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

Maurizio Guido Paoletti1*, Darna L. Dufour2, Hugo Cerda3, Franz Torres4, Laura Pizzoferrato5 and David Pimentel6

1Department of Biology, Padova University, 35100 Padova, Italy
2Department of Anthropology, University of Colorado, Boulder, CO 80309, USA
3Universidad Simon Rodriguez, Caracas, Venezuela
4Fondo Nacional de Investigaciones Agropecuarias Amazonas, Puerto Ayacucho, Venezuela
5Istituto Nazionale di Ricerca per gli Alimenti e la Nutrizione, 00178 Roma, Italy
6Department of Entomology, Cornell University, Ithaca, NY 14853-0901, USA

At least 32 Amerindian groups in the Amazon basin use terrestrial invertebrates as food. Leaf- and litter-consum ing invertebrates provide the more important, underestimated food sources for many Amerindian groups. Further, litter-consum ing 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 (10300 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 1b).

(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 (*Eristylis 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 japonica* spruce, a wild-growing tree which produces...
In order to estimate the consumption of edible insects by the Tukanoans, we focused on the following major food items:

(a) Edible Seeds

Edible seeds of *Inga* sp. and a species of Notodontidae were also consumed by the Tukanoans. For estimating the foliage consumption by the caterpillars, we used the conservative figure of 450 kg ha$^{-1}$ year$^{-1}$ or about 4% of the standing living leaf biomass. We estimated that the Tukanoans consumed about 0.17 kg ha$^{-1}$ year$^{-1}$ of caterpillars, which represents about 0.01% of the total biomass of edible caterpillars.

(b) Litter-Cutter Termites

Most of the termites eaten by the Tukanoans belong to the genus *Syntermes*, of which there are some 23 species in South America (Costantino 1995). These are the largest termites in the region. Estimates of their biomass are based on data collected by Martius (1998) from Manaus, Brazil. We estimated that the Tukanoans consumed about 2.46 kg ha$^{-1}$ year$^{-1}$, which represents about 0.001% of the standing biomass.

(c) Earthworms

In focusing on litter, it is important to establish if the earthworms that dominate litter consumption in most tropical forests are a significant food source. The earthworms inhabiting river edge environments, such as *Andiorrhinus motto* and *Glossoscolecidae*, 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$^{-2}$.

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

<table>
<thead>
<tr>
<th>group</th>
<th>bees and wasps</th>
<th>caterpillars</th>
<th>beetles</th>
<th>grasshoppers</th>
<th>ants</th>
<th>termites</th>
<th>earthworms</th>
<th>decapods</th>
<th>spiders</th>
<th>other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yanomamo$^a$</td>
<td>89</td>
<td>43</td>
<td>25</td>
<td>5</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Guajibo$^b$</td>
<td>31</td>
<td>12</td>
<td>4</td>
<td>4</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Piaroa$^c$</td>
<td>28</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Yukpa$^d$</td>
<td>25</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Ye’Kuana$^e$</td>
<td>23</td>
<td>5</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Tukanoan$^f$</td>
<td>23</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Curripaco$^g$</td>
<td>11</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ 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 Ocabo 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 *Scaraeidae*, *Cerambycidae*, *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 (Tok, Guatamo and Buna Vista) and Curripaco (Cucurital) (1997–1999).


$^c$ The information comes from Zent (1992) and from interviews and collections on site or in near villages (especially in Caño Tigre, Babilla de Pintado and Gavilán, Amazonas, Venezuela).

$^d$ Ruddle (1973).

$^e$ Four species are added to Dufour (1987); one Homoptera Membracoidae, *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.

$^f$ Data for the Ye’Kuana are based on the literature (Lizot 1993; Chagnon 1968) and especially on personal interviews of seven Ye’Kuana from Yapu (Rio Papuri, Vaupes, Colombia) composed of about 100 people.

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

<table>
<thead>
<tr>
<th>name</th>
<th>mean fresh weight (g)$^b$</th>
<th>total (kg year$^{-1}$)</th>
<th>per cent of total weight</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Atta</em> soldiers and queens (three species)</td>
<td>0.1–0.9</td>
<td>100</td>
<td>29.3</td>
</tr>
<tr>
<td><em>Syntermes</em> soldiers (three species)$^d$</td>
<td>0.28</td>
<td>133</td>
<td>39.0</td>
</tr>
<tr>
<td>Caterpillars (five species)</td>
<td>1.46–3.06</td>
<td>96</td>
<td>28.1</td>
</tr>
<tr>
<td>Vespidae larvae and pupae (three species)</td>
<td>0.2–0.4</td>
<td>2</td>
<td>0.60</td>
</tr>
<tr>
<td>Melaphorinae larvae and pupae (one species)</td>
<td>0.1</td>
<td>1.5</td>
<td>0.44</td>
</tr>
<tr>
<td>Rhyynchophorus palmarum larva</td>
<td>8–12</td>
<td>6</td>
<td>1.7</td>
</tr>
<tr>
<td>Beetle larvae boring on wood and dead wood (four species)$^e$</td>
<td>2–8</td>
<td>2.5</td>
<td>0.73</td>
</tr>
</tbody>
</table>

$^a$ 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.

### Notes

- Four species are added to Dufour (1987): one Homoptera Membracoidae, *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.

- The data were collected by M.G.P., H.C. and F.T. (1997–1999) in Puerto Ayacucho and field collections in Mavaka, Boca de Padamo and Boca de Ocabo.

- Ye’Kuana (Tok, Guatamo and Buna Vista) and Curripaco (Cucurital) (1997–1999). The information comes from Zent (1992) and from interviews and collections on site or in near villages (especially in Caño Tigre, Babilla de Pintado and Gavilán, Amazonas, Venezuela).

- Ruddle (1973).

- Four species are added to Dufour (1987): one Homoptera Membracoidae, *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.

- 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.

- Mean fresh weight of individual organisms.

- Weight of soldiers and queens is 0.1 g and 0.9 g, respectively.

- Data based on Martius (1998); estimations of dry weight of *S. spinosus* multiplied by 5 to obtain the fresh weight.

- Scarabaeidae, Buprestidae, Cerambycidae, Passalidae.
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 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.)

<table>
<thead>
<tr>
<th>mean production (kg dry weight ha⁻¹)</th>
<th>litter and leaf consumption (kg ha⁻¹ year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>earthworms</td>
<td>Syntermes</td>
</tr>
<tr>
<td>Syntermes</td>
<td>caterpillars</td>
</tr>
<tr>
<td>Atta</td>
<td></td>
</tr>
<tr>
<td>leaves 10,300</td>
<td>none</td>
</tr>
<tr>
<td>litter 5,410</td>
<td>none</td>
</tr>
<tr>
<td>(437–420)</td>
<td>(437–420)</td>
</tr>
<tr>
<td></td>
<td>450 (18)</td>
</tr>
<tr>
<td></td>
<td>500 (80)</td>
</tr>
</tbody>
</table>

(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 (Ersinyis 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.
value oysters, and smoked earthworms can be sold for almost double the price of smoked sh 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 inquiring 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 Tikanoan 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.

We are grateful to the following for their valuable help in providing information for this research: at Guatamo, Simon Garcia and his family; at Toki, Elia Tiron and Lorenzon Santiño; at Buena Vista, Annibal Baceco and his family; at Babilla de Pantado, Martin; at Caño Tigre, Capitan Enrique, José Jimenez and their families; at Mawaka, Renato Moi and Ignatio Vaivitowe; and at Mototema, Tito. For information on different ethnic groups, taxonomic expertise and various literature, we are indebted to many people, in particular: Paul Patmore, Fredrick W. Stehr, John Moser, Rainer Wirth, Giovanni Onore, Rui Sergio Sereni Murrieta, Carlo Foglia, Virginia Scott, Thomas K. Wood, Reginaldo Costantino, Christopher Martius, Thymoty Myles, Carl Jordan, Deane Bowen, Stenford Zent, Darrell Posey, Napoleon Chagnon, Jacques Lizot, Juan Finkers and Raymond Hames. Susanne Elliott helped in improving the manuscript. We are grateful to two anonymous referees who helped to improve the manuscript with their observations. Comitato Nazionale Ricercche, Consejo Nacional de Investigaciones Científicas y Tecnológicas, and International Foundation for Science from Sweden partially supported the fieldwork in Venezuela of H.C., F.T. and M.G.P.

An Organization for Economic Co-operation and Development grant provided M.G.P. with support for research at the University of Colorado and at Cornell University in 1999.

REFERENCES


De Foliart, G. R. 1999 Insects as food: why the Western attitude is important. *A. Rev. Entomol.* 44, 21–50.


