses about prey availability, prey distribution, and cultural traditions, it is interesting to consider nutritional hypotheses about the distribution of tool use (51). Because insects provide a rich source of protein for the predominantly frugivorous chimpanzees (see below), an important question is whether the frequency of tool use is related to the availability of alternative protein sources, such as leaves and vertebrate prey. In areas where extractive tools are never or infrequently used, such as Kibale and Budongo Forests in eastern Uganda (97, 116), monkey hunts are frequent (115), and in general the protein content of leaves is higher than in western forests (35, 71, 82), suggesting that ecological pressures to develop more elaborate tool technology to obtain more protein may not be needed (51). However, because primates require amino acids, not protein per se, the most comprehensive test of this hypothesis would be to examine the amino acid profiles of leaves and insects eaten by chimpanzees across a range of habitats. In an early

analysis Hladik (43) presented amino acid data on *Macrotermes bellicosus*, eaten by chimpanzees at Gombe Stream National Park, Tanzania, and suggested that the concentrations of histidine, leucine, lysine, and threonine are higher in the termite than in the plant-based portion of primate's diet.

Other primates also use tools to extract insects. Sumatran orangutans manufacture tools and/or use twigs, sticks, and branches to extract insects and their products (32, 110), and capuchins (*Cebus* spp.) use sticks to access insect nests and fish for termites and use stones to dig for tubers (73, 102). Notably, the other great apes—gorillas (*Gorilla* spp.) and bonobos (*Pan paniscus*)—do not use tools to obtain insects, although gorillas do deliberately eat them in small quantities (19, 34, 114, 117). Entomophagy is less frequent among mountain gorillas, which live in forests with high-protein foliage (95), than among western gorillas, which have a more frugivorous diet (93). Bonobos eat limited amounts of insects, even though similar arthropod species eaten by chimpanzees are available in their habitats, as are potential tools (58, 60). Because terrestrial herbaceous vegetation is abundant in their habitats, bonobos probably meet their protein needs from this source (53). In our view, investigations into the nutritional ecology of entomophagy and other diet portions may elucidate interspecies and population differences in extractive tool use.

Humans

A large proportion of the insect species eaten by humans are collected from the wild (48), often using technology. This technology sometimes closely resembles the tool use of nonhuman primates, as is the case for several Amazonian tribes that have developed a form of “termite fishing” similar to that used by chimpanzees (76). In other cases, uniquely human technologies are used, including the use of lights, nets, fire, water-filled bins, and sticks tipped with glue (121).

The most distinctive use of technology to increase the availability of insects for humans involves the manipulation of the environment to increase insect yields. One form of manipulation is where edible insects are concentrated as a by-product of human interactions with the natural environment for other purposes. For example, the Tatuyo Indians of the Amazon cut palms to harvest their fruits, and in so doing expose the starch-rich pith to colonization by edible palm weevil larvae (*Rhynchophorus* sp.), which are later collected (26). Similarly, large-scale insect pests of agricultural crops are sometimes harvested for human consumption, for example, grasshopper plagues in Mexico (11). Humans also manipulate the natural environment specifically to concentrate insects—a practice known as semicultivation. Thus, the Tatuyo Indians fell palm trees for the specific purpose of attracting insects, which then form a food cache for hunters (26), and similar practices have been developed in tropical Africa and New Guinea (109). A further step in manipulating the environment to concentrate insects is growing crops specifically for this purpose. An example is found in Thailand, where the collection of locusts (*Patanga succincta*) from maize fields inspired the planting of maize specifically to feed these insects rather than to harvest (39).

The most extreme form of manipulating the environment to increase the availability of insects is through farming domesticated species. Bees and silkworms, the most fully domesticated insects, are farmed principally for the products they produce, honey and silk, respectively, but both insects are also eaten (5, 39, 101). Increasingly, other species are being domesticated in several countries. Some of these species, including water beetles (*Hydrophilus* sp. and *Cybister* sp.) in China and crickets (*Gryllus bimaculatus* and *Acheta domesticus*) in Thailand, are produced commercially (120), sometimes on a large scale. For example, 400 families in two villages in Thailand produce 10 metric tons of crickets in the peak production period, both for the domestic market and export (48). Paoletti & Dreon (78) suggested that most of the edible insect species collected from the

wild could be domesticated, although in many cases seasonal challenges and technical difficulties must be overcome (98, 120).

NUTRITIONAL IMPLICATIONS OF ENTOMOPHAGY

Is availability the primary determinant of the patterns of entomophagy in primates (22, 90), or is nutritional quality also important? This question mirrors a debate concerning food selection by predators in general. Specifically, it has long been assumed that the nutritional quality of animal tissue is generally high, and therefore predators are limited by the amount of prey they can capture rather than the specific composition of different prey. Studies have shown, however, that the composition of prey animals can vary appreciably (87), that both invertebrate (47) and vertebrate (42, 55) predators feed selectively from prey according to their nutrient composition, and that there are fundamental fitness benefits from so doing (47). These findings suggest that not only the quantity but also the quality of prey is important to predators. In this section we consider whether the patterns of consumption of insects by primates are similarly influenced by variable nutritional quality.

Nonhuman Primates

A comprehensive study of prey choice by chimpanzees and gorillas in Cameroon provides a robust dataset on the nutritional composition of several ants and termites, including both species that are eaten and species that are accessible but not eaten (17–20). Some interesting nutritional results emerged. First, ants have higher gross energy, moisture, crude protein, and available protein than termites do. Chimpanzees preferentially selected insects that were higher in energy, protein, and dry weight over insects that were accessible but not eaten, but gorillas did not appear to have similar preferences (18). Second, ants and termites have much higher concentrations of protein compared with other foods in gorilla and chimpanzee diets (20). Although data are not available from the same site where the insects were collected for nutritional analysis, the typical concentration of protein in the ape diet is around 10% for chimpanzees (15) and 17% for gorillas (94), but the protein concentration of ants and termites is considerably higher at 40% to 60% (20).

The findings from Cameroon are consistent with data from other primate sites, suggesting insects generally provide a good source of protein for nonhuman primates. In female white-headed capuchin monkeys (*Cebus capucinus*) in Costa Rica, the major source of protein in their diet came from insects, which composed 40% of the diet. Eaten insects were composed of 63% protein, while fruits, seeds, and flowers were 15–16% on a dry weight basis (56). The fat content of insects (15%) was lower than that of seeds (20%) (56). Grasshoppers, weevils, winged ants, and unidentified larvae eaten by Japanese macaques (*Macaca fuscata*) (46), and by patas and tamaris monkeys, are also high in crude protein, the content of which varies from 30% to 65%. Larvae, which were high in fat (33–44%), were eaten less often than adults (7.85%) (65), but no data on the availability of these foods were provided.

Because we know very little about the mineral concentrations of primate diets, it is difficult to assess the role of insects, but from the few data available, provision of minerals by insects is significant. The concentration of sodium in the larvae eaten by aye-ayes (*Daubentonia madagascariensis*) is much greater than that of typical plant-based food sources; sodium values of large larvae eaten were 999 ppm and that of small larvae was 2,140 ppm (104). In a comparison of the top staple foods and insects of redbellied monkeys (*Cercopithecus ascanius*) in Kibale National Park, Uganda, concentrations of sodium, iron, and copper were higher in insects (91, 92). Both sodium and copper are limited in this forest (91) and have been suggested to limit redbellied monkey population densities (92). No

single plant food met the guidelines for sodium intake set by the National Research Council (66), and sodium intake from the typical plant diet fell well below suggested requirements throughout the year.

The incorporation of insects into the redtail diet in Kibale National Park provides an alternative source of sodium (and other minerals), which may be obtained more easily than rare high-sodium vegetation (69). Similarly, in Cameroon, gorillas (*Gorilla gorilla*) are likely driven to eat insects because the mineral content, particularly sodium, of plant foods in these forests is low. The mean concentration of sodium in consumed termites and ants is 6,235 ppm, with a range of 300–44,100 ppm (20). Gorillas do not hunt, and aside from practicing occasional entomophagy, they are vegetarian. The plant portion at this site was not studied, but in nearby forested habitats where gorillas reside, sodium in plants was much lower at 30–500 ppm (mean: 145 ppm), indicating that insects serve as an important source of sodium (9). More data on the mineral compositions of primate foods, including vegetation, fruit, and insects, are needed.

Humans

Bukkens (8) has reviewed the literature on the nutrient composition of insects eaten by humans. The data presented suggest that insects are a high-quality food, being an excellent source of protein, fat, and micronutrients, with amino acid compositions that are generally balanced for humans. The few available measures of fatty acid profiles showed that insects contain significant levels of the essential fatty acids linoleic acid (omega-6) and linolenic acid (omega-3), but not of the long-chain polyunsaturated acid derivatives of linoleic and linolenic acid, arachidonic acid and docosahexanoic acid, respectively. In terms of degree of saturation, insect fatty acid profiles are equivalent to those of fish and poultry (21). The carbohydrate content of insects, which is often not measured or even estimated by difference, was not reported by Bukkens, but some studies report high concentrations. For example, eight species ranged from 6.7% (the longan stink bug, *Tessaratoma papillosa*) to 16% (cicada, *Meimuna opalifera* Walker) (83), whereas the dry weight concentration of carbohydrate in raw larvae of the African rhinoceros beetle (*Oryctes monoceros*) was a surprising 51% (28). The limited data for micronutrients showed that the minerals iron and calcium were present in concentrations greater than those found in beef, and many insects also had good levels of B vitamins, beta-carotene, and vitamin E. Insects also contain structural carbohydrates equivalent to those found in fiber, in the form of the chitinous exoskeleton, in proportions similar to cellulose in grain-based foods such as whole wheat flour (8). Overall, the synthesis of Bukkens thus supports the now widely accepted view that for humans insects are generally a good source of calories, protein, fat, vitamins, and minerals (52, 120).

There is, however, also considerable variation in the nutritional composition of insects. Across all species tabulated by Bukkens (8), crude protein ranged from 7.5% dry weight (raw flying ant females, *Carebara* sp.) to 91% (dried rice grasshopper, *Oxya velox*). There was also appreciable variation among species within orders. For example, within the Orthoptera, protein ranged from 41% (*Locusta migratoria manilensis*) to 91% (*O. velox*), and the reported range in ants was 8% to 52%. Composition varied appreciably even among replicate samples of the same species, with reported protein concentrations of palm weevil larvae (*Rhynchophorus* sp.) spanning 23% to 36%.

The amino acid profiles also differed among insects, with the majority having limited amounts of lysine or tryptophan, whereas in other insects lysine and tryptophan were well represented. Particularly variable were the fatty acid profiles, even between related insects collected in different locations, suggesting that diet is a strong determinant of fatty acid levels in insects. Subsequent studies have also demonstrated the variability of fatty acid profiles in edible insects. For example, the total level of polyunsaturated fatty acids across six species of insects eaten in Thailand varied

between 726 and 2,883 mg/100 g, whereas the total level of saturated fatty acids ranged between 653 and 5,432 mg/100 g (119). The limited data suggest that cholesterol levels in edible insects are variable, ranging from none detectable to approximately the levels found in mammals (8, 22). The levels of some micronutrients, including retinol and beta-carotene, also vary considerably among edible insects (8).

An important question is whether specific insects are selected to complement the particular nutritional profiles of the diets of different human populations, or to offset changes (e.g., seasonal) in the diet. Little is known about this, but there is some evidence that the amino acid profiles of edible insects in Zaire and Papua New Guinea complement specific deficiencies in the staple foods of these countries (8).

THE CHALLENGE AHEAD: A NUTRITIONAL PERSPECTIVE

We consider it an important goal to determine how variability in the nutritional composition of edible insects influences patterns of entomophagy among primates. This question will be addressed most likely by meta-analyses, which draw data from multiple studies. The recent literature demonstrating the powerful role of two-way and higher-order interactive effects of nutrients on animals (86, 89, 99, 100) suggests that such analyses should be performed within a multidimensional framework that detects these interactions. In this section we recommend a geometric approach, known as the right-angled mixture triangle (85), and present some illustrative analyses of entomophagy in primates.

One approach to nutritional geometry, which is particularly powerful for experimental studies but has also been used for observational field studies (30, 95), models the absolute amounts of various nutrients required and eaten by animals (88, 89, 100). However, our literature search failed to provide data to perform this kind of analysis for primate insectivory. We therefore collated data on the compositions of insects eaten by human and nonhuman primates, and subjected these data to a preliminary proportions-based geometric analysis using right-angled mixture triangles (RMT) (85). RMTs enable the relationships between three or more components of mixtures, such as food compositions or diet compositions, to be compared and interrelated within a single two-dimensional plot using standard quantifiable vectors (**Figure 1**).

To illustrate, we plotted the data in table 28.2 from Bukkens' (8) review of entomophagy in humans (**Figure 2**). These data represent the composition of the edible portions (i.e., as actually eaten) of 49 common food insects. The model includes the two macronutrients presented in the table, crude protein and fat (x and y axes), and on the third axis is the sum of the water-free nonmacronutrient components. This last vector represents the inverse of the dry weight concentration of macronutrients in the insects (85). Several patterns emerge from this plot. First, the protein-to-fat ratio (P:F) varied considerably, from 27:1 (*O. velox*) to 0.32:1 (female flying ants, *Carebara* sp.). Second, the combined concentration of protein and fat (P+F) spanned a wide range: 29% for male *Carebara* sp. to 101% for a termite listed as a species of *Termes*, the latter value clearly reflecting some measurement error. However, the distribution was heavily skewed toward the high end, with only 4 of the 48 insects having a P+F concentration less than 50%. Third, the composition of the samples varied with insect group. Termites and beetles tended to have a low P:F ratio (<1), whereas all other groups tended toward a ratio greater than one. Finally, the Hymenoptera stand out as having a low overall P+F content; the only species that fall below 50% are ants and bees.

The above analysis suggests that although the P:F ratio of edible insects in the sample varied widely, with the exception of some ants and a bee sample, the combined concentration of these macronutrients tended to be high ($>50\%$). To address whether the high macronutrient content is

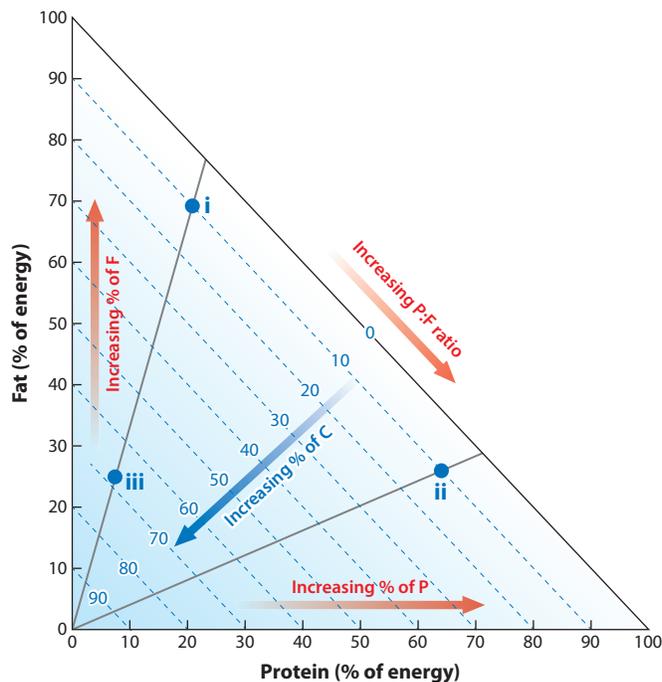


Figure 1

Right-angled mixture triangles depict three components in two-dimensional plots (85). In this hypothetical example, each blue point represents a mixture of protein (P), fat (F), and carbohydrate (C). %P and %F increase along their respective axes, as shown by the horizontal and vertical red gradient arrows. For example, mixture *ii* has a higher concentration of P than mixtures *i* and *iii* do, and *i* has the highest concentration of F. The concentration of the third component (C) is denoted by the dashed blue lines and increases along the blue gradient arrow. For example, *i* and *ii* have the same %C (10%), which is less than %C in *iii* (68%). The dashed blue lines also give the concentration of protein and fat combined (P+F), with the P+F given by the number at which the line intersects the P and F axes. For example, *i* and *ii* each have a P+F concentration of 90%, and *iii* has a P+F concentration of 32%. The P:F ratio of a mixture is given by the slope of the radial that connects the point to the origin. For example, mixtures *i* and *iii* have the same P:F ratio, which is lower than that of mixture *ii*.

a feature of the insects deemed by humans to be edible or whether it is influenced by preingestive processing (e.g., selective removal of parts), we extracted additional data from the literature. This dataset consisted of the gross compositions (i.e., the insect per se, with no indication of preingestive processing) of 86 insects eaten by humans, and compositions of 79 samples presented specifically as edible portions. These data showed that the unprocessed insects were highly variable, both in regard to the concentration and ratio of protein and fat (**Figure 3**), compared with processed samples, which were overrepresented in the upper end (>50%) of the P+F concentration range (likelihood ratio = 7.756, $P = 0.005$). By contrast, the number of processed samples with a P:F ratio greater than or less than 1 did not differ from random samples (likelihood ratio = 1.244, $P = 0.265$). Thus, there is no indication from these data that humans preprocess edible insects to alter the P:F ratio, but preprocessing did have the effect of concentrating both nutrients.

It therefore seems that humans target insects with wide-ranging P:F ratios. Is the same true for nonhuman primates? To address this question we compared the compositions of insects eaten by humans with equivalent data for insects eaten by some nonhuman primates (**Figure 4**). In contrast with the broad range of P:F ratios in insects eaten by humans, all except one insect eaten

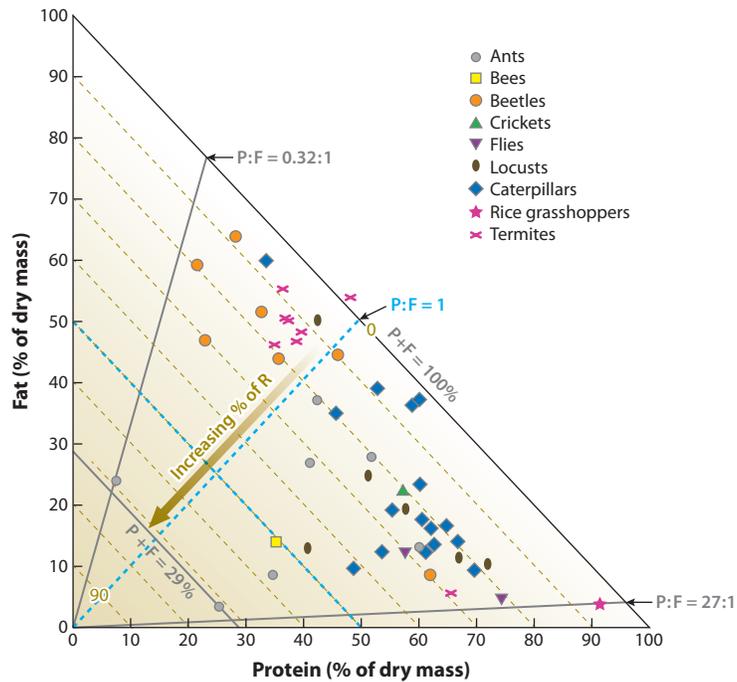


Figure 2

Right-angled mixture triangle plotting the protein (P) and fat (F) content of the edible portions of 49 insects from table 28.2 in Reference 8. Plotted on the third axis is the remainder (R) (*brown gradient arrow and diagonal dashed brown lines*) once %P and %F have been deducted from the total dry mass; this variable is inversely proportional to the dry mass concentration of protein and fat combined (P+F). The labeled, solid gray lines delineate the extreme values in the data. For macronutrient concentration this was P+F = 29% (ant), and P+F = 102% (termite, this value is clearly exaggerated by measurement error). For macronutrient ratio (P:F) the range was 0.32:1 (rice grasshopper) to 27:1 (ant). For reference, the positive-sloped light blue dashed line shows P:F = 1, and the negative-sloped light blue dashed line shows P:F = 50%. The plot shows that most insects had P+F > 50% (to the right of the negative-sloped dashed diagonal), with only ants and bees having P+F < 50%. Most beetles and termites had a P:F ratio less than 1, whereas for other insects P:F exceeded 1.

by nonhuman primates had a P:F ratio greater than 1, with most substantially greater than 1 (likelihood ratio = 9.522, P = 0.002). It thus appears that in our sample the major macronutrient derived from insects by gorillas, chimpanzees, monkeys, and, to a lesser extent, aye-ayes was protein, whereas humans obtained a significant proportion of both protein and fat depending on the insect eaten.

The above analyses are primarily illustrative and are suggestive at best. One limitation is that we could not find sufficient data to control for nonindependence of data points in our analyses. For example, insect nutritional composition is to some extent taxon specific (**Figure 2**), but there were insufficient data to control for this in our comparison of preprocessed and unprocessed insects (**Figure 3**) and human versus nonhuman primate diets (**Figure 4**). Another limitation is the scope and quality of chemical analyses of insects in the published literature. Thus, the majority of studies neither measured nor estimated the carbohydrate content of edible insects. Yet in the 61 insects for which these data were reported, the percentage of macronutrient energy

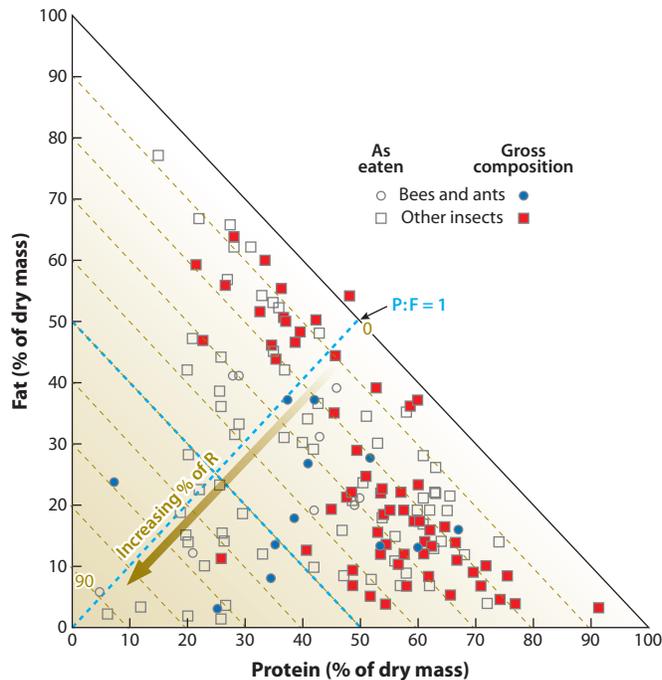


Figure 3

Right-angled mixture triangle plotting protein (P), fat (F), the dry mass remainder (R) for the as-eaten portion (*colored symbols*) of 79 edible insects, and the gross composition (i.e., where the entire animal was measured) of 86 edible insects (*hollow symbols*). For reference, the positive-sloped light blue dashed line shows $P:F = 1$, and the negative-sloped light blue dashed line shows $P+F = 50\%$. Bees and ants (*circles*) are distinguished from other insects (*squares*) to show their preponderance among the as-eaten samples with a low proportion of $P+F < 50\%$. The plot shows that the samples specified in the literature as “as eaten” were overrepresented among those with high $P+F$ concentrations ($> 50\%$), whereas measures of the whole insect spanned the full range (likelihood ratio = 7.756, $P = 0.005$). There was no difference in the distribution of $P:F$ ratios, suggesting that preprocessing of edible insects increases macronutrient concentration but does not systematically alter macronutrient balance. The single non-hymenopteran as-eaten sample with $P+F < 50\%$ is *Oryctes monoceros*, which was reported to have a carbohydrate content of 51% (28). Because at least a portion of carbohydrate would contribute toward dietary energy, this suggests that the true macronutrient content was higher and the non-macronutrient remainder lower than indicated, and on biological grounds the sample should fall among the other red squares. This highlights the importance of estimating all three macronutrients in studies of edible insects.

contributed by carbohydrates ranged from 81% (the honey ant, *Myrmecocystus melliger*) to not detected, with a mean of 10.5%. If these estimates are reliable, insect-derived carbohydrate might well be a significant component of the diet of entomophagous primates, and omitting it could be misleading (e.g., **Figure 3**). Likewise, specific amino acids, fatty acids, or micronutrients might be important, and more information on these is needed. The methods used in the composition data reported above also varied considerably, and in the interests of future comparative studies we encourage researchers to use standardized nutritional analyses of insects (1). Finally, in addition to nutritional proportions, we need to learn more about the absolute amounts of nutrients contributed by insects to the diets of primates. For this, measures of the rates of intake, as well as nutritional compositions, are needed (72).

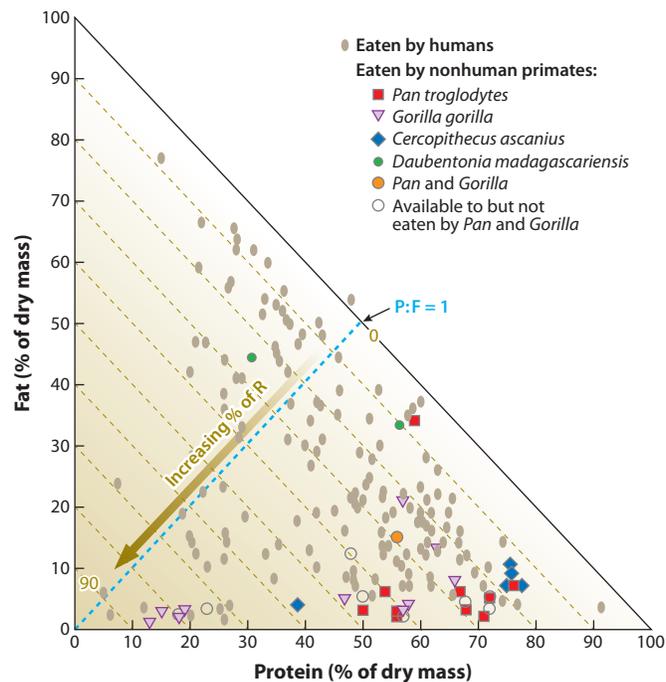


Figure 4

Comparison of the nutrient composition of insects eaten by humans (*small gray vertical ellipses*) and nonhuman primates. Axes are identical to those in **Figures 2 and 3**, and the light blue-dashed diagonal line represents a protein-to-fat (P:F) ratio of 1. The plot shows that insects eaten by nonhuman primates were overrepresented among insects with higher P:F ratios (likelihood ratio = 9.522, $P = 0.002$). However, that a sample of insects available to but not eaten by chimpanzees or gorillas (*hollow circle*) had a composition similar to that of insects eaten by gorillas (*triangles* and *orange circle*) shows that other factors, such as nutrients not included in the analysis or nonnutritional factors, also play a role.

CONCLUSIONS

Both humans and nonhuman primates show diverse patterns of entomophagy, but the factors that drive this diversity are poorly understood. Compared with most conventional food animals, individual insects are small, and their exploitation is thus dependent on their abundance and the ease with which they can be harvested. There is, unsurprisingly, substantial evidence that entomophagy is influenced by insect abundance (absolute as well as relative to primate body size). Both nonhuman primates and humans use extractive technologies to increase the harvest rate of insects, and humans also use various environmental manipulations to do so. Less certain, however, is the effect of insect compositions on the patterns of entomophagy. Existing data suggest that insects are generally high-quality foods for primates, but they also vary substantially in their nutrient composition. To understand the influence of this variation on the patterns of entomophagy among primates, we recommend the use of multidimensional models that disentangle the interactive effects of food components on consumers. However, for this to be effective, future studies should standardize the methodology used to measure insect compositions, adopting procedures that are biologically relevant (1). They should also, where possible, derive estimates of absolute amounts eaten.

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58. Synthesizes the importance of insects in diets across the order Primate, conducts a comprehensive analysis of the types and amounts of insects in primate diets, and explores implications of insectivory for the early human diet.

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