



Energy Consumption of Termite Colonies of *Nasutitermes ephratae* (Isoptera: Termitidae)

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MURADIAN, R., S. ISSA AND K. JAFFE. *Energy consumption of termite colonies of Nasutitermes ephratae (Isoptera: Termitidae)*. *PHYSIOL BEHAV* 66(5) 731–735, 1999.—Measurements of CO₂ production of whole termite colonies showed that respiration intensity varies slightly during the daily cycle, that the relation between standard metabolism and colony size is best described with a negative exponential, taking into account the proportion of the various castes. Larger colonies were more efficient in their energy use, suggesting that energetic considerations may contribute in explaining the maintenance in evolution of complex societies. © 1999 Elsevier Science Inc.

Colony energetics Respiration Termites Castes

THE respiratory rate reflects the total sum of all energetic costs of the metabolic processes involved for the maintenance and activity of the organism and may also serve to estimate the effort of the organism in covering the demands imposed by the environment (9). Very little is known about the demands on energy consumption imposed by social life. Studies with ant colonies (6) have shown that energy requirements may serve to characterize key aspects of social life.

Theoretically, three outcomes may be expected when comparing per capita energy consumption (EC) of isolated organisms with those forming a society (6): (a) EC is independent to the type of social life: null hypothesis; (b) EC decreases with socialization as social life optimizes the utilization of resources: optimization hypothesis; and (c) EC increases with socialization as social life implies increased complexity, which in turn, demands increased energy consumption: thermodynamic hypothesis.

The hypothesis commonly assumed as true by default is hypothesis (a). In the case of termites, the scant data on whole colony respiration available [(15), for example], does not allow testing of these hypothesis. Despite this lack of data, hypothesis (a) has been assumed implicitly as valid for termites [(8,14,15) for example]. In addition, the thermodynamics regulating the formation of social units may differ to that controlling the growth of established societies. These may depend on the proportion of organisms participating in social activities, on the existence of castes, and on the specific social structure. In the case of ant colonies, the transition from isolated individuals to ever

larger groups of ants is analogous to a phase transition in terms of EC and seems to fulfill the thermodynamic hypothesis. Experimental data showed that once a critical number of individuals has been achieved, EC decreases exponentially, fulfilling the optimization hypothesis (3). The mechanisms causing this optimization of EC with colony size are not clear, but have been related to increasing proportions of inactive ants (3) and to a greater synchronization of their activity (10).

To test for these hypotheses in termite colonies, interfering variables have to be controlled, the most important of which are temperature, intake of nutrients, and caste composition of the colony. The respiration of isolated workers are known to be very sensitive to temperature (8), and caste composition may affect EC. Hebling-Beraldo and Mendes (4) showed with ants that EC does vary with castes, and that this variation cannot be explained solely by their differences in size. Tschinkel (12) also found EC differences among castes in *Solenopsis invicta*, where large major workers had the highest EC.

Here we aim to measure EC in fully functional termite colonies of different sizes to test the hypotheses presented above, taking into account variations in EC along the daily activity cycle and the proportion of the various castes forming the colony.

MATERIALS AND METHODS

Termite colonies of *Nasutitermes ephratae* (35 nest) were collected in FONAIAP, Miranda, Hacienda Padrón, Estado Miranda, Venezuela, between March and September of 1996.

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N. ephratae nest have normally only one central nest structure, although exceptionally they can have more than one. We selected nests in the field with only one visible central nest structure, and collected them together with the tree branch on which they were built, placed them into a plastic bag and transported them to the laboratory in a thermal container. Nests were then placed on a Plexiglas sheet of 1.5 m², and were offered water and humid and decomposing birch wood ad lib. Nests were kept in the laboratory under controlled conditions, as close as possible to those in their natural habitat, at 90–98% RH, normal photophase and 26 to 31°C for at least 15 days. During that period we discarded 11 nests that did not forage or that showed high worker mortality. We measured the shortest and longest diameters of the nests and estimated the volume assuming ellipsoid shapes (11). The estimated volumes varied largely among nests from 1438 cm³ to 32696 cm³, reflecting the large variety of sizes found in the field.

The CO₂ production was measured using an infrared spectrometer (Li-Cor) with constant air flux. Twenty-four hours before measurements, termite nests were placed into a hermetically sealed respiration chamber 60 cm wide, 100 cm long, and 60 cm in height, made of aluminum and Plexiglas. Termites were offered food and water, a fixed photoperiod of 12 h, and temperature fluctuated between 26 and 31°C. The air flowing through the chamber was pumped from the outside of the building. Mean CO₂ concentration of fresh air was measured independently and assessed at 353.6 ppm. The respirometer was calibrated before each measurement. Larger nests were submitted to higher air flows so that absolute CO₂ concentrations in the chamber remained below 370 ppm, as ambient oxygen concentrations are known to affect respiration rate in termites (13). Thus, air flux was fixed for each experiment but varied depending on colony size between 30.5 and 131 mL/s.

The measurements were performed for each nest on 2 different but consecutive days. Each measurement took 24 h, and consisted of continuously monitoring atmospheric pressure, air temperature, air flux, and CO₂ concentrations of the air coming in and out of the respiration chamber. With the help of the differential infrared detector and a special computer software (Datacan V) the difference between the CO₂ of fresh air (going into the chamber) and that exiting the respiration chamber was calculated, taking into account the atmospheric pressure, air flux, and temperature. The air current leading to the spectrometer was dried with barium hydroxide.

At the end of the last CO₂ measurement the nests were cut into small pieces and vigorously shaken to extract the termites. Termites remaining in unbroken pieces of nest were extracted manually. The termites with some remaining small pieces of nest material, were kept in a freezer at -5°C. This material was then mixed uniformly and we took six samples (8 mL) from each nest. The material and the samples were dried in an oven at 60°C. Each sample was carefully examined and the various castes counted in detail before drying them. The castes were grouped as follows: worker nymphs having a cephalic capsule of less than 0.1 cm in length, soldier nymphs having a cephalic capsule of 0.07 cm, and adult sexuals, workers, and soldiers, which were recognized by their characteristic morphology. The dry material was weighed, and the biomass of each caste in each nest was then calculated by extrapolating the data for the proportions of the weight of each caste in the sample, to the total weight of each sample, to the total weight of the nest. Data of 17 nests were used as we discarded nests containing reptile eggs. Controls (measuring the noise in CO₂ production measurements) consisted in pieces of nest structures representing

about 80% of each nest, from 10 of the nests used above, after the termites had been extracted, placed with food and water in the respiration chamber, and submitted to the same experimental measurement for CO₂ production as described above.

Data are presented as the normalized respiration intensity (NR) expressed as ml of CO₂ production per gram of dry biomass. Values of NR used were the average of the values for a whole day (NR_{mean}), the maximum values for a daily cycle (NR_{max}), the minimum values for a daily cycle (NR_{min}), and the difference between NR_{min} and NR_{max} (NR_{diff}).

RESULTS

The controls showed that on average, empty termite nests with wood and water produced $7.67 \times 10^{-4} \pm 1.71 \times 10^{-4}$ ml of CO₂/h. If these values are compared to the average respiration of live termite nests (270.8 ± 212.7 mL of CO₂/h) we may assume that nest respiration is accomplished mainly by the termites, and we may confidently dismiss the contribution of other nest components to the respiration values measured.

Comparing values of temperature and CO₂ production of the whole termite colonies, showed no significant correlation between both ($r = 0.11$, $p = 0.52$), in the temperature ranges used in the experiments.

Figure 1 shows the daily variation in NR for the 17 nests studied. Termites showed a maximal respiration activity at 22 h and a minimum at 11 h, showing that maximal activity was at night.

Figure 2 shows the data for NR (maximum, minimum, and average) for each nest during the daily cycle. Each data point is the mean of two measurements of two different days. Results show an inverse exponential relation between NR and colony size.

The difference between maximal and minimal NR of the colony in the daily cycle (NR_{diff}) is a gross indicator of differences in whole colony activity between maximum and minimum activity levels during the daily cycle. This difference correlated negatively with colony size ($r = -0.757$, $p = 0.001$), suggesting that larger colonies have smaller NR_{diff} (Fig. 3).

Table 1 gives the values of r and p for the best fit to the different models (Quasinevton method of Statistica). Model 1

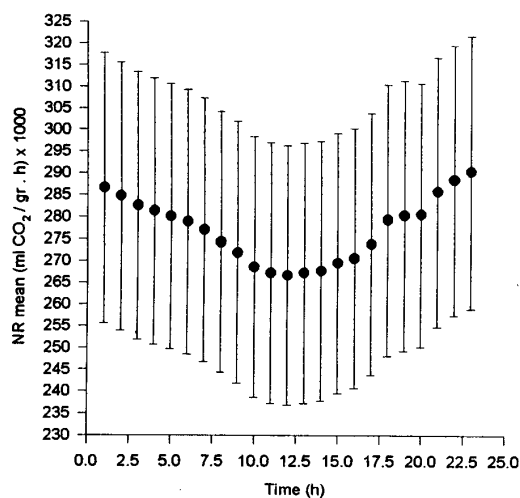


FIG. 1. Daily respiration pattern of termite colonies. Values represent means and standard errors of NR mean from 34 measurements.

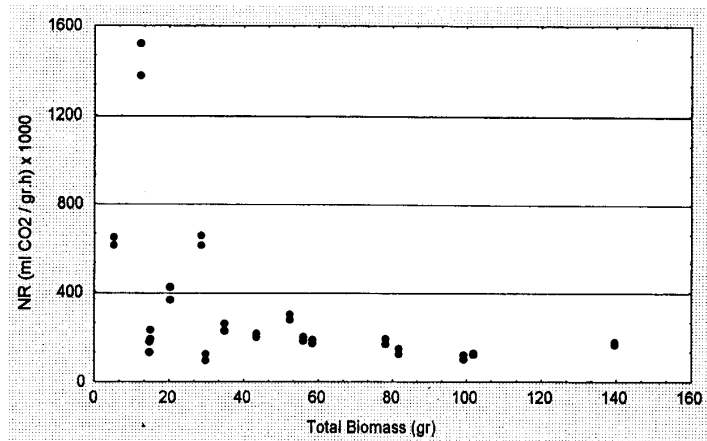


FIG. 2. NR values for nests of different size. Each nests was measured twice. A biomass of 1 g of dw represents approximately 2075 soldiers or 1067 workers with a dw/fw ratio of, respectively, 0.31 and 0.24.

assumes a constant relationship between NR and the colonies biomass. Model 2 assumes that NR diminishes linearly with colony size, models 3-6 assume an inverse exponential relation between NR and colony size, where models 4, 5, and 6 decompose the total biomass into the different components of the colony. In model 4 the NR is the daily average, in model 5 the NR is the minimum of the daily cycle, and in model 6 the NR is the maximum of the daily cycle. The best fit was obtained with models 4-6 and the worst with model 1, suggesting that NR correlates inversely with colony size and that the various castes contribute differently to NR.

DISCUSSION

The results clearly suggest that hypothesis (b) holds for termites. That is, energy consumption per capita in termite colonies decreases with increasing colony size.

Other results give us additional information about the EC colony size relationship in termite colonies. The lack of correlation between CO₂ production of termite colonies and temperature suggests that termite colonies regulate their temperature and are thus unaffected by small changes of environmental temperature. As can be appreciated in Fig. 1, the circadian cycle of NR has a sinusoidal form, with a minimum respiration during the day and a maximum at night. Most Nasutitermitinae are nocturnal foragers. As termites had wood and sufficient space in the respiration chamber to forage, it is probable that these differences in NR are due, at least partially, to differences in foraging activity.

NR measures the total sum of all activities that require oxygen. These activities include basal metabolism, locomotion, growth, food processing, reproduction, etc. In the case of social species, it has been assumed that the energetic requirements of the society are just the sum of the basic requirements

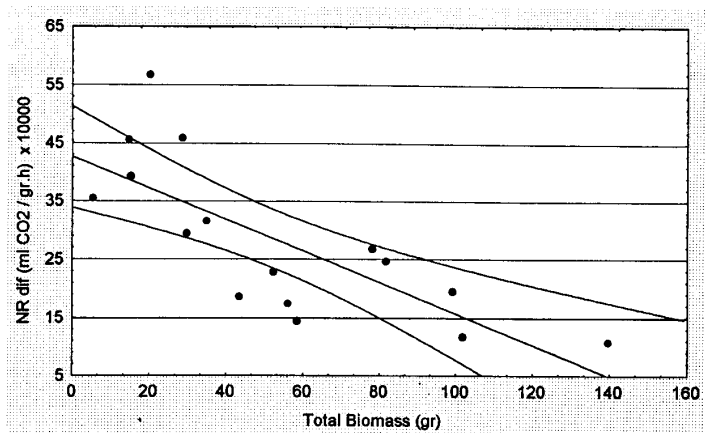


FIG. 3. NR dif values for nests of different size. Each data represents the mean of two measurements.

TABLE 1
REGRESSION COEFFICIENTS BETWEEN NR AND COLONY
BIOMASS USING DIFFERENT MODELS FOR CALCULATING
THE REGRESSION

Model	r	p
1: NR mean = 5.285	0.00	1.00
2: NR mean = 8.8 - 0.07B	0.475	0.054
3: NR mean = 2.3 + 13.9 e ^(-0.04B)	0.590	0.013
4: NR mean = 3.5 + 26.1 e ^(-0.8n - 42.7s - 0.18N + 0.8S)	0.636	0.006
5: NR min = 3.2 + 25.7 e ^(-0.8n - 43.8s - 0.18N + 0.81S)	0.641	0.006
6: NR max = 3.7 + 26.8 e ^(-0.8n - 41.4s - 0.17N + 0.78S)	0.634	0.006

NR = Normalized respiration rate; B = total biomass; n = biomass of worker nymphs; s = biomass of soldier nymphs; N = biomass of adult workers; S = biomass of adult soldiers.

of its individuals. Our results do not support this view; NR values and NR differences between maximum and minimum values of the daily cycle decrease with colony size. We do not know, however, what the activities requiring energy are during minimum and maximum activity levels. NR_{min} does not represent the basal energy requirements of the colony, but we may safely assume that the difference between NR_{min} and NR_{max} includes the foraging activity of the colony, and that the daily NR variations are less than 8.5% of the total NR.

It is interesting to note that NR decreased with colony size independently of the type of measurement (i.e., NR_{diff}, NR_{mean}, NR_{min}, and NR_{max}). Different explanatory hypothesis can be proposed: (a) all colonies need to performed roughly the same amount of work and thus, in larger colonies, this work is proportionally lower than in small ones. That is, larger colonies might have larger reserves of inactive workers, or individual workers work less than in smaller colonies. (b) The degree of individual efficiency increases with colony size. For example, specialization, and thus efficiency, of temporal and morphological castes increases with colony size. (c) Miramontes and DeSouza (7) showed that the survival of individual termites increased with increasing number of workers forming experimental aggregates. By comparing their results with computer simulations, they suggested that this phenomena was related to social interactions, which become more efficient in larger groups. A similar explanation may be applied to our results. (d) Larger nests have a larger proportion of termites in areas of the nest with low air ventilation, which will reduce their respiration rate (13). This may be an indirect way for large colonies to reduce their per capita energy consumption.

Clearly, detailed behavioral studies are needed to understand the phenomena uncovered here and to determine which of the putative mechanisms proposed above are used by termites colonies. Thermodynamic studies only allow to detect basic phenomena, but are useless in explaining causal relationships. However, results in Table 1 suggest that the contri-

bution of the various castes to the NR is different as has been reported previously (4,5,12). Thus, not only colony size is important for explaining NR but also the specific caste composition will affect NR.

The inverse relationship found between colony size and per capita respiration rate, i.e., curves in Table 1, which are derived from data for colony respiration, cannot be extrapolated to individual termites or small groups of termites. For example, the 100 workers mentioned above, measured by Damaschke and Becker (2), weight about 0.03 g. We may thus calculate, using formula 4 of Table 1, that NR mean = 29 mL/g(dw)/h, which is 16 times higher than what was reported by these authors (8). An inverse exponential relationship between NR and the size of the social system, starting from specific minimal sizes of social system, has been reported previously for ants (3,6) and for the relation between energy consumption and number of inhabitants among human settlements [(1) and included references]. The fact that a similar relationship applies to termite colonies, as shown here, suggest that this pattern may be a general characteristic of social systems. Fonck and Jaffe (3) found that in very small groupings of ants the inverse exponential relationship does not appear, but only after a threshold ant group size, which is specific for each species, does the inverse exponential relation becomes evident. A similar phenomenon was evidenced by studying total energy consumption of human settlements (1). In this study, we considered that groupings of a few isolated termites were too artificial to merit experimental study, as termites die very fast when isolated, but similar patterns may also be present in termites.

It seems trivial to suppose that social life has adaptive advantages, the more so when resources are limiting, as they seem to be more efficient in exploiting them. At the same time social behavior may decrease parasitism and predation risks. In addition, life expectancy increases with diminishing standard metabolism. All these factors increase individual fitness with increasing colony size. Here we showed that energy efficiency is also achieved with increased colony size. Although, energy efficiency is not necessarily achieved with social life (6), once social life exists, larger societies seem to be better in using energy than smaller ones. The strong effect that colony size has on NR, suggests that by pure energetic considerations, large societies should be favored in biological evolution. There must be a limit to colony size, as we were unable to locate in the field much larger nests than those studied, but this limit may or may not be determined by energetic considerations.

In summary, our results seem to be consistent with previous data reported in the literature, and factors such as temperature, daily rhythms, or caste composition of termite colonies do not explain by their own the results obtained. It, thus, seems safe to assume that termite colonies optimize their use of energy as colonies get larger. We propose that this optimization is a general principle of social systems as it seems to apply also in ant societies (3,6) and in human settlements (1).

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