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Demography of Termite Colonies as Related to Various Environmental Factors: Nutritional Biochemistry and Physiology of Termites

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FINAL REPORT

DEMOGRAPHY OF TERMITE COLONIES AS RELATED TO VARIOUS ENVIRONMENTAL FACTORS: NUTRITIONAL BIOCHEMISTRY AND PHYSIOLOGY OF TERMITES

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ABSTRACT

A series of studies began in 1975 on the dry-wood termite, *Marginitermes hubbardi*, with a view toward a rather complete evaluation of its role in the Sonoran Desert ecosystem. During 1975, biochemical analyses were carried out on one of its preferred host woods, the saguaro cactus (*Carnegiea gigantea*). Extensive feeding trials were also conducted to determine its rate of wood consumption. By the close of 1976, its oxygen consumption and heat production rates had been measured so that some simple energy budgets could be constructed and the energy flow through a natural population of this termite estimated. Oxygen consumption by larvae and nymphs was highly correlated ($R^2 = 0.93$) with temperature from 16 ↔ 36 C and was predicted by the equation: $Y \log_e = -7.736 + 0.424T - 0.006T^2$; where Y = μl O_2 consumed per milligram termite (fresh) per day, and T = temperature (°C). Mean O_2 consumption by actively feeding termites was 0.453 microliters per milligram per hour with an average RQ of 0.97. Heat production by *M. hubbardi* measured directly at 20 C in a modified drop-heat capacity calorimeter averaged 0.01895 calories per milligram termite (fresh) per 12 hours. Comparative values obtained indirectly by respirometry were considerably lower, averaging 0.0116 calories per milligram termite (fresh) per 12 hours. The differences were attributed to the failure of respirometry to detect heat produced by anaerobic protozoans in the termite hindgut. Energy budgets calculated for groups of 5, 10, 20 and 50 individuals maintained at 22 ↔ 32 C revealed that termites dispersed an average of 0.07 calories per milligram termite (fresh) per day. *M. hubbardi* is an effective detritivore in the Sonoran Desert where it releases nitrogen, carbon and other nutrients which otherwise would remain "locked up" in dead saguaros and other woody detritus. It also facilitates microbial decomposition through the communition of large decay-resistant woody debris. In order to evaluate their protein quality, termites were included as the sole source of nitrogen in a diet fed to weanling mice for three weeks. Although they did not sustain growth as well as a whole-egg reference protein, termites were deficient only in sulfur amino acids. The density of *M. hubbardi* colonies was measured on a 4-ha plot on the Saguaro National Monument (east) near Tucson, Arizona. The estimated termites have a potential to disperse ca. 680 kcal·ha^{-1}·yr^{-1}. This is much less than the value calculated for a common subterranean species, *Gnathamitermes perplexus* (Banks), in an Arizona grassland ecotone (1.5 x 10^6 kcal·ha^{-1}·yr^{-1}).

INTRODUCTION

This series of studies really began during the 1960's with background work on the identity, distribution, biology and behavior of the termites in Arizona. Greatly increased support through the IBP in the mid-1970's stimulated renewed interest and further studies on field populations, forgaging activities, dead-wood production and termite feeding rates, and seasonal production and swarming behavior of the winged forms. In this terminal report we conclude with details of our final investigation of food-energy relations and energy flow through a population of dry-wood termites.

All termites consume cellulose as their primary energy source. The only food for many species, notably the dry-woods of the family Kalotermitidae, is sound, decay-free dead wood. Most of the other termites are subterranean in habit and, according to their specialties, forage for dead wood, grass, plant litter, humus, roots, dung and even fungi cultured on recycled plant material within their nests.

There are two groups of organisms capable of digesting cellulose: those protozoans, mollusks and arthropods that produce their own cellulolytic enzymes; and those that possess a rich fauna and/or flora in their digestive systems which partially degrade cellulose to assimilable components. There is mounting evidence that termites belong to both groups (LaFage and Nutting, in press). This ability to utilize cellulose efficiently accounts largely for the widespread success of termites. It has been suggested that, because their potential food is so abundant, other factors such as availability of suitable nesting sites may be more limiting on the growth and dispersal of termite colonies.

Members of the Kalotermitidae are known as dry-wood termites because, with few exceptions, their nests are permanently excavated within the wood on which their colonies feed. Mature colonies rarely exceed a few thousand individuals. The ecological significance of the dry-wood termites remains poorly understood. In contrast, many of the subterranean termites, belonging largely to two other families, routinely have colonies numbering into the millions of individuals. Many recent studies have shown that subterranean termites may, at times, consume a large percentage of the annual dead wood and forage production, occasionally competing significantly with large herbivores. Yet the large, complex societies of the subterranean termites make it relatively difficult to maintain them in the laboratory, while dry-wood colonies are easily collected and cultured. For these reasons we have chosen to investigate the ecological significance of one common species of dry-wood termite, *Marginitermes hubbardi*, in the Sonoran Desert.

OBJECTIVES

Long-term objectives have been limited to, and centered around, the ecological significance of a single species of dry-wood termite as follows:

1. Determine the nutritive suitability of the termite as food for predators.
2. Assess the role of the termite in the detritus cycle.

Supporting objectives during the final phase of the research on this termite have been:

1. To measure O_2 consumption and heat production.
2. To estimate the composition of the termite's biomass and fecal material in terms of (all or part) calorific content, moisture, ash, C, N, amino acid and lipid content.
3. To determine suitability of termites as a source of dietary protein.
4. To construct energy budgets for small groups.
5. To estimate the annual energy flow through a field population of this dry-wood termite.

METHODS

The Dry-Wood Termite -- *Marginitermes hubbardi* (Banks)

This is probably the most common dry-wood species in the Sonoran Desert. It ranges through central and southern Arizona below ca. 1000 m, adjacent southeastern California, over much of Baja California and the western coast of Mexico, south at least to the city of Colima. It attacks dead branches, stumps and logs of many trees in riparian situations, but favors dead paloverde and saguaro skeletons in the desert. It is also a destructive "house termite."

Termites used in these studies were collected from dead saguaros found along the roads in the vicinity of the Silverbell Validation Site near Tucson, Arizona. Wood samples were taken here at the same time. Information used in estimating energy flow through a natural population of this termite was gathered from a 4-ha plot in section 17 of Saguaro National Monument (east; SNME) near Tucson.

Oxygen Consumption

Fundamental to the understanding of animal energetics is the knowledge that animals dissipate heat as a result of their incomplete utilization of food. Both direct and indirect methods have been developed to measure heat loss. Direct methods always require total enclosure of the animal and involve measurement of temperature rise in some type of surrounding medium. Indirect methods are more widely used owing to their simplicity and reliability. If the protein:carbohydrate:fat ratio of the food being metabolized is known, heat production can be calculated by measuring the liters of O_2 consumed or CO_2 produced (Brody 1945). An animal consuming a 100% carbohydrate diet emits 5.047 kcal for each liter of O_2 respired. Because *M. hubbardi* normally consumes a diet which is close to 100% carbohydrate, it would appear that indirect calorimetry would be a valid method to determine heat production. A constant-pressure differential respirometer (Gilson Medical Electronics, Inc., model GRP20) was used to measure O_2 consumption directly and CO_2 production indirectly for groups of 5 or 10 *M. hubbardi*. Each group incuded one soldier in addition to four or nine nymphs and/or large larvae. Four physiological states were examined: normally faunated/starving, defaunated/starving, normally faunated/feeding and defaunated/feeding.

Normally faunated *M. hubbardi* contain four protozoan species and a variety of bacterial forms are present in awesome numbers. Cleveland (1925) demonstrated that termites held for 1.5 hr at 45 psi O_2 lose their protozoans but they themselves suffer no adverse physiological consequences. When *M. hubbardi* is so treated, the entire protozoan faunule as well as a substantial proportion of the bacteria are killed. Defaunated termites may be completely refaunated and reflorated within 24 hr after being held with normally faunated individuals. Refaunated termites behave normally and appear to suffer no ill effects from the defaunation-refaunation process.

Each group size-temperature treatment combination was tested for 8-12 hr at 16, 20, 24, 26, 28, 30 and 32 C. The respirometer had 18 functioning manometers, which provided space for 14 experimental and 4 control flasks. All measurements were made on termites held in 15-ml reaction flasks containing an internal reservoir and a single side bulb. Flasks containing groups on which O_2 consumption was to be measured contained a few ml of 10% KOH solution (for absorbing CO_2) and a small piece of fluted filter paper in the central reservoir. Those used in conjunction with the indirect method of measuring CO_2 production contained no KOH (Umbreit et al. 1972). Several small saguaro chips were added to the flasks containing feeding termites, while starving groups were provided with small pieces of rubber tubing for footing.

Barometric pressure and room temperature were recorded at the beginning of each 8-12 hr experiment. Gas uptake measurements were recorded hourly and the readings corrected to STP using the following formula:

$$\text{true gas change} = [273(P - P_W)\,\Delta V_g]/760T$$

where P = barometric pressure in mm Hg corrected for temperature and latitude; P_W = vapor pressure of water at temperature T; T = temperature in °K at the level of the manometer; and V_g = μl of gas change measured.

A total of 672 replicates were tested. A computer program was written to reduce the resulting hourly readings to STP and check linearity of gas-consumption rates over time. Final results were expressed as average μl of O_2 consumed per mg termite (fresh wt) per hr. Respiratory quotients (RQ's) were calculated according to the method described by Umbreit et al. (1972). Gas exchange data were examined by an analysis of variance utilizing a completely randomized design with a factorial selection of treatments. Means were tested for significance at the $\alpha = 0.05$ level and separated using Student-Newman-Keul's test. Regression equations were developed by the method of orthogonal polynomials (Little and Hills 1972).

Termite Thermogenesis

The gradient-type calorimeter has been used for many years for direct mesurements of heat production under equilibrium conditions (Hammel and Hardy 1963). The early instruments were relatively insensitive to rapid fluctuations in heat formation owing to low thermal

conductivity of the air-space gradient layer. As such, these instruments were well suited only to studies on rather large animals over long periods. Prat (1954) described a modified Calvet-type microcalorimeter suitable for measureing the heat production of very small animals, bacteria, germinating seed and other tissues. A commercially produced version of this instrument is currently available from Setaram, Lyons, France. More recently, Peakin (1973) used a modified LKB® flow microcalorimeter to study the costs of maintenance in terrestrial poikilotherms. A precise drop-heat capacity calorimeter similar to the one described by Konicek et al. (1971) has been constructed by Dr. J. A. Rupley in the University of Arizona Chemistry Department. This instrument was made available for a study of *M. hubbardi*. Heat production from individuals and groups of five termites was measured at 20 C for 18-24 hr. The sample ampoule in which the termites were tested has a total gas capacity of 5 cc. It was fabricated from stainless steel tubing (0.3-mm wall thickness) and was fitted with a Teflon seal. A simple mechanical lift was used to lower the ampoule into the calorimeter which was allowed to equilibrate for 4 hr or longer to obtain a stable baseline on a 1-mv recorder. The voltage signal output from the calorimeter was amplified with a microammeter (Keithley, model 150B). The amplified signal was sensed by a digital voltmeter (SE Laboratories, model SM213, DVM), integrated every 10 sec, and recorded on paper tape. The tape was read at the University of Arizona Computer Center and the data reduced with a computer program to calories produced. A continuous record of the amplified signal was produced on the 1-mv recorder. Seventeen experiments, each lasting 18-24 hr, were executed with groups consisting of four large larvae or young nymphs and a single soldier. Because normally faunated and defaunated termites were tested while feeding or starving, the relative contributions of host and symbiote to total heat production and the heat increment (Harris 1966) could be estimated. Six additional experiments were performed on single nymphs or soldiers. Where appropriate, the heat production data were subjected to a one-way analysis of variance. Treatment means were separated at the $\alpha = 0.05$ level, using the least significant difference (Steel and Torrie 1960).

Energy Budgets for Laboratory Feeding Groups

Total energy budgets were constructed where possible for all laboratory feeding groups. When more than one replicate was run on a treatment combination involving group size and temperature, mean values were used to calculate budgets. Respiration figures were estimated from indirect calorimetry unless otherwise noted. The following general formula adopts the notation presented by Petrusewicz (1967):

$$C = R + P + FU$$

where

C = ingestion
R = respiration
P = production
FU = egestion (rejecta)

Trophic Level Interactions

The a priori observation that organisms interact with other organisms in both higher and lower trophic levels leads to the inevitable conclusion that energy must flow through ecosystems. Efforts were made to assess the energy flow from *M. hubbardi* populations to higher trophic levels through predation and to lower trophic levels as a result of death and egestion.

Lower Level Interactions

Microorganisms are responsible for a large proportion of the energy flow through any ecosystem (Phillipson 1966). Detritivores represent an intermediate trophic grouping between the decomposers and autotrophs. As such, they facilitate the activity of microorganisms by comminuting litter. It is not clear how, or even if, they alter litter chemically.

A certain amount of material removed by a population from a higher trophic level may be wasted. *M. hubbardi* appears to produce a fine sawdust-like residue while feeding on saguaro. This material was collected and weighed for each intermediate and large feeding group. A total of 123.5 mg collected from the 60 intermediate groups tested represented only 0.27% of the material removed (MR) from the saguaro discs and was thus ignored in subsequent calculations.

Egestion was another variable measured during the intermediate and large laboratory feeding experiments. Nitrogen, lignin and calorific content, important indicators of nutritional quality, were determined for several fecal-pellet samples obtained from the intermediate feeding groups. Nitrogen was determined by the method described by Rennie (1965), lignin by the acetyl bromide method (Johnson et al. 1961) and calorific content by oxygen-bomb calorimetry. In addition, several very small (2-8 mg) fecal-pellet samples were analyzed for calorific content using a commercial version of the Phillipson microbomb calorimeter (Gentry Instruments, Inc.) according to the manufacturer's recommended procedures.

Although the resultant data are not easily projected for field estimates, biomass records were kept of all dead termite bodies, exuviae and carton produced by the intermediate and large feeding groups. The calorific content of carton was measured.

Termites as Prey

No direct estimates were attempted of annual alate production by *M. hubbardi* or of the loss to predators. However, a series of chemical and biological studies were carried out to assess the nutritional quality of termites.

Chemical Assays—Owing to their cryptic behavior, termites remain well protected from potential predators except during dispersal flights. Ants occasionally penetrate termite galleries to feed upon the wingless castes. It was

necessary, therefore, to determine the nutritional characteristics of larvae, young and old nymphs, and soldiers.

There is no general agreement on a standard method for determining the moisture content of biological meterials. High drying temperatures (> 100 C) may cause a loss in the calorific content of tissues containing large amounts of fat (Wiegert 1968). To avoid this, samples were dried for 7 days at 60 C. Unless stated otherwise, all chemical analyses were carried out on termites dried in this manner.

Two 50-mg samples from each caste were analyzed to determine their carbon content with a high-frequency induction furnace (Leco, Inc.), according to the method outlined by Allison et al. (1965). Samples were weighed into tared ceramic crucibles and a catalyst containing iron, copper and tin was added. The crucible was inserted into the furnace and burned in a stream of oxygen for 3 min. Carbon dioxide released during combustion was trapped in an Ascarite® bulb which was weighed after each combustion. The weight gained by the bulb represented CO_2 (proportionate to carbon) released from the sample. Blanks consisting of a crucible and catalyst were combusted periodically to determine CO_2 absorbed by the Ascarite® bulb from the atmosphere. After every seven determinations, a glycine sample was analyzed to determine recovery efficiency.

Eleven samples (ca. 100-500 mg each), representing each of the castes, were analyzed for inorganic mineral content (ash). Samples weighed into tared ceramic crucibles were burned in a muffle furnace (Thermo Electric Co., model F-1740) at 550 C for 18 hr. The oven was turned off and allowed to cool before the crucibles were transferred to a desiccating jar containing indicating Drierite®. The ash samples were weighed after an additional 24 hr.

Several appropriately sized samples from each caste were ignited in an oxygen-bomb calorimeter (Parr Instrument Co., model 1221) to measure heat of combustion, i.e., total calorific content (A3UNE17). After loading the sample, the bomb was charged with O_2 at 30 psi and immersed in a water jacket. The system was closed and allowed to equilibrate before firing. Corrections for heat generated from the fuse wire and formation of H_2SO_4 and HNO_3 in the bomb were applied to the observed heat rise of the water surrounding the bomb.

Micro-Kjeldahl digestions were performed on 20-50 mg termite samples in 30-mm Kjeldahl flasks (A3UNE15). Two ml of digesting solution [H_2SO_4 and H_3PO_4 (1:3 v/v) and ca. 20 mg of catalyst (0.125 g methyl red, 0.0825 g methylene blue, 100 ml ethanol)] were added and slow heating commenced on electric digesting racks. Digestions were complete after 2 hr.

Total amino acids were quantified using the same procedure for the woody tissues (Scurfield and Nicholls 1970), except that smaller samples (100 mg) were analyzed (A3UNE15). An alternate procedure (LaFage et al. 1974) which employed sealed hydrolysis tubes was used for early determinations. Total lipids were measured using the Goldfisch apparatus (Arthur H. Thomas Co., 6-unit model). Termite samples initially weighing 0.4-3.2 g were extracted continuously for 6 hr with ca. 40 ml of ethyl ether, dried, and reweighed. The fatty acids of these lipids were identified and measured using the following procedure.

Fatty-acid methyl esters were identified and measured using a gas chromatograph (Tracor, model MT220) equipped with a flame-ionization detector. A 6-ft glass column (1/4-inch ID) was packed with 15% EGSS-Y (Applied Sci. Lab., Inc.), a copolymer of ethylene glycol succinate containing methyl-silicone, on 100/120 mesh Chromosorb AW-DMCS (Supelco, Inc.) as suggested by Christie (1973). The carrier gas, nitrogen, was delivered with a head pressure of 40 psi and a flow rate of 70 ml/min. The column was held at 170 C (isothermal) and the detector temperature was 250 C. Straight-chain, even-numbered methyl esters of fatty acids from C_8 to $C_{18:3}$ (Supelco, Inc.) were used as internal standards. Methyl esters prepared from the dried insects were injected into the gas chromatograph in hexane with a 1-μl syringe (Hamilton Co., model 7101N). Peak areas were measured by triangulation (Bartlet and Iverson 1966) and results expressed as percentages of total fatty acids in the sample.

Biological Assay—Although the analyses outlined in the previous section can rapidly provide useful information about the nutritional characteristics of a particular food, they fail to answer a number of questions, especially regarding digestibility. The capacity of a food source to support animal growth is often considered the most important measure of nutritional quality. Generally this capacity is directly dependent on the amino acid composition of the protein in food (Eggum 1970). It was not possible to collect sufficient *M. hubbardi* to carry out practical feeding trials, nor to find a method for performing such trials with any of its known predators. Munck (1970) recognized several advantages in using mice as test animals for screening protein quality: well-defined breeding stocks are available; they require much less food than rats or chickens more commonly used in such experiments; and their protein requirements correlate well with those of the rat. Since the amino acid composition of *M. hubbardi* is remarkably similar to that of *Reticulitermes flavipes* (Table 1), the latter species was considered suitable for the determination of termite protein quality. Fourteen mice (Charles River CD-1), weaned at an age of ca. 20 days, were paired (1 male, 1 female) and fed a diet containing *R. flavipes* as the sole nitrogen source ad libitum. The complete diet is described in Table 2. Food intake was monitored and the supply replenished twice weekly. The mice were weighed weekly. The results were compared with values obtained from feeding a whole-egg control diet to similar mice. Several indices of protein quality were calculated, including protein efficiency ratio (PER; Sebrell 1963), net protein retention (NPR; Bender and Doell 1957), protein score (Frost 1959) and essential amino acid index (EAAI; Oser 1959).

Table 1. The amino acid composition of two termite species; values represent the percentage of total amino acids in the sample

	Marginitermes hubbardi						*Reticulitermes flavipes*
Amino Acid	Alate (St)[a]	Alate (Ot)	Old Nymph (Ot)	Young Nymph (Ot)	Larva (Ot)	Soldier (Ot)	Mixed Castes (Ot)
Lysine	6.1[b]	5.3	5.7	5.9	5.5	4.2	5.6
Histidine	2.9	2.4	2.3	2.4	2.2	2.2	2.3
Arginine	5.9	4.2	3.9	4.3	4.1	3.8	4.1
Aspartic Acid	8.2	8.6	8.5	9.0	8.5	7.4	8.3
Threonine	3.9	4.9	5.1	4.8	5.3	5.3	5.2
Serine	3.4	5.2	5.2	5.0	4.6	4.4	5.1
Glutamic Acid	12.6	11.7	10.6	10.5	10.6	9.4	11.3
Proline	6.6	7.4	6.9	6.4	7.5	7.0	6.7
Glycine	12.0	10.8	9.3	13.3	13.6	13.0	10.4
Alanine	8.7	11.9	10.8	10.7	11.5	16.3	11.9
Cystine	0.0	0.0	0.0	0.4	0.4	0.0	0.6
Valine	6.4	7.1	7.0	6.4	6.4	6.9	7.4
Methionine	1.6	1.8	2.1	1.8	1.5	1.2	1.7
Isoleucine	4.7	4.6	4.7	4.5	4.7	4.9	4.8
Leucine	7.6	7.6	7.6	7.2	7.0	7.4	7.6
Tyrosine	5.7	4.0	5.9	4.7	4.6	4.3	4.4
Phenylalanine	3.8	3.3	3.9	3.5	3.0	2.3	3.1
% AA[c]	--	40.17	29.84	38.89	39.93	49.90	51.60
% EAA[d]	--	42.76	40.67	44.39	46.21	35.84	53.76

[a] St = Sealed hydrolysis tube; Ot = open hydrolysis tube.

[b] Values are means for 2-10 replicates/sample.

[c] % AA = Total amino acids as a percentage of sample weight (dwb).

[d] % EAA = Percentage of total amino acids that are dietary essentials.

Estimates of Energy Flow Through a Field Population

The possibility of using laboratory measurements to estimate energy flow through a field population of *M. hubbardi* was not foreseen during the early stages of this study. However, when it was learned that long-term records on the demography of a saguaro forest were available (Alcorn, pers. comm.), it appeared that energy flow estimates might indeed be possible.

During 1941-42, six 4-ha plots on SNME were selected to study population dynamics of the saguaro cactus (Alcorn and May 1962). At that time, maps were prepared which identified the location of every saguaro on the 24-ha study area. The plots were inspected annually and records made of the location of saguaros which had died during the previous year. It was possible to inspect the total population of dead saguaros on plot F2 during a single morning in June 1976. On the basis of previous experience, each skeleton was assigned to one of three categories (A, B, C) according to the following criteria: **Group A** included plants which were considered too young to support *M. hubbardi* (LaFage 1976). Typically these skeletons remain upright with a firm footing in the soil although the plant may have been downed by wind or lightning. The basal third or more is generally covered with intact, but very dry, cortex. Also in this region, an abundance of fibrous material (dried pith) adheres to the ribs. **Group B** skeletons retain less or, at times, no intact cortex, less fibrous material and, if standing, a loose and easily disturbed footing in the soil. Quite often they have become dislodged and lie on the soil surface or propped up against some other vegetation. There remains, in practically every instance, a soil connection with part of the root system. Those skeletons that rest on the surface often have been attacked by subterranean termites at points of soil contact. Group B skeletons frequently contain one or more *M. hubbardi* colonies. **Group C** plants are older and more decayed than the others. They are always prone, rarely retain soil connections with the root system, and at times have lost their roots and basal sections completely. In advanced decay, little structural integrity remains; ribs are fragmented, and the assaults of weather and fungi are extensive. Skeletons in this category never contain active colonies of *M. hubbardi*, but often show evidence that they did at an earlier time. Due to the potential for future study, it would not have been prudent to dismantle the skeletons on this study plot to verify the presence or absence of *M. hubbardi*. Every skeleton assigned to category B is assumed to contain an active *M. hubbardi* colony.

Table 2. Constituents of diet fed to seven pairs of weanling mice for 21 days to assess the quality of *Reticulitermes flavipes* protein

Ingredient	Amount	Percentage
R. flavipes	233.3	10.9
Corn oil	57.0	2.7
Cerelose	1396.7	65.3
Cellulose	297.2	13.9
NaCl	7.6	0.4
Purified Vitamin Mix	76.0	3.6
Dicalcium Phosphate (USP)	57.0	2.7
Trace Mineral Mix	3.8	0.2
Potassium chloride	3.8	0.2
Choline chloride (50%)	3.8	0.2
Cr_2O_3	3.8	0.2
Total	2140.0	100.0

Percent Crude Protein
Termite = 64.20
Diet = 7.00
Percent Crude Fat
Termite = 12.37
Diet = 4.00
Metabolizable energy supplied by diet = 3.086 kcal/g dry wt.
% Calcium = 1.00
% Available phosphorus = 0.5

Nutting (1969) reported actual counts of individuals present in 10 *M. hubbardi* colonies. The mean of these counts was used as an estimate of individuals per colony in this study. The caste composition of a large number of groups from field colonies was recorded during the present study. In addition, calorific values were determined for each caste. Sellers (1960) presented mean annual air temperatures for Tucson between 1895 and 1960. The consumption rate at 22 C for a large group (500 individuals) of *M. hubbardi* was judged to be the closest estimate of a mean annual field consumption rate. Collectively, the preceding information permitted an estimate of total calories dispersed and stored by *M. hubbardi* on the F2 plot during a single year.

RESULTS

Oxygen Consumption

The results of 336 oxygen-consumption tests, each lasting 8-12 hr, are presented in Table 3. These values are means for the total duration of the experiments. There appears to be no standard for expressing metabolic activity, although dry weight, fat-free dry weight, unit-protein nitrogen content and fresh weight are measures often encountered in the literature. Since "dry" tissue is almost always partially hydrated, Keister and Buck (1974) suggest that fresh weight is as good a measure as any. As it was not possible to obtain initial dry weights for the groups, oxygen consumption is expressed in terms of fresh weight.

To estimate an oxy-caloric equivalent (Brody 1945), it is necessary to know the chemical nature of nutrients being metabolized by the termites. A respiratory quotient (CO_2 evolved ÷ O_2 consumed) near 1.0 suggests that carbohydrate is being utilized. Starving animals, deriving their energy exclusively from stored fat, show RQ's near 0.7. The consumption of mixed protein produces RQ's around 0.83. The mean RQ for normally faunated *M. hubbardi* (Table 3) was 0.97. This is sufficiently close to 1.00 to select 5.05 kcal/l O_2 as the oxy-caloric equivalent. As the O_2 consumption rates reported in Table 3 suggested a predictable relationship with temperature, polynomial tests for trends were attempted. The dependent variable (μl O_2·mg fresh termite^{-1}·hr^{-1}) was transformed to $\log_e$ and regressed, step-wise, on the linear, quadratic and cubic components of temperature. The resulting prediction models and their coefficients of determination (R^2's) are listed in Table 4.

Two gas chromatographic procedures were undertaken to identify hydrogen and/or methane in termite respiratory gases. Should these gases by found in large amounts, their specific calorific equivalents would necessarily have to be considered in energy budgeting. Although no serious attempt was made to assess gas production quantitatively, a few statements can be made regarding the relative rates of H_2 and CH_4 evolution. While CO_2 concentrations reached as high as 5.0% of the total gas volume of the respiratory chambers, in no case did H_2 concentrations exceed 1.0%. Methane production was equally unimpressive. The highest CH_4 concentrations measured (22 ppm) were achieved after 4 hr in a closed chamber by normally faunated/feeding groups on filter paper (Whatman No. 2). Termites which fed on saguaro wood produced less than 11 ppm CH_4. The combined H_2 and CH_4 production was less than 1% of the respiratory gas output from *M. hubbardi* and thus was not considered in energy budgeting.

Termite Thermogenesis

The results of *M. hubbardi* thermogenesis experiments are reported in Table 5 as calories produced per mg termite (fresh) per 12 hr. The period for which heat production was recorded began after a stable baseline response had been achieved by the empty calorimeter. The ampoule which housed termites during heat measurements has a gas volume of ca. 5 cc and contained enough O_2 for a 75-mg *M. hubbardi* group to survive almost 47 hr at 20 C. Since CO_2 levels would have become fatal after ca. 24 hr, heat measurements were made only during the initial 16 hr. Although termites removed from the ampoule after this period showed no immediate ill effects, they were held for observation under normal rearing conditions for several days.

Figures 1a and 1b show parts of thermograms produced by a single young nymph. The event pictured, a sudden fall and rise in heat production, is remarkably similar to a thermogram produced by *Galleria mellonella* (L.) during adult emergence (Prat 1954).

Energy Budgets for Laboratory Feeding Groups

The following equations were used to calculate energy budgets for incipient colonies, and the intermediate and large-sized laboratory feeding groups. The notation is that of Petrusewicz and Macfadyen (1970) and Petrusewicz (1967).

$$MR = C + NU$$
$$C = A + FU$$
$$A = P + R$$
$$P = G - L$$

where

- MR = material removed
- C = total intake of food during a defined time period
- A = assimilation, the sum of production and respiration
- FU = rejecta, that part of consumption not used for production and respiration
- P = production, the total amount of body tissue generated (G) by a population less weight losses (L) during a defined period of time
- R = respiration, that part of consumption converted to heat and dissipated in life processes (metabolism) during a defined period of time

Direct measurements were available for the following variables: MR, NU, C, FU and P. Respiration (R) was estimated on the basis of observed and predicted O_2 consumption (Tables 3 and 4). For incipient colonies, caste biomass was partitioned according to the percentages

Table 3. Mean oxygen consumption by groups of *Marginitermes hubbardi*. Values represent means of 14 replicate groups, each containing 5 or 10 individuals. Data were obtained by manometry and expressed as μ l O_2 consumed per mg termite (fresh wt) per hr[a]

Temperature (°C)	Feeding				Starving			
	Normally Faunated	R.Q.	Defaunated	R.Q.	Normally Faunated	R.Q.	Defaunated	R.Q.
16	0.083	1.07	0.041	0.93	0.072	0.63	0.060	1.28
20	0.225	0.97	0.176	0.76	0.145	0.75	0.114	0.76
24	0.398	0.96	0.219	0.84	0.195	0.64	0.152	0.75
28	0.578	0.96	0.378	0.85	0.202	0.69	0.224	0.79
32	0.597	0.98	0.482	0.81	0.326	0.71	0.283	0.78
36	0.839	0.85	0.542	0.75	0.399	0.69	0.456	0.71
$\bar{X}$	0.453[a]		0.306[b]		0.223[c]		0.215[d]	

[a]Means in the same row which are followed by the same letter are not significantly different at the $\alpha = 0.05$ level as determined by the Student-Newman-Keul's Multiple Range Test.

Table 4. Prediction models which estimate oxygen consumption (Y) (μ l O_2·mg fresh termite^{-1}·hr^{-1}) for the four physiological stages tested by manometry. The dependent variable, Y, is regressed on T, temperature (°C)

Treatment	Equation	R^2
Normally faunated		
Feeding	$\log_e Y = -7.737 + 0.424\ T - 0.006\ T^2$	0.927
Starving	$\log_e Y = -3.815 + 0.0830\ T$	0.891
Defaunated		
Feeding	$\log_e Y = -9.431 + 0.513\ T - 0.008\ T^2$	0.895
Starving	$\log_e Y = -4.315 + 0.0976\ T$	0.935

Table 5. Comparison of heat production by *Marginitermes hubbardi* determined by calorimetry and respirometry

Treatment Groups of 5 Termites	No. Replicates	Mean Heat Production[a] (cal·mg fresh termite^{-1}·12 hr^{-1}) (Calorimetry)	(Respirometry)
Normally Faunated			
Feeding	5	0.01895[a]	0.0116
Starving	4	0.00770[c]	0.0070
Defaunated			
Feeding	4	0.01419[b]	0.0057
Starving	4	0.00903[c]	0.0057
Single Individuals			
Large Nymph	3	0.01513	
Soldier	3	0.00768	

[a]Means followed by the same letter are not significantly different at the $\alpha = 0.05$ level as determined by the least significant difference.

[b]Oxy-caloric equivalent = 5.050 kcal/L O_2.

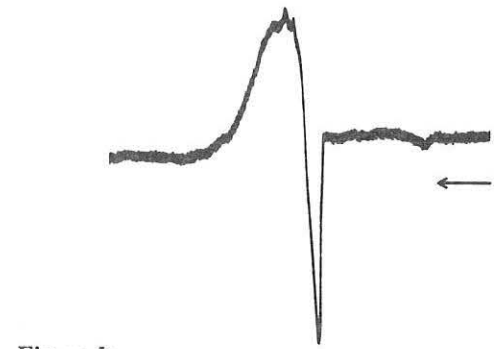

Figure 1a

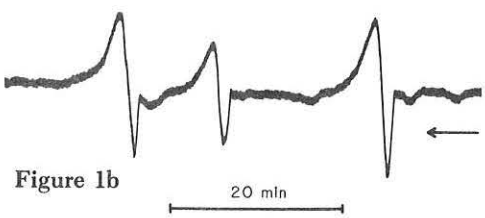

Figure 1b

Figure 1. Parts of a thermogram produced by a single, young *Marginitermes hubbardi* (Banks) nymph during a 12-hr recording of heat production. (a) Isolated event which shows maximum amplitude. (b) Three successive events of lesser intensity.

reported in Table 6. Estimates for dry weights and calorific content of termite castes were made using the values presented in Tables 7 and 8, respectively. With these data, it was possible to calculate energy budgets for all laboratory feeding groups.

Incipient Colonies

An energy budget for 16 incipient colonies was constructed. Although fecal-pellet production data were not recorded for these colonies, a regression equation had been developed earlier which predicts wood consumption on the basis of fecal-pellet production by *M. hubbardi* at 32 C. Consumption data for the incipient colonies were substituted into the following equation to predict fecal-pellet production:

$$\text{wood consumption} = 70.77 + 2.8\,(\text{fecal-pellet production})$$

from Nutting et al. (1973). The data presented in Table 9 suggest that the incipient colonies dispersed slightly more energy (9.9%) than they consumed. However, considering the large number of estimates involved in computing the budget, this error is small.

Intermediate-Sized Groups

Mean energy budgets were calculated for 15 feeding units in each of the four group-size categories (5, 10, 20 and 50 termites). All energy terms were measured directly except respiration (R). Oxygen consumption was estimated for energy budgeting from Table 4. An oxy-caloric equivalent of 5.05 kcal/l O_2 was used because normally faunated/feeding termites had RQ's near 1.00 (Table 3). One additional variable, biomass days, was used to calculate R estimates which appear in Table 10. The calculation of production by these groups is sufficiently complex to warrant further explanation. Production (P), as defined in this study, is the sum of weight gained minus weight lost during a defined period of time. However, the concept of ecological productivity has several additional definitions, one of which measures the total generation of organic matter during time, regardless of whether this matter remains in the population to the end of the observation period (Petrusewicz and Macfadyen 1970). Two types of growth are recognized in ecological studies. The first, P_r, is a measure of biomass of new individuals, i.e., natality. The second, P_g, is production resulting from weight gained by individuals present at the start of the observation period. Several forms of weight loss are also recognized. Among these are losses through death and ecdysis, glandular secretions and endogenous (body) and metabolic fractions of the urine and feces, respectively. Since they are recycled quickly by the termites, very few exuviae were noted among any feeding groups. Although they are generally recycled, a measurable quantity of dead termites or body parts was present when the feeding trials were terminated. Productivity for the intermediate-sized groups was partitioned into three components: P_r, P_g and weight losses (L; Table 11). Only one of the four groups showed positive production values. Since negative production has little ecological meaning, all negative cases were assigned 0 values in the construction of energy budgets (Tables 12 and 13).

Table 6. Mean biomass (by caste) of *Marginitermes hubbardi* colonies collected on or adjacent to the Silverbell site during 1974-75[a]

Caste	Sample Wt (g dry wt)	Percent Total Termite Biomass	Mean Biomass of Individual (mg dry wt)
Nymph (Old)	10.1638	60.73	6.31
Nymph (Young)	5.8604	35.02	3.64
Larva	0.3671	2.19	1.57
Soldier	0.2925	1.75	4.22
Supplementary Reproductive	0.0527	0.31	4.98

[a]Dried at 60 C for 7 days.

Table 7. Moisture content (by caste) of *Marginitermes hubbardi*[a]

Caste	No. of Samples	Mean Sample Wt (mg dry wt)	Mean % Moisture[b]	SE
Alate				
Newly Emerged	12	4.5	72.46	0.64
Pre-dispersal	5	48.5	66.17	0.59
Post-dispersal	6	369.4	61.34	0.26
Nymph (Old)	7	34.3	67.41	1.21
Nymph (Young)	5	32.8	76.33	1.03
Larva	8	25.8	78.49	0.54
Soldier	4	38.0	67.33	0.40

[a]Determined as difference between fresh weight and dry weight after 7 days at 60 C.

[b]The first three values listed in this column are significantly different from one another at the $\alpha = 0.05$ level as determined by the least significant difference.

Table 8. Calorific content (kcal/g dry wt) by caste of *Marginitermes hubbardi*, determined by micro- and macrobomb calorimetry

Caste	No. of Samples	Mean Calorific Content	SE	Range	Method
Alate	10	6.41	0.31	5.87-7.02	Micro
Nymph, Old	11	6.78	0.15	5.76-7.39	Micro
Nymph, Old	3	6.84	0.04	6.77-6.90	Macro
Nymph, Young	10	6.26	0.21	4.89-7.12	Micro
Nymph, Young	3	6.35	0.35	5.89-7.02	Macro
Larva	5	5.82	0.20	5.31-6.29	Micro
Soldier	5	4.43	0.14	3.94-4.72	Micro

Table 9. Mean energy budget for 16 incipient colonies of *Marginitermes hubbardi*. The colonies were maintained at 32 C and ca. 100% RH for 3 years and 1 month

Source	Energy of Biomass (kcal/g dry wt)
Input	
MR	27.57
NU	0.00
C	27.57
Output	
P	0.3166
R[a]	16.52
FU	13.47
Total	30.31

[a]Based on estimate from Table 3.

Table 10. Calculation of respiration (kcal) by intermediate-sized *Marginitermes hubbardi* groups; O_2 consumption rates are based on direct manometric measurements at 28 C for groups of 5-10 termites. Mean biomass days were used for a weight-time factor. Oxy-caloric equivalent = 5.05 kcal/l O_2 consumed with RQ = 1.00

Group Size	Biomass Days	Total O_2 Consumed (L)	Calorific Equivalent (kcal)
5	2471.93	0.034	0.173
10	6742.67	0.094	0.472
20	13551.40	0.188	0.949
50	38181.80	0.530	2.675

Table 11. Calculation of production (P) for intermediate-sized groups of *Marginitermes hubbardi*

	kcal			
Group Size	P_r Larvae + Eggs[a]	P_g Biomass Change (ΔB)[b]	L Dead Bodies[c]	P
5	+0.00000	-0.048	-0.023	-0.071
10	+0.00124	-0.042	-0.018	-0.059
20	+0.00122	-0.037	-0.005	-0.041
50	+0.00415	+0.022	-0.017	+0.009

[a]P_r = Production from birth of new individuals or eggs.

[b]P_g = Changes in biomass of individuals present at the beginning of the experiment.

[c]L = Loss of biomass due to death and ecdysis.

Table 12. Mean energy budgets for intermediate-sized groups of *Marginitermes hubbardi*

	Energy (kcal)			
	Group Size (No. of Termites)			
Source	5	10	20	50
Input				
MR	1.060	1.740	3.250	7.530
NU	0.010	0.040	0.040	0.050
C	1.050	1.700	3.210	7.480
Output				
P[a]	0.000	0.000	0.000	0.009
R	0.173	0.472	0.949	2.675
FU	0.180	0.510	1.170	3.330
Total	0.353	0.982	2.119	6.041

[a]Production estimates $\leq$ 0.00 have been assigned 0 values in the calculation of total energy flow.

Table 13. Energy budgets for the large laboratory feeding groups of *Marginitermes hubbardi*. A single replicate was used for each temperature. Groups were allowed to feed for 92-97 days at ca. 100% RH (kcal)

	Energy (kcal)					
	Temperature					
Source	22	24	26	28	30	32
Input						
MR	48.115	41.754	61.421	57.926	78.400	70.918
NU	0.000	0.000	0.020	0.505	0.054	0.394
C	48.115	41.754	61.401	57.421	78.346	70.524
Output						
P	0.047	0.000	2.162	0.001	0.492	0.007
R	21.189	21.034	31.430	36.769	45.485	46.827
FU	28.015	22.559	33.425	29.010	44.496	35.403
Total	49.211	43.593	67.017	65.779	89.981	82.230

Table 14. Nitrogen and lignin content of *Marginitermes hubbardi* fecal pellets produced during intermediate feeding trials. Nitrogen was determined by the micro-Kjeldahl method (Rennie 1965), and lignin by the acetyl bromide method (Johnson et al. 1961)

Temperature, °C	No. of Samples	Lignin (%)	No. of Samples	Nitrogen (%)
24	2	60.52	3	0.225
26	1	66.56	3	0.175
28	2	61.12	3	0.225
30	2	60.40	3	0.195
32	2	59.55	3	0.195
Mean	9	61.63	15	0.203

Table 15. Ash content of *Marginitermes hubbardi*. Values represent residues of termites combusted in a muffle furnace at 550 C for 18 hr

Caste	No. of Samples	Mean wt of Sample (mg dry wt)	Mean Ash Content (% of Sample wt dry wt)
Alate	5	206.2	4.29
Nymph (Old)	4	509.8	4.37
Nymph (Young)	2	152.4	5.20
Larva	1	363.3	6.19
Soldier	1	84.3	4.27
All	11	263.2	$\bar{X}$ 4.86

Table 16. Carbon content of *Marginitermes hubbardi* determined by the dry-combustion method of Allison et al. (1965)

Caste	No. of Samples	Mean % Carbon	SE	Range
Alate	6	52.90	0.54	52.14-55.52
Nymph (Old)	10	53.31	0.36	51.17-54.79
Nymph (Young)	10	51.62	0.41	49.03-53.45
Larva	6	48.06	0.08	47.85-48.36

The other variable, carton, affects the value of both input and output energy. The carton and calorific contents were determined respectively as follows: carton, 50% and 5.0 kcal/g; saguaro wood, 45.5% and 4.48 kcal/g; and feces, 51.8% and 5.37 kcal/g. These values suggest that carton is a mixture of feces and undigested wood. For energy budgeting, it was assumed that the mixture was half wood and half feces. Half of this energy was added to FU and the other values to NU. The final energy budgets for the intermediate-sized group are given in Table 12.

Trophic Level Interactions

Lower Level Interactions

The nitrogen and lignin content of *M. hubbardi* fecal-pellet material was determined for samples from each of the five temperatures used to test intermediate-sized groups. Pellets from all group sizes had to be combined to provide adequate samples. The results appear in Table 14.

The mean carbon content of four carton samples was 50.03%, and for 10 fecal-pellet samples, 51.84%. Calorific content was determined on fecal-pellet subsamples from the total pellets of all 60 intermediate-sized groups. The micro- and macrobomb determinations on carton had a mean and standard error of 5.44 $\pm$ 0.24 kcal/g dry wt. Very little carton was collected from the intermediate and large groups. Carton samples had an average calorific content of 5.00 kcal/g dry wt, $\pm$ 0.295. So few dead bodies or body parts remained in the feeding units after 90 days that no measurements other than biomass were recorded. For the purposes of energy budgeting, dead bodies were assigned a mean calorific value for all castes of 6.02 kcal/g dry wt.

Termites as Prey

A large number of field-collected colonies of *M. hubbardi* provided the termites for the chemical analyses described below. Although time did not permit a complete census of each colony, a large number of individuals were collected, separated into castes and weighed. Thus, it was possible to estimate how termite biomass is partitioned into castes in natural colonies. These data were summarized in Table 6.

Chemical Assays—The moisture content of *M. hubbardi* is given in Table 7. Animal tissues generally contain less than 10% mineral ash (dry wt). To minimize weighing error, a few large samples were analyzed instead of many smaller ones. The ash content of *M. hubbardi* castes appears in Table 15. Differences in the calorific content of *M. hubbardi* apparently reflect a gradual deposition of energy-rich fat as larvae develop into nymphal and adult stages. The results of numerous micro- and macrobomb calorimetric determinations on *M. hubbardi* castes appear in Table 8. Table 16 contains the results of 32 carbon determinations performed on *M. hubbardi* samples. Too few soldiers were available in stock cultures to permit their inclusion here. The recovery efficiency of the carbon analyses was very high (96-98%), as determined by the

Table 17. Nitrogen content of *Marginitermes hubbardi* castes

Caste	No. of Samples[a]	% Nitrogen (dry wt)	SE	Range
Alate	5	8.65	0.19	8.18-9.24
Nymph (Old)	7	6.95	0.33	5.46-8.18
Nymph (Young)	16	8.49	0.51	6.18-11.69
Larva	15	9.45	0.40	6.62-11.63
Soldier	12	12.88	0.27	11.32-14.21

[a]Each sample represents 2 replicates.

combustion of glycine samples. Carbon determination by combustion in oxygen is much more accurate than wet oxidation with dichromate, a procedure often used for biological material. Strickland and Parsons (1968) state that the latter method often causes the oxidation of compounds other than carbon.

Kjeldahl-nitrogen content was determined for several castes (Table 17). Since protein contains about 16% nitrogen, many authors predict a quantity called "crude protein" which is equal to nitrogen content x 6.25. Nitrogen-to-protein conversion factors, based on measurements of the true protein content of animal tissues, vary widely between 5.18-7.46 (Merrill and Watt 1955). Tassoni (1951) determined that the nitrogen-to-protein conversion factor for the true protein in the pupa of the moth *Telea polyphemus* Cramer was 6.19. He also determined that the factor for the whole insect, including exoskeleton, was somewhat higher than 6.41. Since a true conversion factor was not determined for the termites in this study, a value of 6.25 was used when it became necessary to estimate protein.

The amino acid compositions of *M. hubbardi* and *R. flavipes* appear in Table 1. The two hydrolytic methods used were designated by ST for sealed tubes and OT for open tubes.

Table 18. Termite lipids extracted by ethyl ether in a Goldfisch extractor[a]

Species and Caste	No. of Original Samples	Mean % of Weight (dry wt)	SE	Range
Marginitermes hubbardi				
Alate	1	46.43	--	--
Nymph (Old)	3	42.38	0.54	41.60-43.42
Nymph (Young)	3	22.07	0.25	21.70-22.56
Larva	1	17.05	--	--
Soldier	1	6.24	--	--
Reticulitermes flavipes				
Mixed Castes	3	12.37	0.15	12.22-12.66

[a]Samples were extracted during 2 successive periods totaling 8 hr.

The lipid content of *M. hubbardi* and *R. flavipes* was determined for several castes. Measurements using a modified "Folch" technique were largely unsuccessful due to weighing error and large numbers of quantitative transfers required by the procedure. The Goldfisch extractor, however, provided rapid and reproducible means to determine total lipid content. Termite samples were initially extracted with ethyl ether for 6 hr, dried and weighed. They were then extracted for an additional 2 hr. In no case was additional weight loss greater than 1.0% of the already extracted lipid weight. The results of this experiment are summarized in Table 18. Lipid extracts prepared in this manner were esterified and analyzed with the gas chromatograph. The results are presented in Table 19.

Biological Assay—The results of the biological assay in which termite protein was fed to mice are summarized in Table 20.

Table 19. Fatty-acid composition of *Reticulitermes flavipes* and *Marginitermes hubbardi*[a]

Species and Castes	No. of Samples	Mean Percent Fatty Acids						
		Group 1	C16:0	C16:1	Group 2	C18:0	C18:1	C18:2
M. hubbardi								
Alate	1	5.03	19.84	2.44	1.60	5.15	55.14	10.54
Nymph, Old	2	4.02	21.06	1.98	1.31	3.92	60.64	7.06
Nymph, Young	3	3.91	16.35	1.81	1.53	4.19	63.31	8.84
Larva	1	4.91	14.19	1.98	1.69	6.24	63.61	7.37
Soldier	1	3.67	8.69	2.27	3.20	8.43	63.11	10.77
R. flavipes								
Mixed castes	3	4.94	2.31	11.24	2.79	8.75	61.19	9.86

[a]Each sample value is the mean of 2-4 replicates.

Group 1 fatty acids are the combined percentages for compounds with retention times less than C16:0. Group 2 fatty acids had retention times greater than C16:1 and less than C18:0. There were only traces of compounds beyond C18:2, and these were not included in the table.

Estimates of Energy Flow Through a Field Population

Saguaro density is highly variable from one location to another. In 1941, section 17 of SNME had ca. 37 live saguaros per hectare. Since that time, however, mortality has greatly exceeded natality (principally because of bacterial necrosis). On plot F2 (Fig. 2) more than 80% of the original plants have succumbed. Of the 44 dead skeletons inspected there during early July 1976, only seven, all dead for four years or less, had not been attacked by *M. hubbardi*. We have estimated that 13 skeletons contained active colonies. Nutting (1970) reported actual counts for 10 colonies. The mean number of termites per colony (1173.7) has been partitioned into castes and assigned energy equivalents according to the values presented in Tables 6-8. Based on Nutting's data, 14% of the termites should be alates awaiting dispersal flights. Thus, a single *M. hubbardi* colony would have a mean weight of ca. 6.00 g dry wt, and contain an equivalent of 39.51 kcal. The 13 colonies on plot F2 (4 ha) SNME would weigh 78 g and contain an energy equivalent of 513.63 kcal. The mean annual temperature for Tucson during the period 1895 to 1960 (61 of the 65 years were recorded) was 19.65 C.

Daily wood consumption was calculated using estimates for large feeding groups at 22 C (Table 21). The 13 colonies on plot F2 would then consume ca. 1.557 kg dead wood annually (0.38 $kg \cdot ha^{-1} \cdot yr^{-1}$; 172.15 kcal) and, through respiration, would dissipate 3094.14 kcal (764.3 kcal/ha). Data were insufficient to compute either production or rejecta. These figures would suggest that more than four times as much energy would be dissipated by respiration than would be consumed (764.3 vs. 172.15). Respiration energy appears to have been underestimated at low temperatures and overestimated at high temperatures for the large feeding groups (Table 13). If this pattern holds true for the present situation, the gap between intake and respiration energy for termites on SNME would be even greater. Thus, it appears that wood consumption must be underestimated.

DISCUSSION

Oxygen Consumption

The respiratory rate of *M. hubbardi* is highly correlated with temperature. Oxygen consumption rates for old larvae, nymphs and soldiers were statistically similar for groups of 5 and 10 individuals tested in the Gilson® differential respirometer. Consequently, group size and biomass were eliminated as factors in statistical analyses.

Oxygen consumption and CO_2 evolution were measured at 4 C intervals from 16-36 C. At 16 C, *M. hubbardi* appears to assume a state of respiratory torpidation (an average of

Table 20. Biological assay of *Reticulitermes flavipes* included as the protein source in a diet fed to mice for 3 weeks

Evaluation Technique	Dietary Protein Sources: Whole Egg (Control)	Dietary Protein Sources: *R. flavipes*
Third week body weight (g)	24.1	13.1
Gain in body weight (g)	15.4	4.4
Mean feed intake ($g \cdot day^{-1} \cdot mouse^{-1}$)	4.2	3.3
Apparent protein absorption[a]	81.0	73.0
Protein efficiency ratio[b]	2.50	1.1
Net protein retention[c]	1.78	0.7
First limiting essential amino acid	none	sulfur amino acids
Protein score	100	40
Essential Amino Acid Index[d]	100	78
Biological value[e]	97.3	73.3

[a] Determined according to the Cr_2O_3 method of Schürch et al. (1950).

[b] Sebrell (1963). P.E.R.'s adjusted to 2.50 for egg standard.

[c] Determined by the method described by Bender and Doell (1957).

[d] Determined by the method described by Oser (1959).

[e] Calculated by the formula: BV = 1.09 (EAAI) - 11.73 (Oser 1959).

Table 21. Wood consumption, fecal-pellet production, biomass and carton production by six large groups (490-500 individuals) of *Marginitermes hubbardi* fed saguaro wood for 90 days. Experimental units were maintained at ca. 100% RH

Rearing Temperature (°C)	No. of Groups	Initial Group No.	Final Group No.	Wt Change of Group (mg fresh)	Wood Consumption (mg·g fresh termite^{-1}·day^{-1})	Fecal-Pellet Production (g)	Carton Production (mg dry wt)
22	1	500	444	+26.8	16.53	5.2170	0.00
24	1	500	348	-613.5	19.44	4.2010	0.00
26	1	500	387	+1251.7	24.48	6.2207	8.10
28	1	490	334	-280.1	23.97	5.3082	201.80
30	1	500	324	+284.9	30.73	8.2760	21.60
32	1	500	355	-808.7	29.93	6.5193	157.50
Mean		498.33	365.33	-23.15	24.18	5.9570	64.83

only 0.083 μ l·mg fresh termite^{-1}·hr^{-1}). The lowest O_2 consumption (0.060 μ l·mg^{-1}·hr^{-1}) for any of the four physiological states was recorded at 16 C for the defaunated/starving groups. The 16 C replicates were, at times, greatly influenced by minor changes in the room environment, especially when the air conditioning was shut off daily at 2100 hr. Even though reaction vessels were submerged in a constant temperature water bath, gas exchange measurements, monitored by a micrometer device at a level several centimeters above the water bath, were affected by changes in room temperature. Measurements of very low respiratory rates were inaccurate. This is substantiated by the rather erratic RQ's reported for 16 C groups in Table 3, especially for the defaunated/starving groups which could not possibly have attained an RQ of 1.28. The remaining treatment combinations followed the expected patterns. The treatment with the highest rates of O_2 consumption (normally faunated/feeding) had RQ's near 1.00, suggesting that pure carbohydrate was being metabolized. Keister and Buck (1974) compiled a large table of O_2 uptake for insects. These values, expressed on a fresh weight basis, ranged from a low of 0.037 μ l·mg^{-1}·hr^{-1} for *Cryptocercus punctulatus* Scudder, to a high of 22.1 for actively feeding *G. mellonella* larvae. At 16 C the defaunated/starving groups actually consumed less O_2/hr than many diapausing insects listed by the same authors. Several literature reports of O_2 consumption rates by termites are presented in Table 22.

The O_2 consumption data for normally faunated/feeding *M. hubbardi* are comparable to those in Table 22. They are, however, low by comparison with other insects. Wiegert and Coleman (1970) concluded that termites have low rates as physiological adaptations to conditions of crowding. Also, if alates did not feed during the initial stages of colony development, a low, fasting metabolic rate would be advantageous to conserve energy. The normally faunated/feeding termites consumed more O_2 ($\overline{X}$ = 0.453 μ l·mg^{-1}·hr^{-1}) and had a higher RQ (ca. 1.0) than any other treatment. The mean rates for the starving treatments were 0.223 μ l·mg^{-1}·hr^{-1} (faunated) and 0.215 μ l·mg^{-1}·hr^{-1} (defaunated) (Table 3). While these values differed statistically, it is doubtful if the difference was biologically significant. Since starving termites (and most other animals) rely on stored fats for energy, it is unlikely that the presence of starving protozoans in the gut would affect overall oxygen consumption. This conclusion is especially warranted in view of the evidence which suggests that these protozoans are anaerobic (Honigberg 1970).

The most interesting result of this experiment concerns the defaunated/feeding groups which, though lacking their protozoans, consumed oxygen at a rate approximately intermediate between the normally faunated/feeding and starving individuals. The observed O_2 consumption differences between the normally faunated/feeding and defaunated/feeding treatments could thus not be directly

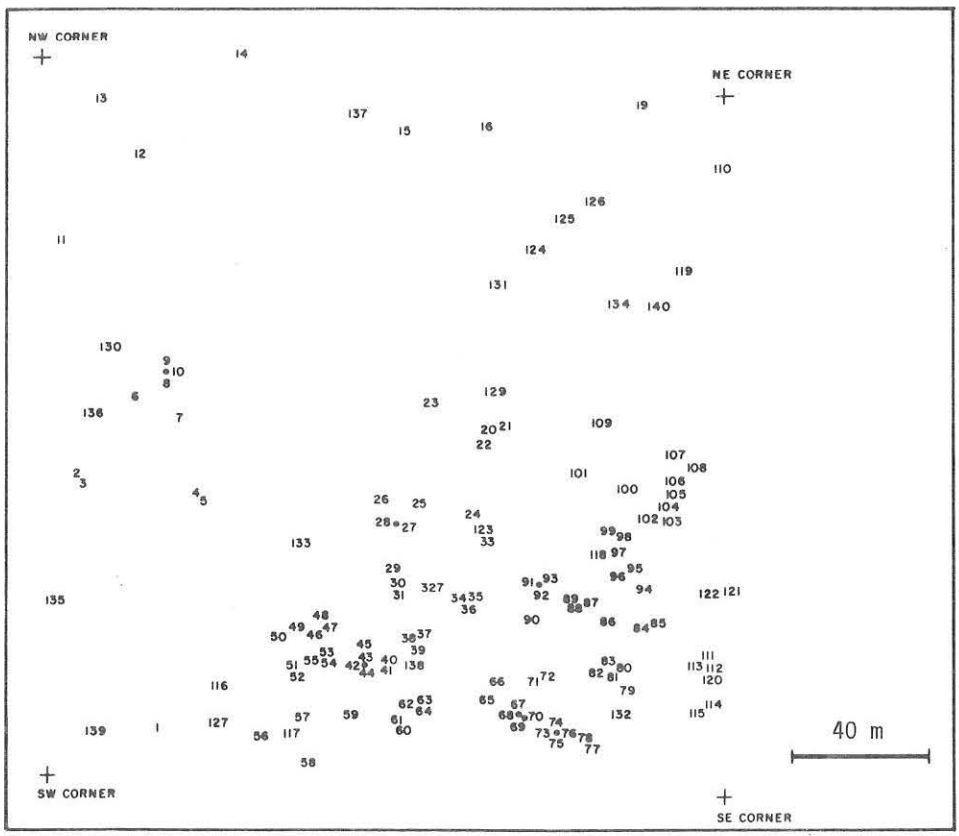

Figure 2. Map which shows the location in 1976 of all live and dead saguaros (*Carnegiea gigantea* [Engelm.] Britt. & Rose) on plot F2 of the Saguaro National Monument (east) near Tucson, Arizona.

Table 22. Summary of literature reports of oxygen consumption by termites (μ l·mg fresh termite^{-1}·hr^{-1}); modified from Hebrant (1970)

Species	Caste	Temp, (°C)	O_2 Consumption	Reference
Kalotermes flavicollis	--	26	0.54	Lüscher (1956)
Zootermopsis nevadensis	--	32	0.81	Cook (1932)
		20	0.42	Cook (1932)
		19	0.51	Lüscher (1956)
		23-25	1.01	Hungate (1938)
		3	0.037	Gilmour (1940)
Z. angusticollis	--	12-32	.140-.655	Cook and Smith (1942)
Reticulitermes lucifugus	worker	20	0.182	Ghidini (1939)
	unpigmented imago	20	0.173	Ghidini (1939)
	soldier	20	0.057	Ghidini (1939)
	1st stage nymph	20	0.086	Ghidini (1939)
R. santonensis		24-30	.62-.99	Damaschke and Becker (1964)
R. flavipes		24-32	.53-1.24	Damaschke and Becker (1964)
Heterotermes indicola		24-32	.64-.89	Damaschke and Becker (1964)
Nasutitermes ephratae		22-30	.20-.58	Damaschke and Becker (1964)
N. costalis		21-25	0.6	Wiegert and Coleman (1970)
Macrotermes bellicosus	large worker	30	0.29	Ruelle (1962)
	small worker	30	0.28	Ruelle (1962)
	large soldier	30	0.17	Ruelle (1962)
M. ukuzii		28	.11-.14	Rohrmann (pers. comm.)

due to the loss of protozoans. The difference resulted from lower levels of available nutrients in the gut as a result of losing the protozoans. The important observation here, however, is that termites assimilate a respectable quantity of wood constituents on their own without the aid of their symbiotes. It should be noted that although most of the gut microfauna was removed by the 45 psi O_2 defaunation treatments, surviving species may have digested some cellulose. Few efforts have been made to assess the cellulolytic capability of the microflora of the hindgut, or of completely defaunated and deflorated termites. Brief reviews of these attempts have been given by McBee (1959) and Mannesmann (1972).

There are, however, some data which suggest termites have the ability to produce their own digestive enzymes. Cleveland (1924) noted that, following defaunation, workers of *R. flavipes* died within 10-20 days when fed sound wood. On a diet of somewhat decayed wood, however, their survival was prolonged and, when fed dextrose (glucose), peptone and starch, either separately or together, defaunated individuals survived considerably longer. These observations suggested that the defaunated termites were indeed capable of digesting and absorbing certain nutrients and, thus, must possess digestive enzymes of their own. Hungate (1938) quantified the relative importance of protozoans and host in digestion and utilization of wood by *Zootermopsis angusticollis*. Although *Zootermopsis* might be able to oxidize about one-third of its total wood intake independently of its symbiotes, he showed that it would have to oxidize ca. seven-eighths of its intake to satisfy its energy requirement. Trager (1932) was the first to demonstrate a cellulase from the intestinal flagellates of the wood-feeding cockroach, *Cryptocercus punctulatus* Scudder, *R. flavipes* and *Z. angusticollis*. He maintained one of the cellulolytic flagellates, *Trichomonas termopsidis* Cleveland, for three years, a feat yet to be equalled. Honigberg (1970) discusses Trager's work in detail along with several other less successful culture attempts. Other data which support the independent elaboration of cellulolytic enzymes by termites come from the family Termitidae which do not possess symbiotic protozoa. An adequate discussion of the mechanisms involved here would require more space than can be reasonably allocated. The reader is directed to the review by LaFage and Nutting (in press) for further information.

As a result of the present study, we have concluded that *M. hubbardi* can assimilate a significant amount of saguaro constituents without its gut fauna. It remains unknown, however, whether a termite-produced cellulase is elaborated.

The observed O_2 consumption data were transformed to $\log_e$ and regressed on temperature (°C). The resulting prediction models (Table 4) were useful in energy budgeting. Over a similar temperature range, both feeding groups responded in a curvilinear fashion while the starving groups followed a simple linear pattern. No biological significance is assigned to these differing responses, however.

Termite Thermogenesis

Table 5 shows estimates of *M. hubbardi* heat production obtained by calorimetry and by calculations based on O_2 consumption predicted from the equations in Table 4 and the oxy-caloric equivalent of 5.05 kcal/l O_2. Discrepancies between the calorimetric and respiration estimates can be explained only partially. Although they are anaerobic, the

Table 23. Caste composition of six large feeding groups (490-500 individuals) of *Marginitermes hubbardi* maintained on saguaro wood for 90 days at ca. 100% RH

Temperature (°C)	Initial No. in Group	Final No. in Group	Production		Caste Composition of Survivors				
			Eggs	New Larvae	Supplementary Reproductives	Larvae	Young Nymphs	Old Nymphs	Soldiers
22	500	444	0	0	4	20	156	250	14
24	500	348	0	0	6	40	126	170	6
26	500	387	0	0	1	1	83	291	11
28	490	334	0	1	9	2	38	268	16
30	500	324	0	0	3	1	87	231	2
32	500	355	13	0	3	2	104	220	13
Column Total	2990	2192	13	1	26	66	594	1430	62
% of Grand Total			0.59	0.05	1.19	3.01	27.10	65.24	2.83

protozoans must, as a result of their metabolic processes, give off heat which cannot be estimated on the basis of oxygen consumption. One would expect and, indeed, does observe, that heat production estimates by calorimetry are higher than those calculated from respirometry. One other study has used both of these methods to estimate heat production by insects (Peakin 1973). Although he found that the two methods produced similar results, his experimental insect (*Tenebrio molitor* L.) contains few, if any, anaerobic symbiotes. By contrast, the termite may contain as much as one-third of its total fresh biomass in protozoans. Only one person has used calorimetry extensively in the study of insect thermogenesis. The now retired Professor H. Prat of Marseilles, France, has, through personal communication, reaffirmed our belief that calorimetry should discern heat production by termites more efficiently than classical respirometry (Prat, pers. comm.).

The thermogram in Figures 1a and 1b is part of a 12-hr record produced by a single *M. hubbardi* nymph. The thermogenetic event pictured occurred repeatedly, though irregularly, during several, but not all runs on single termites. It is both possible and probable that the same event occurred in the group runs but, because these thermograms were composites of five individuals, individual events were difficult to resolve. A possible explanation of the phenomenon pictured might involve a mode of discontinuous respiration in which a sudden burst of moisture-laden respiratory gases escapes and cools the ampoule wall. The sudden increase and subsequent leveling off of the heat record remain unexplained.

Energy Budgets for Laboratory Feeding Groups

Energy budgets developed for the differently sized feeding groups will be discussed collectively.

Since heat production was measured only at 20 C, O_2 consumption measurements (Tables 3 and 4) were used to estimate R for all energy budgets. As R was the only variable not measured directly, it is probable that it was responsible for unbalanced budgets (Tables 9, 12 and 13). On the positive side, none of the budgets was off by more than a factor of two. R was overestimated for the incipient and large groups while underestimated from the intermediate category. As biomass days were calculated with higher accuracy for the intermediate-sized groups than the others, R estimates for the midsized groups were probably the most realistic, in spite of the fact that energy budgets for these groups do not balance as well as those for the others. The components of productivity (P) used in energy budgeting have been noted for the intermediate-sized groups in Table 23.

Trophic Level Interactions

Lower Level Interactions

M. hubbardi fecal pellets represent a rather poor quality nutrient for lower trophic levels in that they are low in nitrogen (0.203%) and high in lignin (61.63%). Although it was not confirmed analytically, the remainder is probably cellulosic in nature. Fecal pellets are probably nutritionally suitable only for a few wood-destroying fungi (white rots) and specialized bacteria. Nevertheless, pellets are small enough that abiotic degradation may proceed rapidly as a result of the large ratio of surface area to volume. Our observations indicate that *M. hubbardi* does not practice coprophagy as do some millipeds to obtain adequate energy from their feed (McBrayer 1973).

Termites as Prey

Many animals consume termites as the opportunity arises. Nutting (1969) reviewed the available literature on the kinds of animals which eat termites. *M. hubbardi* is high in nitrogen and, depending on caste, fat and thus energy. The larvae and young nymphs contain more than 75% moisture and therefore could provide occasional water for desert

Table 24. Nitrogen content of termites

Species	Sex[a]	Caste	% N (dwb)	Author
Pterotermes occidentis	M	Alate	9.94	LaFage (unpubl. data)
Pterotermes occidentis	F	Alate	10.32	LaFage (unpubl. data)
Zootermopsis angusticollis	M+F	Larva & nymph	9.07	Hendee (1935)
Zootermopsis nevadensis	M+F	Alate	14.7	Hungate (1941)
Zootermopsis nevadensis	-	Nymph	9.1	Hungate (1941)
Undetermined	-	Alate	5.71	Leung (1968)

[a]M = male, F = female.

animals. Although *M. hubbardi* larvae and nymphs are generally unavailable as prey as a result of their protective nesting habit, other termites such as *Gnathamitermes perplexus* (Banks) which contain more water and forage near the surface, are habitually eaten by birds and reptiles.

Chemical Analyses—Moisture content tends to be highest in nonreproductive castes, i.e., larvae, workers and soldiers. In *M. hubbardi*, moisture content is a function of fat deposition with the possible exception that differently aged alates possess differing quantities of water while maintaining approximately the same fat content. Newly emerged, unflown alates (predispersal; Table 7) contained more moisture (72.46%) than older unflown (65.17%) or flown individuals (61.34%). Water lost during the preflight maturation period would tend to lighten subsequent flight loads and consequently aid in the conservation of energy required later for brood production.

The ash content of all *M. hubbardi* castes averaged 4.86% (Table 15). Although no statistical analysis was done to determine differences among the castes, the range (4.27-6.19) was considered narrow. Humus-feeding or soil-ingesting termites are the only species which have a high ash content. This results from soil in the gut. Matsumoto (1976) found that workers of *Dicuspiditermes nemorosus* (Haviland), a humus-feeding species, contained as much as 65.6% ash, dry weight.

The calorific content of the individual castes generally reflects their lipid content. In *M. hubbardi* the alates and nymphs have the highest energy content (6.41 and 6.56 kcal/g dry wt). Although high for insects, these values are much lower than the mean (7.79 kcal/g dry wt) for very fat fall migrant birds reported by Odum et al. (1965). Nevertheless, *M. hubbardi* alates, the caste most often preyed upon, are definitely energy rich. The carbon content of *M. hubbardi* castes follows the same relative pattern as calorific content and total lipid content and is, in our opinion, a reflection of the higher carbon content of lipid-rich compounds.

The nitrogen content of *M. hubbardi* (Table 17) is close to that reported for other termite species (Table 24). Amino acids reported for the various castes of *M. hubbardi* (Table 1) are present in essentially similar ratios among all castes tested. The results of determinations on *R. flavipes* also given in this table suggest an extraordinary resemblance in the amino acid profiles of the two species.

The whole-body lipid content and constituent fatty acids of *M. hubbardi* and *R. flavipes* presented in Tables 18 and 19 represent termite body lipids plus the small quantities held in the gut contents. Lipids tend to accumulate in those individuals destined to participate in dispersal flights. Owing to their very high energy-to-mass ratio, but unlike carbohydrates, lipids can be stored in nearly anhydrous form. They are the most commonly stored metabolic fuel and, for fasting and hibernating animals, the only energy source (Lehninger 1970). When oxidized, they generally yield twice as much energy per unit mass as either carbohydrates or proteins. As with most other animals, it appears that lipids, probably as triglycerides (TGL), constitute the most important long-term energy reserve for *M. hubbardi*. Because of their small size and the diffuse nature of the fat body, few analyses have measured the lipid content of specific insect organs or tissues.

Basalingappa (1970) studied the quantitative variation in lipids among the castes of *Odontotermes assmuthi* Holmgren. On a dry weight basis lipids constituted 9.7% of workers, 17.8% of soldiers, 26.4% of royal pairs, 17.8% of the undifferentiated instars and 48.4% of alates. In *Paraneotermes simplicicornis* (Banks), a North American subterranean kalotermitid, older nymphs contained 45.5% lipid; younger nymphs, 39.3%; larvae, 22.0%; pseudergates, 28.4%; and soldiers, 16.6% (dry wt) (LaFage, unpublished data). In this species, as in *M. hubbardi*, there appears to be a progressive lipid buildup in the reproductive line. From data given by Hewitt et al. (1972) it can be calculated that unflown alates of a termitid, *T. trinervoides*, contain approximately 42% dry wt lipid in the form of neutral and phospholipids, with the former predominating. Alates of another termitid, *G. perplexus*, caught in flight, are also lipid rich, containing 56.3% dry wt (Dimmitt, pers. comm.). Unspecified winged termites offered for sale in a Leopoldville (Kinshasa) market contained 44.4% fat (Tihon 1946).

Among these admittedly random observations, only one trend seems to surface: the subimaginal instars and alates contain substantially more lipids than other castes. These stores are undoubtedly used both for energy and for egg production during the critical period of colony foundation and early development by many of the Termitidae and perhaps, on occasion, by the lower termites. The belief that thoracic flight musculature is rapidly mobilized for nutrient requirements during this period, as in the ants, requires further investigation, since Noirot (1969) has noted that this

process continues over a period of years and probably contributes very little to the nourishment of the royal pair. Hewitt and Nel (1969) also noted that primary reproductives of *H. mossambicus* had lost only one-third to one-half the mass of their dorso-ventral thoracic musculature after 18 months. From the data available, it appears that TGL is quantitively the most important lipid class stored by termites and C_{16} and C_{18} FA the most important TGL constituents (Table 19).

Biological Assay—Although a number of authors have extolled the virtues of eating insects (Bodenheimer 1951; DeFoliart 1975; Ruddle 1973; Tihon 1946), only one study (Teotia and Miller 1973) has attempted to analyze insect protein by actual feeding trials. These authors used housefly pupae as the protein source for 135-day-old broiler chicks. The weight gained by the birds during four weeks was statistically similar to that gained by birds on a control diet containing corn, milo, soybean meal (44% protein), fish and bone meal, and alfalfa. It is doubtful, however, that much information regarding protein quality can be gained from this type of experiment as both diets contained more than 25% crude protein. Protein quality should be assessed when supplied at a rate of 7-10% in the diet, i.e., suboptimum levels.

Several conclusions were drawn about the quality of termite (*R. flavipes*) protein as a result of the feeding trials (Table 2). Perhaps most important is the observation that the protein diet was both nontoxic and palatable as it was consumed at a rate (3.3 $g \cdot mouse^{-1} \cdot day^{-1}$) which was close to that for the whole-egg control diet (4.2 $g \cdot mouse^{-1} \cdot day^{-1}$). Mice which were fed termites did not gain as much weight during the three-week feeding period as those on the standard diet, suggesting that one or more essential amino acids were in short supply. The protein score of *R. flavipes* protein (40) indicates that the most limiting amino acid was present at 40% of its optimum concentration. The amino acid profile of *R. flavipes* protein reported in Table 1 indicates that methionine and cystine (considered collectively in calculating protein score) are the most limiting amino acids.

Although protein scores abound in the literature, techniques and animals used in various laboratories differ to the extent that comparisons with *R. flavipes* would be suspect. Many additional analyses on amino acid composition and protein quality have been performed by the laboratory which tested *R. flavipes* (Department of Nutrition and Food Science, The University of Arizona). The following protein scores provided by Dr. C. Weber (pers. comm.) are for conventional proteins: casein, 47; isolated soybean, 21; lactalbumin, 52; blood fibrin, 53; wheat (cajeme-71), 40; cottonseed meal, 36; brewer's yeast, 35; pinto bean, 21. Among the less conventional proteins, but all of which have been tested as possible food additives, are the following: paloverde bean, 22; mesquite bean, 22; mesquite pods, 28; buffalo-gourd seed, 28; papago pea, 14. A quick examination of these protein scores shows that *R. flavipes*, with a score of 40, is a better protein than all of the nonconventional sources and a few of the conventional ones. On the basis of Oser's (1959) essential amino acid index (ESSI) which, unlike protein score, evaluates all the amino acids in a protein, *R. flavipes* also compares well with other proteins evaluated in Dr. Weber's laboratory.

Although some proteins appear quite adequate from their protein scores or EAAI's, they are not readily absorbed by the animals, and are thus of little nutritional value. Chromic oxide (CR_2O_3) was added to the diet as a marker to determine the digestibility of *R. flavipes* protein (Schürch et al. 1950). Ca. 73% of the termite protein was absorbed. The calculated biological value (Oser 1959) suggests that 73.3% of the absorbed protein was retained by mice; i.e., not excreted in the urine. On the basis of the above data, we have concluded that *R. flavipes* by itself is a good, but not wholly adequate protein. However, it is unlikely that any predator would depend entirely on a single protein source. Termites could be considered an excellent protein supplement. The addition of sulfur-containing amino acids would undoubtedly raise their protein quality to a level adequate for normal growth in weanling mice and a variety of other animals. It is little wonder that *M. hubbardi* and other desert termites are routinely eaten.

Field Estimates on Energy Flow Through a Population of M. hubbardi

The density and distribution of dry-wood termite colonies depends to a large extent on the availability of suitable nesting sites which, for *M. hubbardi*, are few and scattered. As a result, this species and many other dry-wood termite populations are far less impressive numerically than subterranean termites. The foraging populations alone of *G. perplexus* can, under favorable environmental conditions, exceed 7×10^5 individuals per ha (LaFage et al. 1974). This is compared with 1.5×10^3 individuals per ha for *M. hubbardi* on plot F2 of SNME, an area which probably has a very high density for this species. The total annual respiration (kcal/ha) for *M. hubbardi* was estimated at 764.3 kcal. Based on Haverty and Nutting's (unpubl.) estimate that the subterranean termites in a desert grassland annually consume 413.9 kg of dead wood (4.116 kcal/g dry wt) we have calculated that more than 1.5×10^6 kcal/ha would be dispersed in a single year. This amounts to 2.0×10^3 times the energy released by *H. hubbardi* on SNME. The above-mentioned subterranean termites display approximately the same metabolic activity/m^2 (150 $kcal \cdot m^{-2} \cdot yr^{-1}$) as other small decomposers and herbivores such as mites, Collembola and nematodes (175.7 $kcal \cdot m^{-2} \cdot yr^{-1}$) and large decomposers such as earthworms and arthropods (128.5 $kcal \cdot m^{-2} \cdot yr^{-1}$; Lee and Wood 1971). Assuming an oxy-caloric equivalent of 4.8 kcal/l O_2, Engelmann (1966) reported that 46 species of oribatid mites with a biomass of 5.377 g/m^2 released 21.54 $kcal \cdot m^{-2} \cdot yr^{-1}$ in forest soil in Belgium. He also summarized respiration data for "mice" (*Reithrodontomys*, *Peromyscus* and *Microtus*) which released ca. 743.6 $kcal \cdot ha^{-1} \cdot day^{-1}$ during the summer.

The ecological importance of *M. hubbardi* need not be diminished on the basis of its low respiration per m^2 per yr, since organisms interact with each other and the environment in many and unsuspected ways. For example, it is possible that some relationship exists between swarming ter-

mites and seed-harvesting ants of the genus *Pogonomyrmex* which favors brood production by the ants. Throughout much of the year, harvester ants in new Mexico rely solely on seeds for food. In summer months, however, these ants supplement their seed diet with termite alates. It so happens that termite dispersal flights occur during the period of greatest brood-rearing activity. Whitford (pers. comm.) has suggested that the protein supplementation by the termite prey may indeed be necessary to meet the increased nitrogen requirements of tissue production in the young ant larvae.

Traditionally, the study of dry-wood termites has been largely restricted to taxonomic control and a few physiological considerations. We hope that the above experiments and speculations stimulate others to perform more in-depth studies on these interesting animals in neglected areas of ecology and behavior.

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