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The importance of leaf- and litter-feeding invertebrates as sources of animal protein for the Amazonian Amerindians

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At least 32 Amerindian groups in the Amazon basin use terrestrial invertebrates as food. Leaf- and litter-consuming invertebrates provide the more important, underestimated food sources for many Amerindian groups. Further, litter-consuming earthworms are also an important food resource for the Ye'Kuana (also known as Makiritare) in the Alto Orinoco (Amazonas, Venezuela). By selecting these small invertebrates the Amerindians are choosing their animal food from those food webs in the rainforest which have the highest energy flow and which constitute the greatest renewable stock of readily available nutrients. Here we show that the consumption of leaf- and litter-feeding invertebrates as a means of recovering protein, fat and vitamins by the forest-living peoples offers a new perspective for the development of sustainable animal food production within the paradigm of biodiversity maintenance.

Keywords: edible insects; edible earthworms; Amerindian food; animal protein; food web; forest food

1. INTRODUCTION

The role of insects and other invertebrates in human nutrition has generally been underestimated by Western observers (Ruddle 1973; Coimbra 1984; De Foliart 1999). However, work carried out by a number of investigators (Ruddle 1973; Coimbra 1984; Posey 1978; Dufour 1987; Zent 1992; Onore 1997; Cerda *et al.* 2000), even if not exhaustive, provides an idea of what is collected and eaten in the Amazon basin and rim areas. We found from the literature, interviews and direct fieldwork that at least 32 ethnic groups in the Amazon consume consistent amounts of small terrestrial invertebrates. The number of small invertebrates used as food by some 'better'-studied Amerindians is shown in table 1. The numbers are conservative and include only those species observed being consumed or described as edible; the actual number of edible species could be in the hundreds. The array of specializations in these invertebrates is impressive and includes pollinators, frugivores, lignivores, folivores, scavengers and even a few aquatic forms. However, research done with Tukanoans by Dufour (1987), as well as the observations of Zent (1992) and M. G. Paoletti, U. Cerda and F. Torres (unpublished data) on different Alto Orinoco groups, has made it clear that leaf- and litter-eating invertebrates are the primary food sources for the Amerindians (table 2).

2. THE AMERINDIAN FOCUS ON LEAF AND LITTER CONSUMERS

In a rainforest, the annual production of leaves and litter (10 300 kg ha^{-1} and 5400 kg ha^{-1}, respectively) surpasses that of wood and fruits, and provides a readily renewable source of energy for the invertebrates collected and consumed by Amerindians: (i) leaf-cutter fungi-farming ants of the genus *Atta*; (ii) caterpillars having a strict link with leaves of the canopy; (iii) litter-cutter termites of the genus *Syntermes*; and (iv) some earthworms consuming litter on the surface soil (table 3 and figure 1).

(a) *Leaf-cutter ants,* Atta

Most of the ants consumed by the Amerindians are the leaf-cutter fungus-growing ants of the genus *Atta*, of which there are 15 species in the Neotropics (Holdobler & Wilson 1990). These are the largest ants in the Neotropics. Considering only the three species (*Atta cephalotes*, *Atta sexdens*, *Atta laevigata*) consumed by the Tukanoans, we would estimate leaf consumption to be *ca.* 370 dry kg ha^{-1}, based on one medium-sized *Atta* colony per hectare of forest, about 60 kg ha^{-1} of *Atta* fresh weight. We estimate that a Tukanoan village (about 100 people) consumes up to 150 kg year^{-1} of this important resource. This would represent a gathering pressure of 1.85 g ha^{-1}, a negligible portion (0.003%) of the estimated total biomass (table 4 and figure 1*b*).

(b) *Caterpillars*

Little is known about most of the species of edible caterpillars collected by the Amerindians, except that most of the species selected for consumption are found on food plants. For example, the Tukanoan, Yanomamo, Piaroa, Ye'Kuana and Guajibo consume the cassava hornworm (*Erinnyis ello*), a key cassava (*Manihot esculenta*) pest (Bellotti *et al.* 1999), the staple food for most Amerindians; Tukanoans consume a species of Noctuidae hosted by *Erisma japura* spruce, a wild-growing tree which produces

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Table 1. *Number of edible insects (and other invertebrates) in some Amerindian groups*

group	total[a]	bees and wasps	cater-pillars	beetles	grass-hoppers	ants	termites	earth-worms	decapods	spiders	other
Yanomamo[a]	89	43	25	5	0	4	4	0	3	5	0
Guajibo[b]	31	12	4	4	5	3	1	0	2	0	0
Piaroa[c]	28	9	5	4	0	4	2	1	2	1	0
Yukpa[d]	25	7	4	3	7	1	0	0	0	0	3
Ye'Kuana[a]	23	5	6	3	0	1	1	4	3	0	0
Tukanoan[e]	23	3	5	5	0	3	4	0	1	0	2
Curripaco[a]	11	4	3	1	0	1	0	0	2	0	0

[a] Data for the Yanomamo are based on the literature (Lizot 1993; Chagnon 1968) and especially on personal interviews of seven Yanomamo in Puerto Ayacucho and field collections in Mavaka, Boca de Padamo and Boca de Ocamo done by M.G.P., H.C. and F.T. (1997–1999). The numbers reported here, when based just on ethnonames, have been carefully documented as to morphology, behaviour and host plant as being really different species. Only a few wood-boring larvae bear ethnonames belonging to beetles such as Scarabaeidae, Ceramybycidae, Buprestidae and Passalidae; apparently they are not much important in terms of biomass to the Indians but the total number could be several hundred species. Fieldwork and interviews were made for Ye'Kuana (Toki, Guatamo and Buena Vista) and Curripaco (Cucurital) (1997–1999).
[b] We did interviews and fieldwork in Alcabala Guajibo, Sabaneta Guaiabal and Coromoto, Amazonas, Venezuela (1997–1999).
[c] The information comes from Zent (1992) and from interviews and collections on site within or near villages (especially in Caño Tigre, Babilla de Pintado and Gavilan, Amazonas, Venezuela).
[d] Ruddle (1973).
[e] Four species are added to Dufour (1987): one Homoptera Membracidae, *Umbonia* sp. living on *Inga* sp. foliage; one small termite pupa having an above-ground arboreal nest (*Labiotermes labralis*); one stingless bee Meliponinae; one Diptera Stratiomyidae larva living on manioc roots; and a freshwater shrimp *Macrobrachium* sp.

Table 2. *Annual consumption of invertebrates in the Tukanoan village of Yapu (Rio Papuri, Vaupes, Colombia) composed of about 100 people*[a]

name	mean fresh weight (g)[b]	total (kg $year^{-1}$)	per cent of total weight
Atta soldiers and queens (three species)	0.1–0.9[c]	100	29.3
Syntermes soldiers (three species)[d]	0.28	133	39.0
Caterpillars (five species)	1.46–3.06	96	28.1
Vespidae larvae and pupae (three species)	0.2–0.4	2	0.60
Melaponinae larvae and pupae (one species)	0.1	1.5	0.44
Rhynchophorus palmarum larva	8–12	6	1.7
beetle larvae boring on wood and dead wood (four species)[e]	2–8	2.5	0.73

[a] For detailed methods see Dufour (1987). Most data derive from observational, fieldwork and direct recording of all animal and vegetable food consumed in the target village. Possibly insect amounts could be higher because sometimes secretive behaviour does not permit assessment of all insects gathered and consumed directly in the forest.
[b] Mean fresh weight of individual organisms.
[c] Weight of soldiers and queens is 0.1 g and 0.9 g, respectively.
[d] Data based on Martius (1998) estimations of dry weight of *S. spinosus* multiplied by 5 to obtain the fresh weight.
[e] Scarabaeidae, Buprestidae, Cerambycidae, Passalidae.

edible seeds (Dufour & Zarucchi 1979), and a species of Notodontidae lives on *Inga* sp., a cultivated fruit tree. Estimating the foliage consumption by the caterpillars is not easy (Pimentel 1988), but a conservative figure would be 450 kg ha^{-1} $year^{-1}$ or about 4% of the standing living leaf biomass.

We estimate that the Tukanoans consume *ca.* 1.7 g ha^{-1} $year^{-1}$ of caterpillars, less than 0.01% of the total 18 kg ha^{-1} of edible caterpillars.

(c) *Litter-cutter termites*

Most of the termites eaten by Amerindians belong to the genus *Syntermes*, of which there are some 23 species in South America (Costantino 1995). These are the largest termites in the Neotropical rainforests. They forage mostly at night on the soil surface, the workers protected by soldiers, and bring litter fragments to their subterranean nests (Costantino 1995; Martius 1998). We estimated (on the basis of data collected by Martius (1998) from Manaus, Brazil) a living biomass of 70 kg ha^{-1}. *Syntermes* consumption by the Tukanoans was limited to *ca.* 2.46 g ha^{-1} $year^{-1}$, which represents about 0.001% of the standing biomass.

(d) *Earthworms*

In focusing on litter, it is important to establish if the earthworms that dominate litter consumption in most tropical forests, however poorly known in Amazonia (Nemeth & Herrera 1982; M. G. Paoletti, unpublished data), represent an important source of edible biomass. In fact, the Ye'Kuana and to some extent the Piaroa devote particular attention to this group as an important food resource.

The Ye'Kuana collect at least two different edible species. One inhabits river edge environments where litter, silt and sand accumulate. Those referred to as 'motto' (Glossoscolecidae: *Andiorrhinus motto* n. sp.; Righi & Araujo 1999) are found 15–50 cm below the surface, and generally below the water table. The estimated fresh biomass of these earthworms is 437 g m^{-2} in the areas of collection. The estimated Ye'Kuana consumption of motto,

Table 3. *Estimated production (kg dry weight ha⁻¹ year⁻¹) of leaves and litter in Amazonian rainforests and potential biomass consumption by earthworms, litter-cutter termites* (Syntermes)*, leaf-cutter ants* (Atta) *and caterpillars*

(The standing living invertebrate biomass is given in brackets.)

	mean production	litter and leaf consumption (kg ha^{-1} $year^{-1}$)			
	(kg dry weight ha^{-1})[a]	earthworms[b]	*Syntermes*[c]	caterpillars[d]	*Atta*[e]
leaves	10 300	none	none	450 (18)	500 (80)
litter	5410	2500 (437–420)	320 (70)	none	none

[a] Data from San Carlos de Rio Negro, Venezuela (Jordan 1989). Litter production data for Manaus (Luizão & Schubart 1987), and Barro Colorado Island (Leugh & Smythe 1978) are similar.
[b] Based on estimations made near Toki and Guatamo for motto (420 g m^{-2} in 5% of the Ye'Kuana territory) and near Buena Vista for kuru (437 g m^{-2} in 2% of the territory) (Anonymous 1995).
[c] Based on estimations by field observations in the Alto Rio Padamo of ten colonies per hectare, and a living biomass of 70 kg ha^{-1}. These quantities are lower than the evaluations made near Manaus (Martius 1998; Martius & Weller 1998).
[d] Based on estimations by different researchers (Pimentel 1988). The edible species may represent less than 5% of lepidopterans active in the canopy. Their biomass could be estimated as 18 kg fresh weight ha^{-1}.
[e] Three *Atta* species present in Vaupes are consumed by Amerindians. Our conservative estimate is based on one mean *Atta* colony per hectare, leaf consumption data (Wirth *et al.* 1997), and a mean colony weight (Schultz 1999).

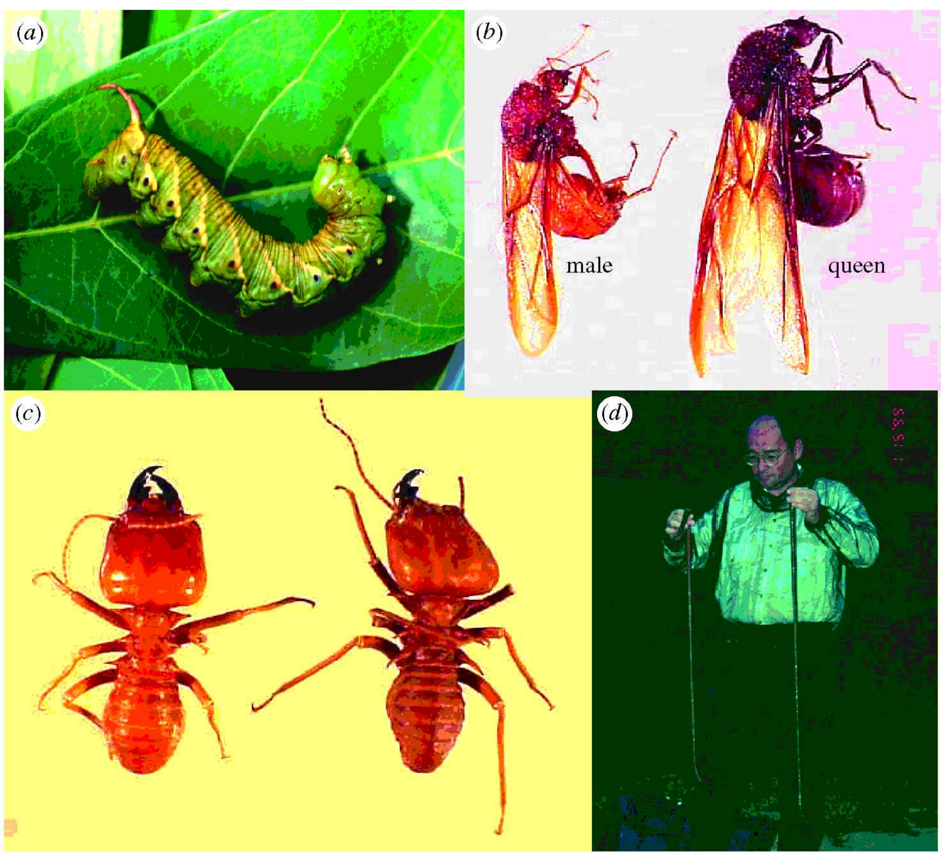

Figure 1. Key edible invertebrates in Amazonia. (*a*) Cassava hornworm (*Erinnyis ello*) an important snack for Amerindians. (*b*) Swarming alatae *Atta* ants (*A. cephalotes*). (*c*) Termite soldiers (*Syntermes* sp.). (*d*) Large edible earthworms (kuru) eaten by the Makiritare in the high Padamo River, Venezuela.

44 g ha^{-1}, is merely 0.001% of the standing biomass. Those referred to as 'kuru' (Glossoscolecidae: Gen.? sp.), are larger (up to 120 cm and 240 g fresh weight) and are reported to live only in the higher regions (250–450 m) of the Ye'Kuana territory, and are collected in the forest from deep (10–30 cm) inside the root mat, where grey soils are present. The estimated living biomass of this species is 437 g m^{-2} while human consumption is estimated to be 131 g ha^{-1} with a low impact on the standing biomass (0.002%).

The Ye'Kuana consumption of earthworms cannot be attributed to a lack of other animal protein resources because there is no shortage of fishes or game in their territory (Schlenkner 1974; Hames 1980). Rather, the Ye'Kuana appreciate these species of earthworms as gourmet foods in much the same way as some Europeans

Table 4. *Estimated consumption of leaf- and litter-eating invertebrates by Amerindians*

group and location	population density (km^{-1})[b]	consumption ($g\,ha^{-1}\,year^{-1}$)[a] leaf eating: caterpillars	leaf eating: *Atta*	litter eating: *Syntermes*	litter eating: earthworms: motto	litter eating: earthworms: kuru
Tukanoan, Vaupes, Colombia[b]	0.2	1.67	1.85	2.46	no	no
Yanomamo, Alto Orinoco, Venezuela[c]	> 0.1	1	0.5	2	no	no
Ye'Kuana, Alto Orinoco, Venezuela[d]	0.13	1	0.5	2	44.7	131

[a] The territory (in ha) on which gathering occurs is estimated here on the land pertinent to the village and that is normally visited. This amount of land represents as well the amount calculated considering a range of 0.1–0.2 people km^{-2}.
[b] Based on Dufour (1987) and unpublished data from the village of Yapu, a population of about 100 people. Villagers collected about 100 kg of *Atta* (three species), 133 kg of *Syntermes* (three species) and 90 kg of caterpillars (five species) in one year. Population density estimates were based on a regional survey.
[c] Data based on direct observations in the villages of Mavaka and Boca Ocamo in 1998 and 1999.
[d] Population density from Ye'Kuana (1995). Consumption estimates from field observations and interviews in four villages (Toki, Guatamo and Buena Vista on the Padamo River, and La Esmeralda on the Orinoco River) visited between 1996 and 1999. Based on data from Toki and Guatamo we assessed motto consumption at about 1.7 kg $person^{-1}\,year^{-1}$. Data for kuru come from Buena Vista, where we calculated consumption to be 2 kg $person^{-1}\,year^{-1}$. The earthworm data is based on only the limited part of the Ye'Kuana territory for motto (5%) and kuru (2%) in which these resources are available. Data on consumption of *Atta*, *Syntermes* and caterpillars are based on per family estimations done in Toki and Guatamo, and assumption that these invertebrate resources are evenly distributed in the entire territory.

Table 5. *Mean foraging efficiencies for some invertebrates compared with those for fishes and game*

animal	foraging efficiency ($g\,h^{-1}$)[a]	foraging success rate (%)[b]	source of data
earthworm motto	388	100	Ye'Kuana: direct measurement in villages Toki and Guatamo (May 1998 and January 1999)
earthworm kuru	446	100	Ye'Kuana: direct measurement in village of Buena Vista (January 1999)
Syntermes spp.	300??	*ca.* 100	Tukanoans (Dufour 1987; D. L. Dufour, unpublished data)
Syntermes aculeosus	200	99	Ye'Kuana: direct measurement in village of Toki (January 1999)
Atta spp.	200	99	Tukanoans (Dufour 1987; D. L. Dufour, unpublished data)
caterpillars	300	99	Tukanoans (D. L. Dufour, unpublished data)
fishes	494	73[c]	Tukanoans (D. L. Dufour, unpublished data)
fishes	927	?	various Amerindians (Beckerman 1994)[d]
game	1003	?	various Amerindians (Beckerman 1994)[e]

[a] Does not include time needed to go to the target place to collect invertebrates. Does include travel and search time for fishes and game.
[b] Per cent of foraging trips successful in procuring organisms sought.
[c] Based on returns from 78 fishing trips observed at various times of the year.
[d] Mean of annual means of five Amerindian groups (table 8.2 in Beckerman 1994).
[e] Mean of annual means of 14 Amerindian groups (table 8.3 in Beckerman 1994).

value oysters, and smoked earthworms can be sold for almost double the price of smoked fish or other meat and game. The Ye'Kuana also actively try to increase the presence of these earthworms: they collect motto (*Andiorrhinus motto*) from locations in which they are abundant, and disseminate them in places (stream or river banks) where they are not found, by inserting the worms into small holes. This is a kind of worm farming that in essence converts a species of the so-called soil macrofauna to a kind of mini-livestock.

3. WHY IS THE STORY OF THE EDIBLE LEAF- AND LITTER-CONSUMING INVERTEBRATES IMPORTANT?

The Amerindian pattern of using invertebrates that feed on leaves and litter as food, and especially as sources of animal protein, is a strategy that takes advantage of the abundance of these highly renewable elements of the rainforest ecosystem, and suggests a finely tuned integration into the natural dynamics of the forest.

The consumption of invertebrates can provide significant amounts of animal protein, especially during the more difficult periods of the year, such as the rainy season, when fishes and game are scarce. We observed that Guajibo living at the savannah border (at Alcabala Guajibo, Amazonas, Venezuela) relied mostly on insects (especially grasshoppers and larvae of *Rhynchophorus palmarum*) during the rainy season of July–August 1998, and estimated that over 60% of their animal protein came from insects. (We made this evaluation based on a few trips around the village, by observing gathering peoples and enquiring of different families in the village during July–August 1998, in Alcabala de Guajibo.) This value is higher than any previously reported (Zent 1992; Lizot 1993) including that of Dufour (1987), who found that 26% of the animal protein in Tukanoan women's diets came from insects in the rainy season. Although it appears that invertebrates are more important in the diet when fishes and game are scarce, it is commonly argued that these small organisms are gathered only because of scarcity of the larger game animals (Denevan 1972). This is simplistic and ignores some Western food habits, such as rating the 'small' fish eggs (caviar) or the tiny escargot much more highly than beef or pork. Indeed, we have observed that the Amerindians value many invertebrates and insects for their taste, and different groups tend to include different species in their cuisine.

Because of the small size of the individual organisms, the average amount of time needed to collect insects for food can be higher than that needed to procure the larger fishes and game animals (table 5). However, because the location and availability of insect colonies and gregarious aggregations is well known, the success rate of foraging for insects is higher (close to 100%) than it is for fishes and game. Both fishing and hunting involve considerable searching, and capture is not assured even when the prey has been located.

In summary, the Amerindian strategy of using leaf- and litter-consuming invertebrates provides a model in which the rainforest supports human populations without the destruction of the biodiversity that has accumulated over millennia.

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