*Human Ecology, VoL 12, No. 2, 1984* 

# **Seasonal Variance in the Diet of Ache Hunter-Gatherers in Eastern Paraguay**

Kim Hill,<sup>1</sup> Kristen Hawkes,<sup>1</sup> Magdalena Hurtado,<sup>1</sup> and Hillard Kaplan<sup>1</sup>

*Seasonal variance in the diet of Ache hunter-gatherers is examined. Fluctuation in the number of calories of honey consumed daily contributed most to the differences in total calories consumed daily during different seasons of the year. Meat, the most important resource in the diet, provided the greatest number of calories daily, and varied little across seasons. The vegetable component of the diet is characterized by low variance in absolute numbers of calories, but high variance in species composition. The mean number of calories consumed daily per capita is high (3827 calories) compared to that reported for other hunter-gathers. Differences in energy expenditure and consumption among modern hunter-gatherers is discussed.* 

KEY WORDS: hunter-gatherers; subsistence; seasonality; energy budget.

# INTRODUCTION

For almost 50 years, seasonality has been considered an important constraint upon many aspects of human foraging societies (Steward, 1938; Thompson, 1939). Recently, quantitative data gathered among the !Kung has clearly documented the importance of seasonality in determining changes in diet, group composition, movement patterns, and possibly reproductive strategy (Lee, 1979; Wilmsen, 1982). Seasonal effects on the diet of foragers

~Department of Anthropology, University of Utah, Salt Lake City, Utah 84112.

101

0300-7839/84/0600.0101503.50/0 9 1984 Plenum Publishing Corporation

## 102 Hill, Hawkes, **Hurtado, and Kaplan**

have also been quantitatively demonstrated in Arnhem land (Meehan, 1975; Jones, 1980). Liebig's Law of the Minimum suggests that perhaps seasonal minimums represent one of the most important constraints for environmental adaptation. The realization that adaptation to occasional periods of severe stress can have major consequences for populations has led to a search for yearly periods of nutritional stress among the !Kung (Lee, 1979; Truswell and Hansen, 1976; Wilmsen, 1982). Seasonal maximums in temperature have also been postulated to be major stress periods, constraining foraging behavior and diet (Blurton Jones and Sibly, 1978), and seasonal gluts may be a key variable in initiating storage (Blurton Jones, 1983).

General descriptive ethnography has frequently noted the importance of seasonality in "culture" and "social structure." For example, several authors (Bowdler, 1981; Damas, 1972; Downs, 1966; Gould, 1977; Hoebel, 1978; Lee, 1979; Watanabe, 1968) report that changes in seasonal abundance of some resources promote a shift from small mobile social groups to large sedentary ones, influencing mating patterns and ritual activity. Where regular seasons of bad weather limit travel, visiting and intergroup conflict may show seasonal fluctuation as well.

Studies in behavioral ecology have demonstrated similar effects of seasonality on the behavior of other organisms. Seasonality of reproduction is one of the most universal phenomena among living organisms. Seasonality also effects a wide variety of other behaviors from foraging and movement to social group composition and, consequently, social behavior. Schaller (1972), for example, has described how sharp seasonal changes in rainfall in the Serengeti region of Tanzania affect social group size and composition, diet, and movement patterns for a variety of herbivores and carnivores. These changes are likely to affect many other behaviors in turn. However, the extent to which seasonality can be seen as a major factor constraining a vast and complex set of interactions between individual organisms and their environment has yet to be determined.

It has been generally assumed that the effects of temporal variability on human populations are greater at higher latitudes and are least pronounced near the equator (Binford, 1980; Yesner, 1980). Ecologists, however, are becoming increasingly more aware that the biological effects of seasonal rainfall patterns in tropical environments can be as important as the seasonality of temperature at high latitudes (Foster, 1973; Harris, 1980; Leigh, 1983; Opler et al., 1976). The belief that tropical environments affect human inhabitants in a temporally uniform way has been seriously questioned by anthropologists as well. Abruzzi (1980) discusses the importance of seasonality to the Mbuti of the Ituri forest, at  $2<sup>o</sup>$  north latitude. It also appears that seasonal effects are very important to human groups living in Arnhem land at 15° south (Meehan, 1975; Jones, 1980) and in the Kalahari desert at about 23° south (Lee, 1979; Wilmsen, 1982). We present data on the seasonal variation in the diet among Ache foragers in neotropical forest near 24° south.

Tropical-forests are frequently considered to display less seasonal variation than any other ecotype on earth. The following study provides a partial assessment of that generalization as it applies to human foragers. The data indicate that although seasonality does have some effects on the Ache diet, they are minor and for the most part qualitative changes rather than fluctuations in the number of calories consumed. The Ache therefore seem less affected nutritionally by seasonality than any other group of foraging people that we are aware of.

# ECOLOGICAL BACKGROUND

The northern Ache were full-time-hunter-gathers in eastern Paraguay until they made peaceful contact with the outside world between 1971-1978 (Hill, \_ 1983). They currently live primarily at a Catholic mission (Chupa pou) but continue to forage frequently in the nearby forest. We have previously described these foraging trips, reported figures on time costs and resources acquired, and begun to formally assess the efficiency of Ache foraging strategies (Hawkes *et al.,* 1982; Hill and Hawkes, 1983).

The northern Ache traditionally roamed the area between  $24-25$ ° south and  $54.5-56$ ° west. The data presented in this paper were collected in a 50 km radius out from a point located approximately  $24.2^\circ$  south and 55.6° west (Fig. 1). From aerial photos taken in January 1982, we estimate that about 80% of this area is covered with forest, between  $15-20\%$  in a strip along the one dirt road traversing the area has been converted to agricultural fields in the past 5 years, and the small residual is natural meadowland. Virtually all foraging is done in the forested areas which we have further subdivided into the following types.

*1. Primary Forest.* This is by far the most common plant community in eastern Paraguay. It is found away from large rivers or meadows wherever there is adequate drainage. It is characterized by tall trees and medium to sparse undercover with considerable densities of hanging vines in some places. Major families of trees found here are *Sapotaceae, Lauraccae, Moraceae, Rutaceae, Myrtaceae, Caricaceae, Combretaceae, Gutliferae, Bignoniaceae, Meliaceae,*  and *Leguminoseae.* Conspicuous ground plants include several types of bamboo (family *Guaduae* and others), various ferns, and spiny plants of the genuses *Bromelia and Dykkia.* One of the largest and most common vines which is used as fish poison by other local indigenous groups (but not the Ache) is *Paullina elegans.* All game animals exploited by the Ache can be found in this ecotype.

*2. Low Scrub Forest. The* trees are considerably shorter and smaller in these areas, with dense ground cover that is difficult to traverse. Common trees are from the families *Rutaceae,* and *Aquifiliceae.* Thick stands of spiny *Bromelia balancea and Dykkia sp. are* common. Armadillos appear to be more abundant in this ecotype than elsewhere.



*3. Riverine Forest.* This type of forest is found along the edges of large rivers, and around the edges of some meadows. It is characterized by a considerable variety of large and small bamboos including one from the genus *Chusquea* which was used by the Ache to make knives before contact, and one large species that yields larva, which the Ache consume. It also has a relatively greater density of palms than the primary forest. Paca and armadillos are more abundant in this ecotype than in the primary forest.

*4. Swamp Forest.* This ecotype is found throughout the primary forest wherever drainage is not adequate. It is characterized by an abundance of palms (genus *Arecastrum* and *Acromia)* and is of considerable economic importance, since palm products are important dietary staples. Small streams or swampy pools provide water. Several species of bromeliads are commonhere as well as large-leaf banana-like plants. Tapirs and peccaries are frequently encountered foraging in this ecotype.

All the above types of forest are encountered frequently and most foraging days include spending at least some time in each (with primary forest and swamp forest being most common). Indeed, it would be difficult to forage in this area without crossing these ecotypes fairly frequently. We hope that future research by qualified ecologists will provide a more accurate detailed characterization of the forest in this area.

Seasonality in eastern Paraguay is marked by both temperature and rainfall. Two weather stations located approximately 100 km east and west have been in operation for the past 5 years. Our own weather data taken during 4 months of 1980 and 6 months of 1981-1982 agree closely with the mean of the two, so we use the more complete data base provided by the official weather records. The extremes in rainfall and temperature are synchronous, with the two major seasons being warm and wet or cold and dry.

Figure 2 shows the mean high and low temperatures, month by month, over the past 5 years. The warm season (November-February) shows mean daily high temperatures in the low  $30s^{\circ}$  C (high  $80s^{\circ}$  F), and mean daily lows in the low 20s<sup>o</sup>C (high 60s<sup>o</sup>F). The cold season (May-August) shows mean daily high temperatures in the low  $20s^{\circ}$ C and mean daily lows around 10 $^{\circ}$ C. Extreme yearly highs are in the upper 30s °C and temperatures usually drop below  $0^{\circ}$ C about 5 days a year. There is very little year-to-year variation in temperature and our field period appears to be representative of the general pattern.

Rainfall in eastern Paraguay is extremely erratic from month to month and year to year. The period from November to January is generally but not consistently wetter, with June to August being generally drier. Figure 3 shows monthly rainfall and yearly totals. Total rainfall has ranged from 1180-2079 mm in the past 6 years. The 4 wettest months of the year have a mean monthly total rainfall of 217 mm while the mean of the 4 driest months is 73 mm. This difference is significant (median test,  $p = .002$ ). During our field period, September 1981 was the driest September in the past several years, and December 1981 was the wettest December. The significance of this is not clear,





Fig. 3. Monthly rainfall totals in millimeters during the past few years. Yearly totals are 1976, 1632 mm; 1977, 1395 mm; 1978, 1180 mm; 1979, 2079 mm; 1980, 1457 mm.

especially since temperature may be more important (and consistent) in determining seasonality. 2 Humidity measurements recorded with a sling psychrometer during the warm season of 1981-1982 showed midday humidities usually between 80-95% and the dew point was usually reached by 1-2 hr after sundown.

Rain can come at any time of day and varies in duration from about 1 hr to more than 3 days. Hard rains of long duration severely limit mobility and foraging. The result is frequently that men forage near the previous night's camp, without weapons for small game (rain destroys their palm wood bows), and women spend considerably more time exploiting nearby vegetable resources.

At the present time, we can only give a crude description of the floral and faunal responses to seasonal fluctuation in temperature and rainfall in this area. We have observed flowering and fruiting during most times of the year although flowering is considerably less frequent in the cold season. Insects are more active in the warm season and insect products (honey and larva) seem rare in midcold season. We observed reptiles (especially teju lizards) to be much more visible during the early warm season and this agrees with one published study (Bertoni, 1941). Mammals appear to be present and active year round although most have young at the beginning of the warm season. Mammals are considerably fatter at the end of the warm season and beginning of the cold season. Bird eggs appear to be more abundant in early and midwarm season.

## **METHODS**

All data presented were collected on 16 foraging trips out from the Catholic mission ranging from 5-15 days in length. We sampled 153 foraging days (137 whole days) during different seasons of 1980, 1981, and 1982 (Table I). The data represent 1578 adult male days, 977 adult female days, and 723 child days (3278 consumer days), in foraging bands ranging from 9-68 Ache (see Table I).

All items brought back to the women-and-children's location (this group is usually moving throughout the day) during the day were weighed with hanging spring scales. Since all meat and most other resources taken in appreciable quantifies were brought back to the main camp, this represented the bulk of the diet. Focal person studies, instantaneous scan sampling, and focused event

<sup>2</sup>Tropical botanists have warned us to be cautious of concluding that temperature is more important than rainfall in determining floral and faunal seasonal responses. Many South American tropical forests clearly cue to rainfall for seasonal phenomena, and some of the flora in our study area are known to cue to changes in rainfall elsewhere (see references on tropical seasonality).



×

sampling also allowed us to record a good deal of the simultaneous acquisition and consumption that took place throughout the day. This "on the spot" consumption was primarily limited to women and children and included only certain vegetable items. When subjects who were out of sight were known to be acquiring and consuming resources for a substantial period of time we extrapolated their consumption from observed acquisition and consumption rates of other similar subjects. These same observations allow us to estimate that the total number of calories consumed "on the spot" is less than 10% (usually about 5%) of the total consumption. Thus, the error introduced by our inability to monitor and accurately record all of this consumption, while unfortunate, does not detract seriously from the results presented. The direction of the error however results in a slight underestimation of the vegetable and small collected component of the diet.

Since all resource items acquired by the Ache are consumed within 48 hr (usually within 24 hr), and since we virtually never observed any acquired resource to be subsequently discarded rather than consumed, we consider total acquisition and total consumption on any foraging trip to be equivalent. Dogs were rarely present and the amount of food brought back to the mission at the end of trips was negligible. Techniques of data collection have been further described elsewhere (Hawkes *et al.,* Hill and Hawkes, 1983).

Plant resources were identified using Cadogan (1973), and animals were identified using the "Key of Paraguayan mammals" (White and Stallings, unpublished manuscript.) All vegetable resources not weighed directly, i.e., those recorded as number of items or liters, were converted to kilograms using a factor calculated from several field samples. Most vegetable and all meat items were Weighed directly with hanging spring scales (I kg, 10 kg, and 50 kg). Caloric equivalents are taken from (1) laboratory analysis performed in Salt Lake City, Utah, (2) food composition tables for use in Latin America (Leung, 1961) and USDA Handbooks 8 and 456 (Watt *et al.* 1950; Adams, 1975), and (3) extrapolations from these sources for some game items where no equivalent is listed. Samples analyzed at Ford Laboratories in Salt Lake City were stored in nalgene bottles containing 25 ml methanol until the field period ended. Control experiments showed that such storage does not appreciably affect food analysis for periods exceeding 6 months. 3 Game items are calculated as 75% edible based on eight field measurements showing the edible portion to be between 68.9%-88.1% for various game items. Hart (1978) calculated edible portions of game items for Mbuti Pygmies at above 80% and our field calculations also suggest that the edible portion of game used by hunter-

<sup>3</sup>Slight discrepancies between our fresh-frozen controls and samples stored in methanol for 6 months were noted. Unfortunately, due to the high cost of analysis we could not run enough independent tests to determine if there really are significant differences between the two. Since the discrepancies did not change the final caloric value of any item by more than about 12% (fat content is slightly lower after 6 months in methanol), we have taken laboratory analysis at face value.

gatherers may have been underestimated in most earlier studies. We have not taken into account the considerable change in amount of body fat for some game items during the year. This has important implications for seasonal effect on diet, and we discuss this more fully in another section. Caloric equivalents for all items are given in Table II.

Due to the skepticism of some colleagues and an anonymous reviewer, we have recalculated some of the values for game items listed in Table II. Specifically, the reported values for opposum, peccaries, pacas, and coatis seem high when compared to values for some East African game animals (Pitts and BuUard, 1968). Precise calculations of body fat for some of the animals in question, however, indicate that the numbers listed in Table II are quite conservative. Based on the body fat measurements of Brazilian specimens (Ledger, 1968) we calculate the caloric value of paca, armadillo, aguti, opposum, and racoon to be 242, 201, 238, 211, and 299 cal/100 g live weight, respectively.<sup>4</sup> This is considerably higher for all items than the numbers we report in Table II. On the other hand, equivalent calculations for the African warthog and the hippopotomus yield 85 and 144 cal/100 g live weight, respectively. Other East African game animals are in this same range (see Pitts and Bullard, 1968). This points out the little-appreciated fact that many South American game animals are substantially fatter than common African or North American game.

Numbers presented on dietary intake are listed as mean daily calories per person. This is calculated by dividing the total calories of resources that we record acquired on a given day by the total number of consumers present on that day. All members of a foraging band greater than 3.5 years of age (including anthropologists) are calculated as equivalent consumers. These numbers therefore represent intake per capita (minus infants). Although individual intake is very difficult to measure, our data on consumption (Kaplan *et al.,* 1984), and our field observations lead us to believe that women and children eat considerably more than has often been assumed. One 5-year-old boy that we monitored ate amounts equivalent to that consumed by the anthropologists. Women's energy requirements, because of constant lactation and pregnancy approach that for adult men (see Discussion). We recorded women in consumption events much more frequently than men (Kaplan *et aL,* 1984)

<sup>&</sup>lt;sup>4</sup>Calculations on calories per 100 g edible portion are made using the formula: calories =  $82.5$  $+ 8.172 \times$  percent fat in carcass. Edible portion is calculated as 75 g/100 g live weight. This is broken into 15 g internal organs and 60 g carcass. Internal organs are calculated at 138 *cal/lO0*  g, the mean of brain, heart, intestines, kidneys, liver, lungs, spleen, and tongue taken from Leung (1961). Percent fat is given for the carcass in Pitts and Bullard (1968) and for the whole animal in Ledger (1968). We assume that all body fat remains with the edible carcass portion, thus carcass fat = body fat/fraction of live weight which is carcass  $(.6)$ . An example calculation is as follows: Paca, of 100 g live weight, 25 g is refuse. Internal organs make up 15 g  $\times$  138 cal/100 g or 20.7 calories. The carcass is 60 g  $\times$  82.5 cal/100 g plus 8.172  $\times$  12.6 percent body fat/.6 (the fraction of the live weight which is carcass). This yields 171.6 calories for the edible carcass, giving a total of 242 calories for the edible carcass and internal organs per each 100 g live weight.



112

urtedo and Kenlan





91.<br>Plote this is cal/kg raw weight. The higher caloric values for edible portion listed in some sources have been adjusted downward in order<br>to subtract out inedible refuse. For example, all game items listed show 75% of to subtract out inedible refuse. For example, all game items listed show 750/0 of the caloric value of the edible portion since 25% of the "Note this is cal/kg raw weight. The higher caloric values for edible portion listed in some sources have been adjusted downward in order carcass weight is refuse.

hA. Ford Chemical Laboratory, Salt Lake City, Utah; B. Handbook of Latin American Foods; C. USDA Handbooks 8 and 456; D. Extrapolated from similar items listed in A, B, or C. and it is possible that they actually consume more calories than men. Because of these uncertainties and a general lack of agreement about what factor should be applied to each age and sex category to calculate nutritional needs for "equivalent consumers," we leave our calculations as per capita (minus infants) consumption. The data in Table I allow for any adjustments appropriate for comparison.

Physical measurements of Ache subjects were done using a digital electronic bathroom weigh scale and a standard tape measure fixed to a vertical wall. All subjects were weighed barefoot in light cotton clothing and the equivalent weight of any extra attire was subtracted. Pregnant women were excluded when calculating mean weights. Subjects weighed before and after foraging trips were weighed in the midmorning. Others were weighed at convenient times throughout the day. Adults are defined as greater than 18 years of age for physical measurements and greater than 15 years or married for foraging trips and consumption.

All statistical tests are described in the text. A probability level of .05 is considered significant unless otherwise stated.

# VALIDITY OF THE SAMPLE

It should be explicitly stated that we are sampling a subset of days throughout the year in order to reconstruct the seasonal pattern of the Ache diet as full-time foragers before contact. We do not, in this paper, examine the current Ache diet or calculate the effects of sedentation on the nutrition of the study population. Since we are attempting a reconstruction of fulltime foraging behavior based on a sample of people who currently only forage part time, the validity of such a generalization should be carefully examined.

The Ache currently live primarily at a Catholic mission and engage in subsistence agriculture while residing there. Some younger males even do occasional wage labor. Nevertheless, all of the Ache in our sample were fulltime nomadic hunter-gathers until between 2-8 years (depending on the individual) before the present study began. They continued foraging frequently even after taking up residence at government or mission colonies. Provisioning was sporadic and agricultural output was minimal until 1980. Although their foraging skills may have declined slightly during this period, the data indicate that they still do exceptionally well acquiring food in the forest. All adults continue to have a thorough knowledge of foraging technology and techniques. The technology employed on foraging trips that we sampled was virtually identical to that used before contact (with a few minor exceptions such as greater numbers of metal tools and use of matches). Hunting pressure on game populations seems slightly higher in areas

that we monitored, especially nearby the mission, than would have been the case in precontact times. At distances greater than a 1-day walk from the mission, the hunting pressure (in hunter days/ $km<sup>2</sup>$ ) is similar to that we calculated before contact. These factors combined lead us to believe that the rates of foraging returns that we measured (kg/hr or cal/hr) must indeed be very close to the return rates the Ache experienced before contact.

The potential problem with data on time allocation and food consumption is more complex. It has been suggested by several critics that current Ache foraging trips may not be representative of the work effort and consumption levels that would have been observed before contact. Specifically, the Ache may be working hard and consuming much in order to satiate cravings for protein and other critical nutrients which are not readily available at the mission settlement. In addition, since most of the current Ache social and political life takes place at the mission, short foraging strips may be seen as special purpose excursions where the only goal is to eat well. while we are quite aware of these and other potential effects of mission life on the foraging behavior that we sampled, we currently believe that our measurements of food consumption and men's work effort are indeed representative of the precontact behavior of full-time Ache foragers (changes in women's behavior may be more substantial; see Hurtado *et al.,*  unpublished manuscript, for discussion). This conclusion is based on several independent observations and impressions that follow.

1. Ache informants claim that the daily routine of behavior that we observed on the trips sampled was indeed quite smilar to that which characterized their life before contact. Specifically, they state that men hunted virtually every day that weather permitted. On the other hand, they do mention occasionally living in larger camps that moved less frequently. The effects of this type of change on the numbers that we report has yet to be determined.

2. Hill observed several Ache bands that were dependent almost entirely on wild foods for more than 3 months. No differences in work effort or food consumption were apparent.

3. Hill also observed Ache foragers less than 2 weeks after initial contact in 1978. Their work effort and food consumption seemed identical to that which we later measured on foraging trips with some of the same people. Some of these Ache, although making peaceful contact, had continued to forage daily. There is no reason to believe that they should have experienced any greater craving for protein or nutrients than they would have before contact.

4. Photos of a great number of Ache, immediately after first contact, show body weights very similar to what they are currently. Therefore, the ratio of energy output to energy consumption must not have changed too radically.

5. We observed no changes in work effort or food consumption on our sample trips, whether they were 4 days in length or 15 days.

6. The assumed craving for proteins and other nutrients may not be as intense as some critics imagine. Although it is true that the Ache prefer to eat as much meat as they can get, they currently eat considerably more than neighboring Paraguayans or Guarani Indians, even when they are at the mission. Small game is brought into the mission every day, and large game is killed about once a week. Chickens, ducks, pigs, and dogs are eaten regularly, and a burro is usually killed about once a month. In addition, wild collected foods (especially larva) are brought in daily by mission residents. Most members of the population spend about 8-10 days per month in the forest. Most members of foraging trips that we sampled were precisely those Ache who tended to go most frequently to the forest, and should thus have the least craving for protein and nutrients. Some of these Ache spent more than 50% of all days in the forest.

7. Foraging bands on trips that we sampled are similar in size to Ache bands before contact. Most of the same "social" opportunities exist. Marriages were formed and broken while on trips that we sampled. Flirting, playing, and joking with potential mates and lovers, as well as close friends, were common distractions from subsistence work. Taking care of children was an important activity, although fewer children of intermediate ages were present in our sample bands than in precontact Ache bands. Although the political arena is considerably more lively at the mission than on foraging trips, it may be the mission behavior that is unrepresentative of the precontact situation. Warfare has of course been eliminated, but probably had little effect on the daily subsistence pattern. The amount of status to be gained from successful hunting is probably lower now than it was before contact (status is now gained at the mission from material wealth, ability to maipulate outsiders and missionaries, etc.). This, however, would tend to depress work effort and consumption levels rather than raise them. The demographic makeup of bands that we sampled seems slightly biased against children and in favor of adult males. This, of course raises food consumption levels, but adjusting for the observed bias changes projected consumption levels very little.

Thus, in short, it appears to us that our sample *is* in fact representative of precontact full-time foraging behavior. However, since all of the above points are based on impressions rather than measurements, the possibility remains that the current mission situation may have affected the data we collected on foraging trips. If one were to hypothesize that such a problem existed, it would be necessary to specify cause and effect between some aspect of the current Ache situation and some foraging behavior that we have measured. The vague belief that mission life or contact has "somehow changed" the foraging behavior that we observed for this group of



Fig. 4. Mean daily kilocalories per consumer: (a) total, (b) from meat, (c) from vegetable, (d) from honey, (e) from mission food. 1980 (X), 1981-1982 (.), all hunters with shotgun  $(\triangle)$ . Vertical bars mark one standard error from the mean.

people who spent most of their lives as full-time foragers, is not a valid criticism of the studies presented. On the other hand, despite our current belief that our sample is representative of the behavior of full-time foragers, we will continue to investigate possible effects that mission life may have on the data we have collected.

# RESULTS

Mean daily total calories per consumer for each foraging trip during the sample period is shown in Fig. 4a, and the mean daily calories per consumer for meat, small collected items (vegetable and larve), and honey are presented in Fig. 4b, c, and d, respectively. Calories of food (mostly manioc and corn) brought from the mission is presented in Fig. 4e, but will not be discussed further as most of this is consumed on the first day of a trip. Due to the small size (in days) for individual foraging trips, and the considerable day-to-day variance in consumption of some items, the standard error is quite large for some measurements. Mission-brought items are only acquired on the first day of foraging trips and thus show no standard error. One trip in 1980 when all men used shotguns is shown for comparison but is not included in any calculations. On all other trips, men used only bows and arrows.

In order to determine whether the differences in mean daily calories consumed between trips was significant a Kruskal-Wallis test (samples were not normally distributed and variance was not equal) was perfomed on each data set (Figs. 4a-d). The test could not reject the hypothesis that total calories and calories from meat are all drawn from equivalent populations, i.e., that the difference between trips is due only to sample error. However, the differences between trips for calories of honey and vegetable items were highly significant ( $H = 42.43$ ,  $p = .0001$  and  $H = 48.74$ ,  $p = .00001$ , respectively).

Figure 5 shows the cumulative number of calories in the Ache foragers' diet as each major resource class is added into the diet (shotgun data and mission items excluded). Differences in honey appear to be most important in determining the differences in total calories consumed on different trips, followed by differences in meat, and finally vegetable items. Meat, however, is consistently the most important resource class in the diet followed by honey during part of the year and vegetable items during other times of the year. The percentage of the total caloric intake that is provided by meat ranges from 47-77%. Honey makes up between .4%-44% of the total calories on different trips and vegetables between  $6-45\%$ . Mean total calories consumed daily on foraging trips ranged Trom 2535-5585. The overall mean is 3827 calories per consumer per day with each trip weighted equally.

Each major resource class is further broken down into individual resource items in Figs. 6-8. Only resources that provided at least 100 calories per consumer on at least one trip are treated separately. Major game items are two species of peccary, deer, monkeys, armadillos, pacas, and coatis. The honey from *Apis melifera* is the major type taken, and major collected resources include palm heart, fiber, fruit, oranges, virella, kurilla, and larva.



Fig. \$. Cumulative mean daily kilocalories per person from foraging (bow only). (A) vegetable items and larvae, (B) honey, (C) meat.

In order to test for seasonal differences in resources consumed, the year was divided into quarters (3 months each) beginning in January, and all data taken within a given quarter of the year were pooled. A Fisher test for equality of variance showed many significant differences, and chisquare goodness of fit test showed that most samples were not normally distributed. For this reason, nonparametric tests were utilized to test for differences in the mean (or median) number of calories consumed of each resource class (meat, and vegetable) per day throughout the year. A randomization test for two independent samples was performed for each pair of yearly quarters for meat, vegetable items, and for total calories consumed. 5 The median test was performed for each pair of yearly quarters for honey, as kurtosis of the combined samples was considered too high to run the randomization test. Because three independent tests were performed

<sup>&</sup>lt;sup>3</sup>The randomization test is a nonparametric test for population location. For large sample sizes, it has been shown to approximate the Student's t distribution (Pitman, 1937) but it does not rely on the assumptions of the classic  $t$  -test. The median test also tests for equivalence of population location but does not assume normality of equal variance of samples.







Mean Daily Catories Honey per Consumer

Fig. 7, Cumulative mean daily kilocalories per person from honey and bee larvae. Numbers refer to resources listed in Table II. (A) honey and lavae from *Apis melifera (25,* 35, 36) (B) honey and larvae from other sources (26, 28, 29, 38).

on each data set, a probability of .01 was considered necessary for statistical significance. Results are presented in Table III.

The number of calories of honey consumed in both the fourth and first quarters of the yearly cycle are significantly greater than for the second and third quarters. The data also suggest (but differences are not quite significant) that the third quarter of the year, when oranges and palm fruit are heavily exploited, may include more vegetable calories in the diet than the other three quarters. No significant differences are found in the calories





123

Mean Daily Calories Vegetables per Consumer



124

of meat consumed during the different quarters but the fourth quarter shows a significantly (or nearly significantly) greater number of total calories consumed daily than for the other three quarters. Although the absolute amount of meat in the diet did not differ significantly between yearly quarters, the relative percentage of calories provided by meat was significantly greater during the second quarter than the other three quarters  $(p < .01$  for all). This is because honey peaks in the fourth and first quarters and vegetable items peak in the third quarter. 6

Many vegetable resources are only in season for a short time and, therefore, differences between yearly quarters for individual resources can be determined directly from Fig. 8. The major vegetable resources are oranges *( Casmiroa sinensis)* and palm fruit *(Arecastrum romanzolfianum)*  in the second and third quarters, and virella *(Campomanesia zanthocarpa)*  and kurilla *(Rheedia brasilense)* in the fourth quarter. Larva appear to be less abundant during the fourth quarter; however, due to small sample size, the differences are not significant. The oranges are not native to South America, but were brought into eastern Paraguay by the Jesuits in the 16th and 17th century and the seeds were subsequently spread into the forest by birds and monkeys. Palm products, particularly of the species *Arecastrum romanzolfianum,* are the most consistent vegetable resource in the diet. Palm fiber and heart are consumed throughout the year in significant quantities. All types of honey show the same pattern of seasonal difference as described above for honey in general.

Game items are generally available throughout the year and although there is considerable variance in consumption of individual resources from trip to trip, there is no significant seasonal difference for most items. The one exception to this is the teju lizard (not identified) which, as mentioned earlier, seems to be prevalent only at the beginning of the warm season. The amount of large game (deer and peccaries) in the diet fluctuates considerably but shows no significant seasonal trend and makes up a yearly mean of 36% of the meat in the diet. Capuchin monkeys, providing 19% of all meat calories, are the most consistent game item in the diet and also the only other resource besides large game (and birds which are insignificant) that is hunted using bow and arrows. The meat resources numbered 64-79

<sup>6</sup>Food consumption on each individual day is treated as an independent measurement. Since the members of a foraging trip, general location, weather, and possible other parameters are probably not completely independent from one day to the next the assumption of independence is probably not warranted. Unfortunately, culling data (using for example, every fifth data point) or lumping data (using only the mean from each trip) would result in too few data points to do meaningful statistical tests. Future fieldwork expanding the data set should allow us to determine if nonindependence of measurements has caused us to attribute a difference to seasonal effect when, in fact, it is due to some other factor.

in Fig. 6 are hunted by hand or with a digging stick. The hand-hunted component of the meat items is quite significant and makes up a yearly mean of 45% of the total meat taken. Ache informants reported that armadillos are dug out of their burrows only in the end of the warm season when they are fat (at other times they will be pursued if encountered above ground only) and we observed that this was partially true. Nevertheless, the number of calories provided by armadillos is not significantly different across seasons in our yearly sample unless adjustments are made for fat content (see discussion).

The major conclusions of this section are (1) there is high seasonal variance in the species of vegetable (or collected) item exploited, but not much variance in the absolute number of calories that vegetables provide, (2) the relative contribution of different species of honey exploited does not vary, but the absolute amount of honey in the diet shows high seasonal variance, (3) there is very little variation in the meat component of the diet throughout the year, and (4) the Ache seem to consume slightly more calories during the warm wet season than during the rest of the year, due to an abundance of honey at that time.

# **DISCUSSION**

We reported previously (Hawkes *et al.,* 1982) that Ache foragers consumed about 3600 calories daily per capita and that the greatest part of these calories was provided by meat. That study, however, covered only 3.5 months of I year and therefore we were reluctant to generalize. The current study allows us to generalize to at least 1 year, and given the weather data collected over a several year period, may be representative of other years. Temperature, which partially determines seasonality, is quite consistent from year to year. Rainfall fluctuates erratically, but appears (at least on a monthly basis) to have very little effect on the major component of Ache diet, meat. Differences in yearly rainfall pattern could have considerable effect on the vegetable or honey component of the diet so we must be cautions about generalizing for these resources.

It is of some interest that no significant differences were found for any resource class (meat, honey, and vegetable) between 1980-1982 during the 1 month (April) that was sampled both years. A single vegetable species, palm fruit, did seem considerably more important in this overlap period during 1980 than in 1982, and the difference between the two years for this resource was significant ( $t = 2.16$ ;  $p = .037$ ). Because this overlap period occurred at the onset of the palm fruit season, however, we were not able to determine if the fruit was actually taken in lower quantities in 1982 or if it was simply later in maturing.

The data suggest that meat is consistently the most important resource in the Ache diet and usually provides more than 50% of the calories consumed. As we pointed out previously (Hawkes et al., 1982), this contradicts widely held notions about hunter-gatherer diets in low latitudes. The *caloric*  importance of game probably becomes considerably greater during the end of the warm season and beginning of the cold season when most game animals are quite fat. Pacas, coatis, and armadillos which are all lean during the early warm wet season, later put on layers of fat greater than 1 inch in thickness. Since the total body weight of these animals is small, the relative proportion of fat is tremendously high, compared to that of larger animals. We have not adjusted the caloric value of meat during this period, as field measurements of fat content were not performed.

Measurements on wild ungulates have shown that fat content fluctuates from about  $2\%$  in the lean season to perhaps  $10\%$  in the fat season (Speth and Speilmann, 1983). The game which the Ache take, however, consists primarily of peccaries, rodents, armadillos, and monkeys, which have a thicker fat layer than most wild ungulates (the Ache consider deer to be the leanest of all game items). It is our impression that the seasonal differences in fat content of Ache game animals are more similar to the difference between thin and fat pork.

The *Food Composition, Table for Use in Latin America* (Leung, 1961) lists whole pork at 1940, 2160, 2700, and 3760 cal/kg for thin, medium fat, fat, and very fat, respectively. This is an increase of  $11\%$ , 39%, and 94% in caloric content for medium fat, fat, and very fat animals. The change in ungulates from  $2\n-10\%$  fat is an increase of 61% in caloric content (the relative change is greater because they are leaner to start with). If we use the mean of the difference between thin, medium fat, and fat pork as a guideline for the difference in Ache game animals between the thin time of the year (beginning of the warm season) and the fat time (beginning of the cold season), then calorie equivalents for game items the Ache exploit should be adjusted upwards about  $25\%$  in April, May, and June.<sup>7</sup> This would of course raise the total calories available to consumers during that period, and the relative importance of meat in the diet.

Honey appears to be considerably more abundant in the early part of the warm wet season and, according to Ache reports, this is due to the abundance of flowers during that part of the year. Some vegetable items and larva are consumed in every yearly quarter and three of the four quarters show major vegetable peaks. Two of the three major vegetable peaks are due to fruits that are frequently found in large groves. These peaks appear to be

7Since the animals are thin for about 9 months and only fat for 3 months of the year, we assume caloric values reported are probably for thin animals.





accompanied by an increase in number of days spent at one campsite before moving. This will be further investigated in subsequent field work.

Based on our sample, we would conclude that a small number of resources provide the great bulk of the Ache diet. Indeed, only seven game species, one type of honey, six vegetable resources, and three types of insect larva provide almost all the calories consumed over a yearly cycle. This can be contrasted to the 52 game spedes, eight types of honey, 34 vegetable resources, and 12 types of larva and insects that we have actually seen consumed, or to food lists from informants that would double the number of resources again. Lengthy food lists of all resources ever-exploited may be of very limited use in understanding the basic economy of foraging peoples.

The total number of calories consumed daily that we report here seem somewhat astounding in light of the considerably lower numbers reported for other hunter-gatherers (Bose, 1964 as calculated in Meehan, 1975; Hart, 1978; Lee, 1979; Jones, 1980; Tanaka, 1980; Wilmsen 1982). Some South American horticulturalists are also reported to consume considerably fewer calories than the Ache (Lizot, 1978), although others show caloric needs not far below ache consumption levels (Montgomery and Johnson, 1977). Several things are associated with the differences. First, the Ache (both men and women), while almost exactly the same height as the !Kung or the Yanomamo, for example, weigh an average of about 10 kg more (Table IV). This is about a 20-25% difference in body weight. Second, nutritional studies have demonstrated that people consuming high protein diets have metabolic rates that can be as high as 30% above those consuming lower protein diets (see Taylor and Pye, 1966; Speth and Speilmann, 1983). The Specific Dynamic Action value of food for the Ache diet is probably around 10%, however, due to their consumption levels of carbohydrate. In addition, the caloric requirements of pregnancy and lactation must be taken into ac-

count. During the foraging days sampled in 1981-1982, 16% of the women days represent pregnant women,  $36\%$  are lactating women, and  $2\%$  are both. Using an increase of 200 calories per day for pregnancy and 1000 calories per day for lactation (Taylor and Pye, 1966, p. 463), we get an overall increase of 416 calories per day for the needs of the adult female population. These factors combined lead to inactive metabolic requirements of about 1591 calories for adult males and 1756 calories for adult females (Calculated as in Taylor and Pye 1966, pp. 45-49; see Table V).

Second, and of equal importance, is the difference in activity regime between the Ache and several other reported groups. Ache men hunt every day (except in extreme weather) and spend an average of 6.9 hr daily in resource acquisition (Hill and Hawkes, 1983; Hill, 1983). In addition they work on tools and food processing virtually every day. The period of time spent foraging is very strenuous, and those of us who sampled men's activities had a very difficult time keeping up even though we expended considerably less energy than did our Ache counterparts. Women's days are less strenuous but are not easy. Because camp moves every day women frequently carry heavy loads through dense jungle. Most women carry one child and it is not unusual for them to carry two. Women's carrying baskets contain all possessions and whatever food is being transported. Although baskets usually weigh between 5-15 kg, we have recorded them weighing more than 40 kg.

Caloric expenditure for different activities is quite difficult to determine when the activities are not analogous to those that have been monitored in modern populations. Specifically, the caloric expenditure of transportation through thick jungle is difficult to ascertain. Montgomery and Johnson (1977) measured the caloric expenditure of several activities in a native population of tropical Peru. We rely on their numbers and those in Taylor and Pye (1966), along with our activity data (Hill, 1983; Hurtado, unpublished manuscript), to make the rough estimate that Ache men probably use 3301 calories per day in activity expenditure, and Ache women probably use about 1414 calories (Table V). This gives a total daily caloric requirement of 4892 calories for men and 3170 calories for women. These numbers are quite rough and they are presented only as a tentative but plausible explanation for the consumption levels we observe. In light of the difficulties in accurately calculating human food needs, attempts to further refine caloric requirements would be premature at this time.

Before beginning our 1981-1982 field period, we were aware of the high caloric consumption of Ache foragers and, therefore, decided to weigh all members of foraging bands at the beginning and end of each foraging trip in order to determine if the Ache were storing excess energy from foraging in the form of fat. Since humans gain 1 kg body fat for every 7700 calories excess consumption (Taylor and Pye 1966, p. 368), we might expect





has indicated for high protein diets in Taylor and Pye (1966, pp. 39-40, and Speth and Speilmann (1983). "Assume mean age of 30 years for adult. Calculations follow Taylor and Pye (1966, pp. 23 -25).<br>
"As indicated for high protein diets in Taylor and Pye (1966, pp. 39-40, and Spelimann (1983).<br>
"Taylor and Pye (1966, p. 463 ~Assume mean age of 30 years for adult. Calculations follow Taylor and Pye (1966, pp. 23 -25). Taylor and Pye (1966, p. 463)  $\times$  16% pregnant, 36% lactating, 2% both.

aEstimated from Hill (1983) and Hurtado *el al.* (unpublished manuscript). From Montgomery and Johnson (1977; calories above basal metabolism).

 $\overline{\phantom{a}}$ 

individual Ache to gain about .8 kg on a 10-day foraging trip if their true caloric needs were only 2500 cal/day and they were actually consuming 4000 cal/day. Analysis of six foraging trips ranging from 6-14 days using a paired t-test showed that weight change was not significant for the population as a whole  $({\bar X} = +.06 \text{ kg}, n = 127, t = 0.57, p = .57)$ . This would suggest that Ache caloric needs are as high as the levels of consumption we observed. Within the population, however, there were some interesting differences. Men lost weight on all but one trip and pooling all data, their weight loss is very significant ( $x = -0.58$  kg,  $n = 45$ ,  $t = -2.97$ ,  $p = .005$ ). Women, in contrast, gained weight on all but one trip, and the results when pooled were also significant  $(x = +0.38 \text{ kg}, n = 32, t = 2.19, p = .036)$ . Children gained weight on all but one trip; however, the results were not significant  $(x = +.14 \text{ kg}, n = 50, t = 1.16, p = .25)$ . The fact that caloric needs estimated for men (Table V) are considerably higher than the mean calories available for all trips, and the caloric needs estimated for women are lower than the mean daily calories available, is quite suggestive. The weight data indicate that men did not quite consume: as much energy as they expended, while women consumed a slight excess. Since body weights were observed to change during foraging trips, we must also conclude that either current body weights at the mission, or male and female consumption and energy expenditure in the forest, are not perfectly representative of precontact times. It is not clear, however, how far the observed trend in weight change would continue before a new equilibrium was reached.

The input-output energy balance that we report for the Ache is likely to be somewhat controversial because of the exceptionally high numbers. Nevertheless, both consumption and energy expenditure calculations are based on quantitative field measurements. Durnin *et al.* (1973) have concluded, on the basis of extensive research and literature review, that "energy requirements of man and his balance of intake and expenditure are not known." The Ache are perhaps another puzzling example of this. Nevertheless, there is some precedent from artic foragers for the numbers in the Ache range. Several different types of Eskimo day hunts are reported to result in daily energy expenditure of greater than 4,000 calories (Shepard and Godin, 1976). In addition, several types of industrial work may result in caloric expenditure of more than 4000 calories per day (Taylor and Pye, 1966, p.49). We therefore conclude that our numbers, while impressive, are within reasonable limits for very active populations.

The startling difference between Ache consumption and activity pattern and that of-the !Kung, for example, leads to some very interesting questions. At permanent water hole camps, the !Kung are relatively inactive compared to the Ache. !Kung men only hunt about 1 day in 3 (Lee, 1979) and women gather only about 3 days per week. The relative inactivity of the !Kung is correlated with a much lower caloric intake which, in turn, pro-

duces a much thinner population (however, see Hill, 1983 for calculations of !Kung activity levels in the bush). The Ache, on the other hand, are extremely active and robust and consume considerably more calories.<sup>8</sup> It could be argued that Ache consumption might be quite a bit lower if they were less active, thinner, or both. This argument is circular yet true, and points out that different ecological circumstances may lead to different time-energy strategies. The adaptive significance for these alternatives has yet to be determined. However, at least one model based on heat stress in the Kalahari desert has been proposed (Blurton Jones and Sibly, 1978). The heat-humidity regime tolerated by the !Kung may not allow an activity level comparable to that of the Ache. Another relevant finding is the fact that Ache men gain weight at the mission within the first week after returning from a foraging trip ( $x = .67$  kg,  $n = 22$ ,  $t = 3.03$ ,  $p < .01$ ) and yet they appear to consume fewer calories than they do in the forest (unpublished data). They also seem to show a much less strenuous activity regime at the mission (unpublished data). This suggests that activity-consumption 'strategies can change extremely rapidly with changing ecological circumstances.

## **CONCLUSION**

The Ache diet shows some seasonal variance in honey and small collected (vegetable) items which do have an effect on the seasonal means of total calories consumed. Meat is the most important component of the diet year round and does not vary significantly in absolute amount season to season. Few resources account for the bulk of the diet. There is no lean time of the year but rather the fourth quarter of the year might be considered a fat time. The number of calories consumed is certainly sufficient, and produces a healthy robust population that maintains a high activity profile. Although seasonality is of some importance, it does not seem as extreme as for many high latitude groups or those in arid environments. It is also possible that some other foragers will show even less seasonality in resource consumption than do the Ache. The importance of meat in the diet as well as the total number of calories consumed seem to contradict frequently held ideas about low latitude tropical hunter-gatherers (but see Ember, 1978). The results raise further questions about the factors responsible for the

<sup>&</sup>lt;sup>a</sup>If the Ache were compared to the !Kung during wet season (Yellen, 1976) this difference would disappear (see Hill, 1983). It should be noted that we are talking about Ache activity patterns while on foraging trips. If the time spent at the mission were included, the activity pattern would be more similar to that reported for the !Kung; however, Ache men report that they hunted virtually every day that weather permitted as full-time foragers before contact.

**observed range of energy expenditure and consumption among modern hunter-gatherers. Future investigation of the diet and activity regimes of other foraging peoples may continue to expand the documented range and variation these exhibit in different ecological settings.** 

## **REFERENCES**

Abruzzi, W. S. (1980). Flux among the Mbuti Pygmies of the Ituri Forest: An ecological interpretation. In Ross, E. (ed.), *Beyond the Myths of Culture.* Academic Press, New York.

- Adams, C. F. (1975). *Nutritive Value of American Foods in Common Units.* Agriculture Handbook 456, U.S. Department of Agriculture.
- Bertoni, M. (1941). Los Guayakies. *Revista de ia Sociedad Cientifica del Paraguay* 2: 2-62. Binford, L. (1980). Willow smoke and dog's tails. *American Antiquity* 45: 4-20.
- Blurton Jones, N. (1983). A selfish origin for human food sharing: Tolerated theft. *Ethology and Sociobioiogy* 4: 145-147.
- Blurton Jones, N., and Sibly, R. M. (1978). Testing adaptiveness of culturally determined behavior: Do Bushman women maximize their reproductive success by spacing births widely and foraging seldom? In Reynolds, V., and Blurton Jones, N. (eds.), *Human Behavior and Adaptation. Society* for Study of Human Biology Symposium #18. Teller and Francie, London.
- Bowdler, S. (1981). Hunters in the highlands: Aboriginal adaptation in the Eastern Australian Uplands. *Archeology in Oceania* 16(2): 99-111.
- Cadogan, L. (1973). Tangy Puku. Centros de Estudios Antropologicos Universidad Catolica "Nuestra Senora de la Asuncion." Asuncion del Paraguay.
- Damas, D. (1972). The copper Eskimo. In Bicchieri, M. G. (ed.), *Hunters and Gatherers Today.*  Holt, Rinehart, and Winston, New York.

Downs, J. (1966). *The Two Worlds of the Washoe.* Holt, Rinehart, and Winston, New York. Durnin, J. V. G. A., Edholm, O. G., Miller, D. S., and Waterlow, J. C. (1973). How much food does man require? *Nature* 242: 418.

- Ember, C. (1978). Myths about hunter-gatherers. *Ethnology* 17(4): 439-448.
- Foster R. B. (1973). *Seasonality of Fruit Production and Seed Fall in a Tropical Forest Ecosystem in Panama.* Ph.D. dissertation, Duke University, Durham, North Carolina.
- Gould, R. A. (1977). *Puntutjarpa Rockshelter and the Australian Desert Culture* Vol. 54, Part 1). Anthropological Papers of the American Museum of Natural History, New York.
- Harris, D. (1980). *Human Ecology in Savannah Environments.* Academic Press, London. Hart J. A. (1978). From subsistence to market: A case study of the Mbuti net hunters. *Human Ecology* 6: 325-353.
- Hawkes, K., Hill, K., and O'Connell, J. (1982). Why hunters gather: Optimal foraging and the Ache of Eastern Paraguay. *American Ethnologist* 9: 379-398.
- Hill, K. (1983). *Adult Male Subsistence Strategies among Ache Hunter-Gatherers of Paraguay.*  Unpublished Ph.D. thesis, University of Utah.
- Hill, K., and Hawkes, K. (1983). Neotropical hunting among the Ache of Eastern Paraguay. In Hames, R., and Vickers, W. (eds.), *Adaptive Responses of Native Amazonians.* Academic Press, New York.
- Hoebel, E. A. (1978). *The Cheyennes: Indians of the Great Plains.* Holt, Rinehart and Winston, New York.
- Hurtado, A. M., Hill, K., Kaplan, H., and Hawkes, K. Womens time allocation to activities among Ache hunter-gatherers of Paraguay. Department of anthropology, University of Utah, unpublished manuscript.
- Jones, R. (1980). Hunters in the Australian coastal savanah. In Harris, D. (ed.), *Human Ecology in Savannah Environments.* Academic Press, London.
- Kaplan, H., Hill, K., Hawkes, K., and Hurtado, A. M. (1984). Food sharing among Ache huntergatherers of eastern Paraguay. *Current Anthropology 25: 113-115.*

Ledger, H. P. (1968). Body composition as a basis for comparitive study of some East African mammals. *Symposia of the Zoological Society of London* 21: 289-310.

Lee, R. B. (1979). *The !Kung San.* Cambridge University Press, New York.

- Leigh, E. G., Rand, A. S., and Windsor, D. M. (eds.). (1983). *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes.* Smithsonian Press, Washington.
- Leung, W-T. W. (1961). *Food Composition Table for Use in Latin America.* National Institutes of Health, Bethesda, Maryland.
- Lizot, J. (1978). Population, resources, and warfare among the Yanomami. *Man* 12:497-517. Meehan, B. (1975). *Shell Bed to Shell Midden.* Ph.D. thesis, Australian National University, Canberra.
- Montgomery, E., and Johnson, A. (1977). Machiguenga energy expenditure. *Ecology of Food and Nutrition* 6: 97-105.
- Pitts, G. C., and Bullard, T. R. (1968). Some interspecific aspects of body composition in mammals. *National Academy of Sciences Publication* 1598: 45-70.
- Opler, P. A., Frankie, G. W., and Baker, H. G. (1976). Rainfall as a factor in the release, and anthesis by tropical trees and shrubs. *Journal of Biogeography* 3:231-236.

Schaller, G. (1972). *The Serengeti Lion.* Chicago: The University of Chicago Press.

- Shepard, R. J., and Godin, G. (1976). Energy balance of an Eskimo community. In Shepard, R. J., and Itoh, S. (eds.), *Circumpolar Health.* University of Toronto Press, Toronto.
- Speth, J. D., and Spielmann, K. A. (1983). Energy source, protein metabolism, and huntergatherer subsistence strategies. *Journal of Anthropological Archeology* 2: 1-31.
- Steward, J. H. (1938). Basin-plateau aboriginal sociopolitical groups. *Smithsonian Institution Bureau of American Ethnology Bulletin,* 120.
- Tanaka, J. (1980). *The San Hunter-Gathers of the Kalahari: A Study in Ecological Anthropology.* University of Tokyo Press, Tokoyo.

Taylor, C., and Pye, O. (1966). *The Foundations of Nutrition.* Macmillan, New York.

- Thompson, D. (1939). The seasonal factor in human culture, illustrated from the life of a contemporary nomadic group. *Proceedings of the Prehistoric Society* 5: 209-221.
- Truswell, A. S., and Hansen, J. D. L. (1976). Medical research among the !Kung. In Lee, R. B., and DeVore, I. (eds.), *Kalahari Hunter-Gatherers.* Harvard University Press, Cambridge.
- Watanabe, H. (1968). Subsistence and ecology of northern food gatherers with special references to the Ainu. In Lee, R. B., and DeVore, I. (eds.), *Man the Hunter.* AIdine, Chicago.
- Watt, B. K., Merrill, A. L., Orr, M., and Wu, W-T. (1950). *Composition of Foods-Raw, Processed, and Prepared.* Agriculture Handbook 8, U.S. Department of Agriculture.
- White, R. T., and Stallings, J. R. Claves para la identification de los Mamiferos del Paraguay. Unpublished manuscript.
- Wilmsen, E. N. (1982). Studies in diet, nutrition, and fertility among a group of Kalahari bushman in Botswana. *Social Science Information 21:* 5-125.

Yellen, J. (1976). Settlement patterns of the !Kung: An ecological perspective. In Lee, R. B.,

and DeVore, I. (eds.), Kalahari Hunter-Gatherers. Harvard University Press, Cambridge. Yesner, D. (1980). Maritime hunter-gatherers: Ecology and prehistory. *Current Anthropology*  21: 726-750.