



The ‘other faunivory’ revisited: Insectivory in human and non-human primates and the evolution of human diet



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ABSTRACT

The role of invertebrates in the evolution of human diet has been under-studied by comparison with vertebrates and plants. This persists despite substantial knowledge of the importance of the ‘other faunivory’, especially insect-eating, in the daily lives of non-human primates and traditional human societies, especially hunters and gatherers. Most primates concentrate on two phyla, Mollusca and Arthropoda, but of the latter’s classes, insects (especially five orders: Coleoptera, Hymenoptera, Isoptera, Lepidoptera, Orthoptera) are paramount. An insect product, bees’ honey, is particularly important, and its collection shows a reversal of the usual sexual division of labor. Human entomophagy involves advanced technology (fire, containers) and sometimes domestication. Insectivory provides comparable calorific and nutritional benefits to carnivory, but with different costs. Much insectivory in hominoids entails elementary technology used in extractive foraging, such as termite fishing by chimpanzees. Elucidating insectivory in the fossil and paleontological record is challenging, but at least nine avenues are available: remains, lithics, residues, DNA, coprolites, dental microwear, stable isotopes, osteology, and depictions. All are in play, but some have been more successful so far than others.

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Introduction

All accounts of the evolutionary origins of human diet highlight *faunivory*, that is, the consumption of animals (versus *herbivory*, the consumption of plants), even if the term is seldom used. However, in most theorists’ minds, faunivory equates to *carnivory*, here defined as the consumption of vertebrate tissue, or, in common parlance, ‘meat-eating’. Sometimes confusingly cross-cut with this is the method of obtaining animal matter, usually termed hunting, or less commonly, scavenging, hence the prominence of ‘Man the Hunter’ in evolutionary scenarios (Lee and DeVore, 1968, but cf. Dahlberg, 1981).¹ One of the aims of this paper is to emphasize the ‘other’ faunivory, that is, the consumption of invertebrates, especially insects,² and their products.

When I wrote a book chapter (McGrew, 2001) on this topic, it was the only one in a volume otherwise devoted to carnivory (Stanford and Bunn, 2001). Perhaps in the ensuing 12 years, one

might expect this imbalance to have been rectified? It appears not. A recent and thorough review of diet in early *Homo* (Ungar et al., 2006) devoted much text to hunting and meat-eating but not a single word to eating invertebrates. A more recent update (Ungar and Sponheimer, 2011) was the same: no insects. Similarly, a popular and successful textbook (Larsen, 2010) has many pages on hunting and meat-eating but only two sentences on hominin insect-eating (and these are likely to be misguided, see below). Thus, the second aim of this paper is to update the relative contributions of the ‘other faunivory’ to hypothetical accounts of the origin and evolution of human diet.

Speculating about the key role of faunivory in hominin evolution, from the last common ancestor to the present day, is an abiding cottage industry (e.g., Stanford, 1996; Pickering and Dominguez-Rodrigo, 2012). However, few of the hypotheses posed are presented in testable terms, that is, few are precise enough about how such ideas can be taken beyond argument by plausibility to empirical testing; even fewer of the hypotheses allow for distinguishing carnivory from insectivory. In McGrew (2001), I raised some possibilities for such enquiry, but at that point, most of the suggestions were only notional. In the meantime, some domains of study have proved more useful than others, and a third aim of this paper is to assess to what extent the evolutionary origins of human invertebrate consumption, or ‘invertebrativory’, have been illuminated.

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¹ Hunting is not the same as faunivory or scavenging or butchery, anymore than gathering is the same as herbivory or collecting or foraging. Some animal prey are particulate and sedentary (such as birds’ eggs), just as some plant prey are too large to be eaten whole and must be dissembled into more manageable parts.

² The terms ‘insectivory’ (from Latin) and ‘entomophagy’ (from Greek) have identical meanings, but somehow the former usually is applied to non-humans and the latter to humans.

Finally, a simple fourth aim of this paper is to update the situation from my previous synthesis (McGrew, 2001). Here I focus on recent findings and seek to avoid overlap with the previous work, so this paper should be read as a complementary sequel, preferably in conjunction with the original.

Primate invertebratory

Among primates, two orders of invertebrates repeatedly crop up as dietary constituents for both humans and non-humans: Mollusca ('shellfish' such as clams, snails, mussels, etc.) and Arthropoda (insects, crustaceans, scorpions, spiders, etc.) (Abrams, 1987).

The former are distinguished by their mechanical defenses against predators, foremost of which are calciferous shells and sometimes stubborn adhesion to a substrate. Shells can be breached by suitable dentition, elementary technology, or clever behavior, and none of these suites of tactics is limited to primates: harbor seals crunch molluscs and crustaceans with specially adapted molar teeth (Scheffer and Sperry, 1931), California sea otters smash abalone against stones balanced on their bellies, as they float on their backs (Hall and Schaller, 1964), and banded mongooses hurl snails against hard surfaces (Mueller, 2010). The latter defensive adaptation is less often mentioned: unless a mollusc can be detached from its hold on the substrate, it cannot be transported to a processing site or manipulated. Thus, it is not surprising that gastropods, which are mobile as opposed to sessile, are favored prey among the molluscs. For example, wedge-capped capuchin monkeys eat snails more often than all other invertebrates combined (Robinson, 1984).

A further constraint on eating molluscs is that the large-bodied taxa are mostly aquatic and found mostly in marine habitats. Either their predators must take to the water or take advantage of their temporary exposure in littoral habitats. Early reports of monkeys preying on shellfish exposed at low tide were anecdotal (Carpenter, 1887; Fernandes, 1991), but later systematic study has shown that long-tailed macaques (*Macaca fascicularis*, also known as crab-eating macaques) habitually use impressive technology. In coastal Thailand, the monkeys move onto tidal flats to harvest a variety of species of molluscs (Malaivijitnond et al., 2007; Gumert et al., 2011). Furthermore, they use different types of stone tools to access different types of prey, e.g., snail versus oyster (Gumert et al., 2009). Some of these food-getting habits seem to be culturally acquired: Japanese macaques (*Macaca fuscata*) on Koshima learned to detach limpets from rocks at the shoreline, after they were lured to the beach by food provided by primatologists (Watanabe, 1989). The researchers sought only to habituate the monkeys to observation, but apparently the provisioning incidentally introduced them to new prey, such as limpets and barnacles.

The arthropods are hugely diverse, with several classes. Their anti-predator defenses often take the form of pain-inflicting stings, bites, or toxins. Some of these anti-predator strategies are robust enough to induce teaching of offspring by adults, e.g., meerkats train their kits to deal with scorpions (Thornton and McAuliffe, 2006). Capuchin monkeys (*Cebus* spp.) in Brazilian *caatinga* forests use a variety of tools to obtain and to process various invertebrate species, including spiders (Canale et al., 2009; Mannu and Ottoni, 2009).

Some taxa, such as the Crustacea (shrimp, crab, lobster, etc.), are notably absent in non-human primate diets but figure prominently in human diets in both traditional and industrialized societies. The taxa most often eaten by humans are primarily marine forms, often from pelagic or benthic habitats, necessitating more than elementary technology (see Oswalt, 1976 for examples). However, the arthropod class most often consumed by primates overall, more than all others put together, is the Insecta (Hexapoda).

Insect prey

The only type of invertebrate prey eaten by primates across the board, by the smallest to the largest primates, is insects (see Tables 8.1 and 8.2 in McGrew, 2001). The frequency of insectivory varies from low to high, both within and across taxa; here I concentrate on hominoids, given limitations of space. Of the African great apes, gorillas (*Gorilla* spp.) appear to eat insects only rarely and without technology (Tutin and Fernandez, 1983; Kajobe and Roubik, 2006); the same seems to be true of the much-less studied bonobo, *Pan paniscus* (McGrew et al., 2007). In Asia, insects compose up to 20% of the feeding budgets of gibbons (Hylobatidae) (Elder, 2009). Fox et al. (2004) did the most detailed and extensive study of insectivory in orangutans (*Pongo* spp.): they found cross-site differences, some related to basic environmental constraints. In swamp forest, edible insects (ants, termites, bees) were concentrated in cavities in the canopy, making these prey accessible to the arboreal ape predators. At the same time, these physical obstacles to harvesting the insects likely encouraged the invention of extractive technology (see below).

Chimpanzees use a variety of tools to obtain a variety of insect taxa (McGrew, 1992). Across chimpanzee populations, even in the same region, insectivory ranges from occasional and rare in Uganda (Kanyawara, Ngogo, Semliki) to regular and habitual in Tanzania (Gombe, Mahale) (Sanz et al., 2014; Webster et al., 2014).

Of the orders of insects, only five stand out as prominent prey for primates, including humans: Coleoptera (beetles), Hymenoptera (ants, bees, wasps), Isoptera (termites), Lepidoptera (butterflies, moths), and Orthoptera (locusts, crickets). This is not merely a reflection of biodiversity, for other orders such as Diptera (flies), Homoptera (cicadas, aphids), and Hemiptera (true bugs) are similarly speciose, but are virtually ignored, except by *Homo sapiens*. Some other orders have a few large-bodied taxa, but these are often ecologically unsuitable (e.g., dragonflies). So, why are these five orders favored?

Beetles present some of the largest individual body sizes among insects and their larvae and pupae are therefore desirable. Immature forms in general are higher in protein and fats than adults, as well as being soft-bodied, except for their mouthparts. This makes them maximally digestible. However, most beetle larvae and pupae taken are encased, e.g., wood-boring beetles, and so must be extracted, sometimes with tools. Other beetles are toxic and so unsuitable (e.g., Chrysomelidae).

Ants, bees, and wasps typically are small individually, but the social (colonial) forms may have high collective biomass, and so are targeted, especially by large-bodied primates (e.g., Gotwald, 1995). All have impressive anti-predator adaptations, including venomous stings or painful bites, or fortified homes, either below ground or in cavities, or both (Schmidt, 2014). Being wingless and mostly terrestrial, ants are more accessible to primates than flying bees or wasps, but some taxa (*Dorylus*, *Pachycondyla*) engage in aggressive, massed defense when disturbed. Others, such as carpenter ants (*Camponotus*), bore into living woody vegetation and are virtually invulnerable, except to elementary technology ('ant fishing') (Nishida and Hiraiwa, 1982; Nishie, 2011). Bees targeted by primates are mostly those that make and store honey, and this high-value prey-item deserves special treatment (see below).

Most wasps are left alone by primates, given their powerful stings and willingness to use repeatedly this chemical defense. However, one of the most frequently ingested hymenopterans is the tiny and humble fig wasp, eaten inadvertently when frugivorous primates consume figs (Redford et al., 1984). Similarly, gall wasps sequester larvae individually on leaves, where they are plucked by primates as if they were plant parts. Interestingly, some of the fiercest wasps, hornets, are exploited by humans for their

tasty larvae; this apparently is enabled by appropriately complex technology, rather than domestication (Nonaka, 2009).

Bee taxa targeted by primates are mostly those that make (by mixing nectar and saliva) and store honey, and this high-value resource deserves special consideration. Honey-producing bees fall into two general types: stinging (*Apis*) and stingless (Melapoini). The latter are small, even tiny, in body size, but in some taxa their honey-stores are large. If the primate predator can solve the problem of access to these stores, the reward is otherwise cost-free (Brewer and McGrew, 1990). Stinging bees present a high-risk, high-payoff prey: the benefits are not only energy-rich honey, but also fat and protein-rich brood-combs, and even adults caught up in the sticky mess. But bee venom is potent, and raiding chimpanzees swell up from being stung, just like humans. Honeybee hives are usually difficult to access, being either inaccessibly elevated or impregnably encased in cavities, such as rock crevices or hollow trees. Only the large-bodied (thus able to metabolize venom?) and large-brained (thus able to exercise self-control in the face of pain?) apes persist in seeking the honey of stinging bees. Such is the irresistibility of honey that the only experimental study of primate insectivory done in nature relied upon honey as a reward to entice wild chimpanzees to take part (Gruber et al., 2009).

Compared with the other orders, termites are fewer in species and more specialized in lifestyle. However, they offer two major advantages as prey: sedentariness and huge collective biomasses (the biggest of any insects) (Wilson, 1971). They are neither winged (except as reproductives) nor venomous, but their colonial homes are impressive fortresses, at least in the large-bodied mound-builders, such as *Macrotermes*. These mounds may persist for decades, offering seasonally predictable sources of food. Apart from primates, only highly specialized fossorial predators such as aardvark and pangolin have solved the puzzle of these 'castles of clay' (McNab, 1984). To harvest termites, primates usually depend on technology, such as the famous 'termite fishing' with probes of vegetation, first described by Goodall (1963) in her pioneering study at Gombe, Tanzania. Apart from great apes, only blonde capuchin monkeys use probes to acquire termites (Souto et al., 2011). This constraint does not apply to the winged reproductives (alates), which are periodically released *en masse*; they have no defensive armaments and are flying fat stores (as much energy is needed for dispersal and initial reproductive effort). Even creatures not normally insectivorous, e.g., ungulates, gorge on termite alates when available.

No primate seems to rely on butterflies or moths, that is, adult lepidopterans, but when their larvae are social in large numbers, they are a major resource. 'Armies' of massed, slow-moving caterpillars are easily plucked from the substrate, but their availability is short-lived, usually only for days. Many primate species, from baboons to bonobos, drop all else to feast on caterpillars. However, not all caterpillars are such easy prey, as many species sequester plant-produced toxins. Many of these distasteful forms are distinguished by warning coloration or conspicuous stinging hairs or venomous spines.

Similarly, large-bodied primates capitalize on sporadic aggregations of migratory locusts or crickets, as do many other organisms (However, for neither of these short-lived bonanzas are there any quantitative data on predation by primates, surprisingly.) For small-bodied primates (with body-weights of circa 1 kg) such as callitrichid monkeys, a large-sized grasshopper may be a meal in itself, big enough even to be shared with other family members. Thus, choice of insect prey among primates that vary in body mass by orders of magnitude (from 200-g pygmy marmoset to 200,000-g gorilla) is also a scaling issue.

Honey is not the only insect product used by primates. Mouse lemurs avidly consume the residual secretions of homopteran

immatures (Corbin and Schmid, 1995). African great apes regularly ingest the concreted mix of saliva and clay in termite mounds, perhaps to buffer the toxic effects of plant secondary compounds, such as tannins. Finally, some primates, especially both genera of capuchin monkeys (*Cebus*, *Sapajus*) anoint their body surfaces with a wide variety of crushed arthropods, mostly insects, but also millipedes and worms. This seemingly bizarre self-directed behavior may be a form of self-medication (Alfaro et al., 2011). Verderane et al. (2007) hypothesized that, by anointing themselves with formic acid from carpenter ants, capuchins gain protection from ectoparasites. For *H. sapiens* (see below), some Indian tribes crush black ants (*Bothroponea rufipes*) into a paste that is applied to the skin to treat scabies, wounds and boils (Chakravorty et al., 2011).

Finally, a sobering point: There seem to be almost no comparative studies of sympatric human and non-human primates competing for invertebrate resources. (For a rare and instructive example, see Kajobe and Roubik, 2006.)

Human entomophagy

McGrew (2001, Table 8.4) cited 19 published sources³ of insects being eaten by traditional human societies in Africa, the Americas, and Australasia. These comprised foragers and horticulturalists inhabiting ecotypes from desert to rainforest. Some of these studies were focussed ethnographies of the subsistence of particular ethnic groups, while others were regional surveys. Data were extracted on the 'Big Five' orders listed above, all of which featured prominently, as well as on other taxa of insects and other invertebrates. Some findings were brief and descriptive, but a few were substantial and quantitative. My trawling of the vast ethnographic literature then was opportunistic and piecemeal, as I found no recent, comprehensive review.

Conveniently, 10 years later, Crittenden (2011) published a review article that included ethnographic findings on a particular aspect of entomophagy, that is, honey-eating. Surprisingly, of the sources used by her that were published before 2000 (and so *could* have been included in my chapter), only three were common to both reference lists. She listed an additional 16 references published before 2000 that I had missed, and that was just for honey; and of course she added newer publications, too.

Examples of human acquisition, processing, and consumption of insects can be found in McGrew (2001) and Crittenden (2011), but a few generalizations are worth reiterating, as they have stood the test of time. The Big Five orders remain predominant, and certain types crop up repeatedly: beetle larvae, social caterpillars, termite alates, honey, etc. For quantitative and systematic studies of entomophagy in traditional societies, see Schiefenhoefel and Blum (2007) for the Eipo of New Guinea, Hawkes et al. (1982) for the Ache of Paraguay, and Kajobe and Roubik (2006) for the Batwa of Uganda.

The key difference between human and non-human primate predation on insects is advanced technology (Sutton, 1995). This can best be appreciated with reference to Oswalt's (1976) taxonomy of subsistence types, such as instruments, facilities, etc. No non-human primate uses or makes natural containers for the collection, transport, preparation, or storage of assembled particulate food items, such as individual insects. Only human primates use fire in entomophagy, to control, stupefy, process, or cook insect prey. Another key difference is domestication, for example, artificial

³ Here I refer only to traditional human societies and ignore industrialized ones. In the latter, insect production may amount to agro-business. For an early, impressive example, see Kok (1983).

selection is now underway for cultivation of honey from stingless bees (Youngsteadt, 2012), whereas *Apis* honeybees have been domesticated for millennia (Crane, 1983).

Clearly, an updated, comprehensive, systematic, and (when possible) quantitative synthesis of human entomophagy is needed. The last such review was more than 15 years ago (DeFoliart, 1999).

Insectivory's payoffs

In the previous paper (McGrew, 2001, Table 8.3), I sought to calculate the basic nutritional payoff to a chimpanzee fishing for *Macrotermes* termites. This entailed cobbling together six elements from three species of *Macrotermes* as published in five sources. The result was crude but unprecedented, suggesting that such a meal yielded about 500 calories of energy, 30 g of fat, and 50 g of protein. However, given that the duration of termite fishing sessions ranged from 5 to 200 minutes and the average number (5.65) of major soldiers obtained per minute per individual chimpanzee ranged from about 2.5 to 11.2, the payoffs could vary hugely!

Other sources that give one or more of the six elements involved in the calculation tend to agree with these results. For example, Phelps et al. (1975) found *Macrotermes falciger* to be rich in protein and fat; protein constituted 42% and fat 44% of the wingless dry mass of alates. Bogart and Pruetz (2011) found for 10 adult male chimpanzees at Fongoli that their bouts of termite fishing averaged 27.2 minutes in duration ($n = 145$, range = 15.6–42.9 minutes), which compares favorably with my average of 26.2 minutes ($n = 495$) for Gombe. However, O'Malley and Power (2012) discuss the pitfalls of incomplete, piecemeal approaches to nutritional analysis.

Furthermore, few studies of payoffs combine nutritional data with primate (human or non-human) feeding data (for the most comprehensive such study, see O'Malley and Power, 2012). Many references on basic nutritional composition of insects are available, although fewer of them give details of micronutrients or they concentrate on well-known species used by humans (e.g., Bukkens, 1997; Verkerk et al., 2007). Finally, few studies of insectivory in primates compare the nutritional composition of what is eaten as a subset of what insect prey are available (but see Deblauwe and Janssens, 2008; O'Malley and Power, 2012, 2014). Clearly, such studies need to be done.

At the other extreme, the ultimate payoff for any behavioral pattern is in achieved lifetime reproductive success (ALRS). Mackworth-Young and McGrew (in revision) compared the frequency of fishing for *Macrotermes* termites by 11 female chimpanzees at Gombe with the same individuals' ALRS. The termite fishing data were collected in the 1970s, when the females were early in their reproductive careers, while the data on ALRS came from 2011, after all but one had died. ALRS was measured by five variables: age of first giving birth, offspring survivorship (infancy), offspring survivorship (juvility), inter-birth interval, and age at death. All five yielded positive correlations, three statistically significant. So far as we know, this is the first demonstration of a fitness advantage linked to insectivory in any primate (cf. similar analyses done on meat-eating in chimpanzees, McGrew, 1992).

Technological insectivory

In McGrew (2001), only great apes were described as technological insectivores, and almost all of the examples were of chimpanzees using only the simplest forms of extractive foraging (e.g., McGrew and Collins, 1985). Gorillas and bonobos were characterized as feed-as-you-grab foragers, with the most complex processing being the gorillas' breaking off of pieces of termite mound and picking out the termites contained in these earthen fragments.

In the ensuing decade, no one has yet reported either of these species habitually using instrumental technology.

For orangutans, data have emerged from field sites, especially Suaq Balimbing in Sumatra (e.g., Fox et al., 2004). However, the technical repertoire of orangutans, whether for insectivory or otherwise, remains constrained by their overwhelmingly arboreal lifestyle (Recall that most tool use by primates occurs on the ground, where much of their daily activity occurs, Meulman et al., 2012).

Chimpanzee technological foraging has seen notable new discoveries, many involving more complex (and therefore cognitively challenging) techniques revealed by ongoing field studies (McGrew, 2010a). The typical chimpanzee population's *tool kit* (= repertoire of tools used habitually by a group) numbers about 20 in total, of which many are used in insectivory. Tool kits do not vary greatly across ecotypes but do vary across regions of Africa (McGrew, 2010b, 2013). Chimpanzees use *tool sets* (= two or more tools used in an obligate sequence to achieve a single goal) to obtain ants, termites, and honey (Suzuki et al., 1995; Deblauwe et al., 2006; Sanz and Morgan, 2009; Sanz et al., 2009b). For example, a Gabonese population uses a tool set of five elements—pounder, perforator, enlarger, collector, swab—to obtain *Apis* honey (Boesch et al., 2009). Chimpanzees use *composite tools* (= two or more tools used simultaneously and complementarily to achieve a goal), for example, hammer and anvil stones to crack nuts, but few have been described for insectivory. An example is when chimpanzees bend over a sapling to make a perch, from which to dip more securely for army ants on the ground below (McGrew, 1974). Similarly, chimpanzees use *compound tools* (= two or more components combined as a single working unit), for example, a leaf-sponge, but none has been described for insectivory.

Variation in technological insectivory across chimpanzee populations is now well-established (Whiten et al., 2001; Sanz et al., 2014). Less-well understood is what causes that variation, which in principle could be due to genetic, environmental, geographic or cultural influences (cf. Langergraber et al., 2011 versus Lycett et al., 2011; Kamilar and Marshack, 2012). Only empirical, comprehensive, comparative analyses will disentangle such multiple causal variables (e.g., Schöning et al., 2008). Variation across groups within the same population may result from differing environmental affordances (e.g., Uehara, 1982) or differing cultural knowledge as a reflection of stochastic transmission processes (O'Malley et al., 2012). Variation across individuals within a population is likely to result from differing experiences in ontogeny, especially exposure to the mother as a model (termite fishing, Lonsdorf, 2006; ant dipping, Humle et al., 2009; see also Jaeggi et al., 2010, for orangutans).

Although technological extraction of insects for food by non-human primates was first reported 50 years ago, with Goodall's (1963) description of termite fishing, new findings continue to emerge (Sanz et al., 2009a; Sanz and Morgan, 2011). Other notable discoveries are still at the early stages of investigation, such as bearded capuchins using naturally sharp stones as 'trowels' to dig up subterranean spiders (Mannu and Ottoni, 2009).

Paleo-insectivory

The earliest and best-known empirical claims for insectivory in prehistory are for bone tools recovered at various Lower Palaeolithic sites in South Africa. Backwell and d'Errico (e.g., 2001, 2008; Lesnik, 2014) analysed microwear on tools from Swartkrans, Sterkfontein, and Drimolen and concluded that *Paranthropus robustus* used them to dig into termite mounds to obtain the insects for food. Experimental studies of various bone tool-using activities seemed to confirm this assertion (d'Errico and Backwell, 2009). The

authors refer to chimpanzee termitivory, but no chimpanzee population has been seen to dig up termites; the closest thing to excavation is their use of stout sticks to puncture nests, followed by the insertion of probes (Sanz and Morgan, 2011). An alternative interpretation for the microwear patterns found in South Africa is that the bone tools were used to obtain termite mound earth for geophagy or to dig up other items, such as tubers. Furthermore, the authors made no reference to digging for termites among modern human foragers, although African villagers routinely dig into termite mounds for raw material for brick-making (personal observation).

An alternative approach is to model paleo-insectivory based on the known foraging of living apes and human hunter-gatherers, as Wrangham (2012) has done for honey-eating. He notes that honey is a high-priority food (deemed preferable even to meat in some cases) for all societies, human and otherwise, who have access to *Apis* honey (Kraft et al., 2014). But what is the evidence that this craving extends into the past? Ingeniously, he argues that the mutualism between honey-guide (*Indicator indicator*) and human is a long-standing, co-evolved relationship. He notes that effective *Apis* honey extraction depends on refined technology, that is, at least smoke, axe, and container. Archaeological evidence for management of fire and production of appropriate lithics is unknown before *Homo erectus*, but is present from then on.

Using similar lines of argument, McGrew (2001) outlined six general hypotheses about early hominin insectivory:

1. It made a notable contribution to diet.
2. It was seasonal, providing regular top-ups of key nutrients.
3. It was less risky than hunting or scavenging.
4. It entailed intermediate technology, such as the container.
5. It yielded collected products that were transportable and exchangeable.
6. It encouraged sexual division of labor, that is, female gathering and male hunting (except for honey).

All of these hypotheses are fulfilled in living foraging peoples, for example, the Hadza hunter-gatherers of the Tanzanian savanna (Berbesque and Marlowe, 2009; Marlowe, 2010; Marlowe et al., 2014). The first three apply to chimpanzees, but not the last three: apes use technology to get honey, but all of it is simple (as stated in Oswalt, 1976). Captive chimpanzees readily use containers but their counterparts in nature do not. Wild chimpanzees carry food away from bees' nests, after a smash-and-grab raid, and honey is shared with others, but both of these phenomena are trivial by comparison with humans. Apes show sex differences in diet, some of which mirror those of humans, such as male predominance in hunting and female predominance in insectivory, but they show no sexual division of labor.

Hypothetical scenarios about the evolution of human diet, and particularly, the consumption of invertebrates, may be provocative and even entertaining, but are they testable? That is, can they be translated into empirically falsifiable propositions ('postdictions')? McGrew (2001) nominated eight possibilities, and here I consider if these have led to progress over the last decade. (Readers seeking background references should consult the original paper, as these mostly will not be repeated here. See also Sutton, 1995, for a comprehensive and masterly early review.)

Remains

Remnants of invertebrates, however fragmentary, are in principle recoverable from sediments by normal archaeological methods. However, most of these come from historical, not pre-historic, sites (e.g., Carrott and Kenward, 2001). In practice, most

soft tissues decompose quickly and are lost, but hard tissues with sufficient mineral content may persist, such as mollusc shells: Cortes-Sanchez et al. (2011) used shell middens on the Spanish coast to push back the consumption of shellfish to before the arrival of modern humans. With dates of about 150,000 years BP (before present), they established Neanderthal invertebrativory equivalent to that of early *H. sapiens* at Pinnacle Point, in southernmost Africa (Jerardino and Marean, 2010).

Lithics

Tools made of organic materials, mostly vegetation, are unlikely to have been preserved in the deep evolutionary past, that is, the Plio-Pleistocene or earlier. Thus, most of the likely technology for insectivory will be 'archaeologically invisible'. As broached in McGrew (2001), the best candidates for recovery are likely to be wear patterns, both macro and micro, on stones used to obtain or to process invertebrate prey. Just as nut-cracking leaves such signs on the stone hammers and anvils of living primates (Haslam et al., 2009) and apparently of their Pleistocene hominin counterparts (Goren-Inbar et al., 2002), so might similar percussion on the calcareous shells of molluscs (e.g., Cortes-Sanchez et al., 2011). Based on contemporary human foragers, another candidate for lithic 'signatures' for entomophagy might be the microscopic striations left on grinder and grindstone by the chitinous exoskeletons of orthopterans that are ground into meal (Sutton, 1990). Whether such microwear is reliably distinguishable from other polishes apparently remains to be seen.

Residues

Phytoliths from consumed plants have been recovered from the calculus on fossilized teeth of *Gigantopithecus blacki*, an extinct Asian ape (Ciochon et al., 1990). These date to at least 300,000 years BP. More recent research on dental calculus has yielded a variety of plant materials and other compounds from Neanderthals at 30–24,000 years BP (Hardy et al., 2012). Some organic materials from animals may persist similarly: Hardy and Moncel (2011) reported organic residues of fish, birds, and mammals on the stone tools of Neanderthals at 125–250,000 years BP. If feathers, scales, and hair survive at such time-scales, then why not chitinous exoskeleton? For more recent specimens, Flood (1980) used ultraviolet light to detect the proteins of moths that were processed on stone milling tools by Australian aborigines.

DNA

In living primates, recently-developed metagenomic approaches, such as sequencing by basic local alignment search tool (BLAST) comparison may reveal taxa eaten in insectivory. Pickett et al. (2012) assigned taxonomic identities to arthropods eaten by six sympatric species of New World monkeys. It remains to be seen whether or not this can be done with older DNA from coprolites or residues.

Coprolites

As outlined in McGrew (2001), coprolites, either subfossil or fossil, may reveal insectivory, just as does fresh dung (McGrew et al., 2009), when indigestible chitin passes through the gut. Holocene examples from human dung are well-known (e.g., Heizer and Napton, 1969), but what about older coprolites? Backwell et al. (2009) recovered apparent human hair from a fossil hyena coprolite in South Africa, dated to about 200,000 years BP. (All kinds of keratinized tissues, that is, horn, nail, feather, etc., are in principle

recoverable, providing a vertebrate basis for comparison with invertebrate chitin. Similar arguments apply to gut contents.) Andrews and Fernandez-Jalvo (1998) even have suggested that DNA may be retrievable from the remarkably intact bone fragments found in the coprolites of theropod dinosaurs.

Dental microwear

Any chewed foodstuff that is dense and hard enough to leave abrasions on enamel is in principle identifiable, at least to general category, such as siliceous vegetation, hard-shelled fruit, etc. (Strait, 2014). Most research so far has concentrated on plant foods (Teaford and Walker, 1984; Teaford, 1988). As yet, no one seems to have differentiated insectivorous versus non-insectivorous primate species, but Taylor and Hannam (1987) did so for African mongooses.

Stable isotopes

Studies of stable isotopes as indicators of the diets of living primates continue to burgeon (see recent reviews in Crowley, 2012; Sandberg et al., 2012). More and more source materials have proven to be useful, and some of these (see above) are recoverable in the fossil and archaeological record: tooth enamel, bioapatite, feces, hair, etc. The obvious element to focus upon for faunivory is nitrogen, for example, Schoeninger et al. (1998) showed that insectivory could be distinguished from folivory in prosimians. However, the sternest test, as yet unaccomplished, for this hypothesis, is to differentiate consumption of vertebrates from invertebrates. Perhaps the closest result to this is the detection from N isotopic data of wild bonobos (*P. paniscus*) gorging on seasonal 'bonanzas' of social caterpillars (Oelze et al., 2012).

Carbon isotope data may be useful in revealing hominin diet, as they allow the differentiation of herbivory of C4 (mostly grasses) versus C3 (other plants). However, given multi-level food chains, hominid consumption of animals that consume plants complicates matters. Sponheimer et al. (2005) showed that living termites in South Africa are mixed C3/C4 feeders, so their possible consumption cannot account for the C4-biased signature of South African australopiths.

Not pursued so far for seeking insectivory are radioisotopic studies of strontium (but see Copeland et al., 2011 and Balter et al., 2012, for its use in human evolutionary studies). If, for example, mound-building termites prefer certain soil types, especially if these are uncommon, and if these produce a notable isotopic signature in the tissues of consumers, then insectivory may be inferable (Wood and Schroer, 2012).

Osteology

McGrew (2001) cited Skinner's (1991) provocative suggestion that pathological apposition of bone on KNM-ER 1808 (a female *H. erectus* specimen) might indicate over-consumption of bee brood, leading to hypervitaminosis A, which notably disfigures bone. Later, Skinner et al. (1995) effectively falsified that hypothesis, which seems to have been laid to rest (Wrangham, 2012). On the contrary, bee brood may be useful sources of other vitamins and minerals (Finke, 2005).

Depiction

The most direct and graphic evidence for prehistoric entomophagy are representational paintings on Upper Paleolithic cave walls, such as Altamira in Spain, dated to about 14,000 years BP (Pager, 1976). These illustrations (whether artistic or not)

remarkably resemble paintings in rock shelters by modern humans in Saharan and southern Africa. Pager (1973) claimed that they showed nests, combs, ladders, and even honey-gathering, but Mguni (2006) interpreted some of the images as termites and their mounds. Invertebratvory depictions seem ripe for further re-examination.

Conclusions

Over the last decade or so, continuing research has shown the importance of invertebrates, and especially insects, in the diets of living human and non-human primates. Similarly, their extraction and processing, especially with regard to elementary technology, has proven to be more complex and variable than before imagined. Accordingly, these findings have prompted researchers of human evolution to seek for the paleo-counterparts of these extant phenomena, in an effort to understand the origins and evolution of human diet. Some efforts have proven to be more (isotopes, residues) or less (lithic and dental microwear) productive than others, but enough has emerged to make the pursuit worthwhile. Efforts to elucidate the origins of human diet have concentrated mostly on plants (for an exemplary recent example, see Wood and Schroer, 2012) and vertebrates. Now it should be the turn of the invertebrates.

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