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The energetic and nutritional yields from insectivory for Kasekela chimpanzees

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ABSTRACT

Insectivory is hypothesized to be an important source of macronutrients, minerals, and vitamins for chimpanzees (*Pan troglodytes*), yet nutritional data based on actual intake are lacking. Drawing on observations from 2008 to 2010 and recently published nutritional assays, we determined the energy, macronutrient and mineral yields for termite-fishing (*Macrotermes*), ant-dipping (*Dorylus*), and ant-fishing (*Camponotus*) by the Kasekela chimpanzees of Gombe National Park, Tanzania. We also estimated the yields from consumption of weaver ants (*Oecophylla*) and termite alates (*Macrotermes* and *Pseudacanthotermes*). On days when chimpanzees were observed to prey on insects, the time spent in insectivorous behavior ranged from <1 min to over 4 h. After excluding partial bouts and those of <1 min duration, ant-dipping bouts were of significantly shorter duration than the other two forms of tool-assisted insectivory but provided the highest mass intake rate. Termite-fishing bouts were of significantly longer duration than ant-dipping and had a lower mass intake rate, but provided higher mean and maximum mass yields. Ant-fishing bouts were comparable to termite-fishing bouts in duration but had significantly lower mass intake rates. Mean and maximum all-day yields from termite-fishing and ant-dipping contributed to or met estimated recommended intake (ERI) values for a broad array of minerals. The mean and maximum all-day yields of other insects consistently contributed to the ERI only for manganese. All forms of insectivory provided small but probably non-trivial amounts of fat and protein. We conclude that different forms of insectivory have the potential to address different nutritional needs for Kasekela chimpanzees. Other than honeybees, insects have received little attention as potential foods for hominins. Our results suggest that ants and (on a seasonal basis) termites would have been viable sources of fat, high-quality protein and minerals for extinct hominins employing *Pan*-like subsistence technology in East African woodlands.

> *To be filled, wait for the termite.*
> -Malawian Proverb (Morris, 2004)

Introduction

Chimpanzees (*Pan troglodytes*) are social, omnivorous, tool-using hominoids found in a wide range of habitats across central Africa (Pruetz, 2006) and that share a close phylogenetic relationship with modern humans (Chen and Li, 2001). Along with other living mammals, chimpanzees represent useful referential models for inferences about the diet and behavior of extinct hominins (McGrew, 1992; Sept, 1992; Moore, 1996; Stanford, 1996, 2006; Pickering and Domínguez-Rodrigo, 2010; Wood and Schroer, 2012).

All species of great apes are reported to consume insects, most commonly the eusocial insects of the Orders Hymenoptera and Isoptera[1] (see reviews in McGrew, 1992, 2001). Chimpanzees at multiple sites across Africa feed on mound-building termites (*Macrotermes* spp. soldiers and alates, *Pseudacanthotermes* spp. alates), driver ants or siafu (*Dorylus* spp.), weaver ants (*Oecophylla longinoda*), carpenter ants (*Camponotus* spp.), honeybees (*Apis mellifera*) and stingless bees (Meliponini) (McGrew, 1992). Insectivory composes a greater proportion of chimpanzee diets than carnivory at many long-term research sites (Pruetz, 2006). With the

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[1] Inward et al. (2007) advocate nesting Isoptera within the Order Blattoidea (cockroaches).

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apparent exception of *Dorylus*, all of the aforementioned insect genera (and often the exact species within genera) are also consumed by humans. Termite alates (usually of the genus *Macrotermes*) are highly valued foods across sub-Saharan Africa (Fasoranti and Ajiboye, 1993; Bukkens, 1997, 2005; Banjo et al., 2006; Malaisse, 2006; also see Bodenheimer, 1951 for older ethnographic accounts). Termite alates and termite nests are prominent in San mythology and rock art, some of which date to between 1500 and 12,500 years ago, and are culturally associated with health and potency (Mguni, 2006). Termite soldiers are consumed in some cultures in addition to alates (Bodenheimer, 1951). Green weaver ants (*Oecophylla smaragdina*) are raised for commercial sale in Southeast Asia (Offenberg and Witwatwitaya, 2010). *Camponotus* ants were consumed in some Native American cultures and by Caucasian lumberjacks (Bodenheimer, 1951). Several species of honeypot ant (including *Camponotus inflatus*) are consumed avidly by Australians (Meyer-Rochow and Changkija, 1997). Finally, honeycomb and honey (usually produced by *Apis* spp.) are consumed by human cultures around the world (Crane, 1999; Marlowe, 2014).

Why eat insects? Like vertebrate flesh (or 'meat'), insects represent a high-value food item for primates in terms of energy, fat, high-quality protein and some essential vitamins and minerals (Lieberman, 1987; Ladrón de Guevara et al., 1995; Milton, 2003a; Bukkens, 2005). However, despite widespread insect consumption in living hominoids, there is relatively little published research on the significance of insectivory for extinct hominins (for reviews see Sutton, 1990; McGrew, 2001, 2014; Lesnik, 2014). Given the small size of insects on an individual basis (often far less than 1 g), it may seem intuitively unlikely that insects could make a significant contribution to the diet of a 32–60 kg animal like a chimpanzee (or by extension, an australopithecine or paranthropine). For insectivory to be worthwhile, a would-be predator should seek to maximize yields (energetic, nutritional, or both) for the time invested. Consistent with this prediction, humans and apes favor insects that are large-bodied, highly concentrated in time and space, or both (McGrew, 2001). Favored prey include large, sedentary beetle grubs or larvae (Coleoptera), social insects (Hymenoptera and Isoptera), or other insects available in vast numbers at once such as caterpillars (Lepidoptera) or grasshoppers and locusts (Orthoptera). Humans, chimpanzees and orangutans also employ forms of elementary technology to consume insects (Bodenheimer, 1951; McGrew, 1992; Fox et al., 1999, 2004). Technology may allow access to insect prey that would otherwise be unavailable as well as increasing foraging returns.

Data on the nutritional yields for insectivory (either on a per-mass or per-unit basis) by chimpanzees are limited. Hladik (1977) suggested that insects represent a potentially valuable source of fats, proteins, vitamins and minerals for released chimpanzees in Gabon, and provided estimates of nutritional intake for a variety of plant food as well as insects. McGrew (2001; Table 8.3) estimated the foraging yields for termite-fishing by Kasekela chimpanzees, drawing on previously published data (McGrew and Marchant, 1999). However, McGrew's calculations, based on the best data available at the time, overestimated energy content by using dry weight values for energy, fat, and protein for *Macrotermes* alates (not soldiers) that were fried in palm oil, and by using individual weights of *Macrotermes carbonarius* major soldiers (reported as 0.5 g each; O'Malley and Power, 2012 later reported individual weights of *Macrotermes subhyalinus* major soldiers at 0.116 g). Deblauwe and Janssens (2008) provided comprehensive assays of social insect prey consumed by sympatric chimpanzees and gorillas (as well as some other available species) of the Dja Biosphere Reserve in Cameroon. Using insect remains identified from feces as an indirect measure of consumption (which they acknowledge was likely an underestimate), they concluded that only the intake of manganese (Mn) from insects reached the estimated recommended intake (ERI) for chimpanzees, while only iron (Fe) from insects reached the ERI for gorillas. Nishida and colleagues (Nishida, 1973; Nishida and Hiraiwa, 1982) dismissed the estimated protein yields from ant-fishing by Mahale chimpanzees as negligible, though did not rule out that consumption might yield important micronutrients. Using Deblauwe and Janssens' (2008) nutritional data, Nishie (2011) confirmed that the average macro- and micronutritional yields from ant-fishing for *Camponotus* by M-group Mahale chimpanzees were negligible, and concurred with Nishida and Hiraiwa that this behavior may be a leisure rather than subsistence activity for this community.

Though increased meat consumption is often hypothesized to be a critical dietary shift in human evolution (e.g., Bunn, 2007), there is a surprising paucity of data on macro- and micronutritional yields for meat consumed by chimpanzees (though mass intake estimates were provided by Stanford, 1996). Tennie et al. (2009) suggested that for chimpanzees, the value of vertebrate meat is not as a source of energy as it is for many carnivores, but instead is as a package of fats, vitamins, and minerals that are otherwise limited in the diet. This 'meat scrap hypothesis' may explain why chimpanzees choose to incur the substantial risks of hunting even though the estimated energetic costs per hunter are lower than the estimated gains. McGrew (2010) has questioned this explanation on the grounds that insects may provide micronutrients in a more easily acquired and predictable form. We believe it is appropriate to view hunting and insectivory as different, complementary strategies for acquiring animal-sourced nutrients, each with advantages and disadvantages (for further discussion, see Tennie et al., 2014). Unfortunately a clearer understanding of these strategies is limited by the lack of comprehensive nutritional data on the vertebrates and invertebrates consumed by chimpanzees, and limited data on intake rates in the latter (but see Hladik, 1977; Deblauwe and Janssens, 2008; O'Malley and Power, 2012).

The lack of quantitative nutritional yields for faunivory by chimpanzees is a critical issue for any effort to incorporate insectivory into reconstructions of hominin diets. There is no *a priori* reason to assume that late Miocene or Pliocene hominins were incapable of using probes, wands and pestles similar to those employed by modern chimpanzees (McGrew, 1992; Sanz and Morgan, 2007) or orangutans (Fox et al., 1999) to acquire insects and honey. Such activities are unlikely to be preserved in the archaeological record (but see Backwell and d'Errico, 2001, 2008). Similarly, no distinctive isotope signature for insectivory has been identified in hominin bones or teeth (Lee-Thorp et al., 2003; Peters and Vogel, 2005; Sponheimer et al., 2005, 2006) nor has a distinctive insectivorous pattern been identified in hominin dental microwear (Teaford, 2007; but see Strait, 2014). While new lines of evidence are being identified and developed (see McGrew, 2001, 2014), studying the behavior of living apes remains a viable approach to understanding the possible contribution of insects to the diets of early human ancestors.

In a recent manuscript, we provided energetic and macronutrient values for the major insect prey consumed by Kasekela chimpanzees, as well as of some insects that are present in Kasekela and consumed by chimpanzees elsewhere but ignored by this community (O'Malley and Power, 2012). Our conclusions indicated that of the palatable insect prey available in their community range, Kasekela chimpanzees preferentially consume those insects that are high in metabolizeable energy, protein and fat on a per-foraging-unit (insect, dip, or nest) basis. We also found that on a gram-for-gram basis, the insect prey favored by Kasekela chimpanzees have a comparable range of energy, fat and protein values relative to published values for the meat of wild African animals