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A SIMULATION OF WOOD CONSUMPTION BY THE SUBTERRANEAN TERMITE, *HETEROTERMES AUREUS* (SNYDER), IN AN ARIZONA DESERT GRASSLAND (1)

By MICHAEL I. HAVERTY and WILLIAM L. NUTTING

Department of Entomology, University of Arizona, Tucson, Arizona, 85721, U.S.A.

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SUMMARY

A simple model is presented which simulates the consumption of superficial dead wood in a desert grassland by a single termite species over a period of one year. Temperature-dependent functions of termite foraging intensity and wood consumption are most critical. The model was designed to run on mean daily temperature and daily rainfall. The model predicts that *Heterotermes aureus* foragers were able to make 4.61×10^{10} visits to the surface per hectare during the year of simulation. It estimates that there were only seven days during this period that *H. aureus* did not forage. It calculates that this species removed dead wood at the rate of 78.9 kg/ha/yr, which represents 3.7 percent of the standing crop biomass and 17.5 percent of the annual production of superficial dead wood. The importance of this termite is emphasized by its removal of preferred species of wood.

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ZUSAMMENFASSUNG

Mathematisches Modell des Holzverzehrs durch die Termite, *Heterotermes aureus* (Synder), in einem semi-ariden Grasland Arizonas.

Dargestellt wird ein einfaches mathematisches Modell, das die Verzehrung des in einem semi-ariden Grasland in Arizona auf der Oberfläche liegenden abgestorbenen Holzes durch eine einzelne Termitenart im Zeitraum eines Jahres voraussagt. Von höchster Bedeutung sind die temperaturabhängigen Funktionen der Intensität der Futtersuche und der Holzverzehrung der Termiten. Das Modell wurde so aufgestellt, daß es vom Tagestemperaturmittel und der täglichen Niederschlagsmenge abhängig ist. Das Modell sagt voraus, daß futtersuchende *Heterotermes aureus* während des Simulations jahres die Oberfläche $4{,}61 \times 10^{10}$ mal pro Hektar besuchen. Es wird errechnet daß *H. aureus* nur an 7 Tagen im Jahre nicht auf die Futtersuche geht. Ferner lässt sich errechnen, daß diese Termitenart 78,9 K/Ha/J abgestorbenes Holz verzeht, was 3,7 % der stehenden Biomasse und 17,5 % der jährlichen Produktion toten Holzes darstellt. Die Bedeutung dieser Termite wird durch die von ihr verursachte Entfernung von bevorzugten Holzarten betont.

INTRODUCTION

The development of models which describe populations and which can be used for predictive purposes is one of the major goals of an ecologist (HADLEY, 1972). In this paper we present a simple model which simulates the consumption of superficial dead wood by a single termite species over a period of one year. To our knowledge this is one of few attempts at computer simulation of food consumption by social insects (HADLEY, 1972; BARONI-URBANI, 1972), and the first such attempt for subterranean termites. Because of the cryptic behavior of subterranean termites, there are relatively few comprehensive studies which examine their ecology and demography. Most such studies have concerned themselves primarily with the obvious mound builders, or harvesting species which forage above ground, even though subterranean termites may be at least as numerous and ecologically more important (SANDS, 1972).

There are approximately 40 species of termites in the continental United States and at least 16 of these occur in the Tucson Basin in southern Arizona. This represents the largest number and greatest diversity of species in any area of comparable size in this country. Ten are subterranean and feed on a variety of foods including wood, dried vegetation, dung and perhaps humus (NUTTING, 1968). *Heterotermes aurçus* (Snyder) is probably the most destructive of the subterranean termites in this area.

Since it is an economically important species, we have postulated that it must also be an important detritivore in the Sonoran Desert ecosystem. With regard to its function in the detritus cycle we then asked how much wood it

could consume or remove from the ecosystem per unit area per unit time. We chose to develop a simple model to answer this question since it provides input for a larger model designed to evaluate the flow of energy through a termite community and the return of nutrients, released from dead plant material, to the soil.

METHODS

To evaluate the role of *H. areus* in removing superficial dead wood from a desert grassland ecosystem we have used data from many sources, some unpublished (2). Temperature-dependent functions of termite foraging intensity and wood consumption are most critical. Both mean daily, and hourly, temperatures (°C at food-soil interface) were tried with very similar results. To reduce computer time then, the model was designed to run on mean daily temperature and daily rainfall for a period of one year. The data used for running the model here were taken during our field studies of *H. aureus* on the Santa Rita Experimental Range, ca. 40 km south of Tucson, Arizona (HAVERTY *et al.*, 1974).

A description of the model's operation is best illustrated by a detailed outline of the logic involved :

1. Read daily temperature and rainfall.

For each day of the year, 24 hourly temperatures (°C) and daily rainfall (mm) are read in and a daily mean temperature calculated. The model assumes that the termites forage as long as the mean temperature does not fall below 4.0 °C, since this is the lowest daily mean temperature at which *H. aureus* has been observed foraging.

2. Calculate number of foragers visiting food source each day.

Temperature and rainfall values are entered into the equation $\ln Y = -0.985 - 0.0761 (\text{Temp}) + 2.928 (\log_e \text{Temp}) + 0.327 (\log_e \text{Rain})$ to determine Y, the mean number of foragers above the surface per 100 m^2 at any point in time during the day. At temperatures below 4.0 °C, the model automatically assigns the number of foragers a value of 0. Since these data come from a study area of only 0.01 ha (LAFAGE *et al.*, 1973; NUTTING *et al.*, 1973), the number of foragers observed is multiplied by 100 to provide an estimated foraging force/ha.

The above equation does not estimate the number of termites foraging at the surface during a day, but only the number observed at a single point in time

(2) HAVERTY (M. I.), 1974. The significance of the subterranean termite, *Heterotermes aureus* (Snyder), as a detritivore in a desert grassland ecosystem. Ph.D. Dissertation, University of Arizona, Tucson, Arizona, U.S.A., p. 89.

within the day. It therefore becomes necessary to determine how fast the termites above the surface might be replaced by an equal number from below. This required one major assumption : the numbers below the surface are very large; that is, there will always be an ample subsurface force to replace those foraging above. This assumption necessitated the establishment of a forager « turnover rate » based on the speed at which termites travel as a function of temperature. SKAIFE (1955) measured the speed (in cm/minute) of *Amitermes hastatus* (Haviland) between 10-30 °C. On the assumption that *H. aureus* moves at the same speed, these data have been used to develop the following equation to calculate the distance a forager can travel in one day :

$$\text{Speed (cm/day)} = (-1.47 + (1.62 \times \text{Temp})) \times 60 \times 24.$$

To complete one circuit from the underground forager pool (estimated at 2 cm below the soil surface) to the food source (here we have used the height of a toilet paper roll, LAFAGE *et al.*, 1973) and back to the pool, a termite must travel a maximum distance of 26.9 cm. Thus the number of foraging round-trips per day, or turnover rate, may be expressed as follows : Turnovers/day = Speed (cm/day)/Maximum distance (cm).

The model multiplies the number of turnovers/day by the number of foragers observed at some instant during the day; the product represents the total force visiting the food source during that day.

3. Convert termite numbers to biomass.

Numbers are converted to biomass because wood consumption rates have been determined as a function of termite biomass (HAVERTY and NUTTING, 1974), not numbers of termites. Forager biomass is calculated from data on size and caste composition of foraging groups. Proportional caste composition and corresponding individual caste biomass of *H. aureus* foraging groups are given in Table I. The foraging biomass is obtained by summing the products of the numbers of each caste times the average biomass per individual.

TABLE I. — Caste composition and individual caste biomass of an average *Heterotermes aureus* foraging group on the Santa Rita Experimental Range. Data based on counts and measurements of 40 foraging groups.

TABELLE I. — Zusammensetzung der Kasten und Biomassen der einzelnen Kasten einer typischen Furagiergruppe von *Heterotermes aureus* auf der Santa Rita Experimental Range. Die Angaben beruhen auf den Zählungen und Messungen von 40 Furagiergruppen.

Caste	Percent of group	Individual biomass, mg *
Larva	0.1	0.26
Larva-worker	97.2	0.34
Soldier	1.6	0.47
Nymph	1.1	1.05

* Dried to constant weight at 60 °C.

4. Proportion termite biomass to different woods and determine daily consumption of each wood species.

H. aureus preferentially divides its foraging attention toward different species of wood (Table II). Therefore, it follows that its foraging biomass must also be

TABLE II. — Proportion of termite biomass assigned to each species or category of wood. Santa Rita Experimental Range, Pima Co., Arizona.

TABELLE II. — Anteile der Termitenbiomasse an den verschiedenen Holzarten oder -kategorien. Santa Rita Experimental Range, Pima County, Arizona.

Wood species or category	Proportion *
Acacia greggii	.173
Celtis pallida	.061
Cercidium floridum	.017
Ephedra trifurca	.038
Gutierrezia sarothrae	.006
Opuntia engelmannii	.017
O. fulgida	.179
O. spinosior	.355
O. fulgida and *O. spinosior*, joints	.012
Prosopis juliflora	.133
Other woods	.009
Total	1.0

* The proportion is the ratio of the number of units of each species or category of wood attacked by *H. aureus* to all units attacked by it.

partitioned into percentages of the total which will process each of the 11 species or categories of wood in the system. Different species of wood are consumed by termites at varying rates as a result of many factors. These rates have been determined for *H. aureus* on four species of wood at six temperatures (HAVERTY and NUTTING, 1974) and regressed to yield consumption equations for each of 11 species or categories of wood (Table III). At some temperatures above 4 °C it is possible to obtain negative consumption values with the regression equations. This is, of course, biologically impossible; therefore, if the consumption equation yields a negative value, a consumption rate of zero is assumed. Thus the amount of each wood species consumed is the product of a particular consumption rate times its assigned termite biomass.

5. Repeat daily procedure and sum over the year.

The temperature-dependent, daily consumption of each wood species is summed to give a total daily wood consumption, and these daily figures summed over a year to provide the total annual amount of wood consumed by *H. aureus*.

TABLE III. — Equations for consumption (mg wood/g termite biomass/day) of the species or categories of wood by *Heterotermes aureus* as a function of temperature (x).

TABELLE III. — Berechnung des Verzehrs (Mg Holz/g Termitenbiomasse/Tag) von 10 Holzarten bzw. -kategorien durch *Heterotermes aureus* als Funktion der Temperatur (×).

Wood species	Consumption rate mg wood/g termite biomass/day
Acacia greggii *	70.32
Cercidium floridum	$-137.90 + 20.45\ x - 0.338\ x^2$
Prosopis juliflora	$-13.66 + 3.48\ x$
Opuntia fulgida, Opuntia spinosior **	$-310.15 + 27.96\ x - 0.462\ x^2$
Celtis pallida, Ephedra trifurca, Gutierrezia sarothrae, Opuntia engelmanii, O. fulgida and *O. spinosior* joints, Other woods ***	$-165.38 + 20.45\ x - 0.338\ x^2$

* No significant regression obtainable, therefore consumption rate is mean of 6 rates determined between 16-36 °C.

** Because of the similarity between species, *spinosior* was assigned the same consumption rate as that determined for *fulgida*.

*** Specific consumption rates for these six categories of wood were not determined. Rate estimated by combining data for 4 wood species tested between 16-36 °C.

* Es war keine bedeutende Regression festzustellen; daher wird die Verzehrsrate als Mittlewert von 6 zwischen 16° und 36 °C festgestellten Werten angegeben.

** Wegen der Ähnlichkeit der Holzarten wurde für *O. spinosior* die bei *O. fulgida* festgestellte Verzehrsrate angenommen.

*** Für diese 6 Holzkategorien wurden keine spezifische Verzehrsraten festgestellt. Die Verzehrsrate wurde durch Kombination der Meßraten für 4 Holzarten, die bei 16-36 °C gemessen wurden, abgeschätzt.

RESULTS

The model predicts that there were only seven days, all within the month of December, between October 15, 1971, and October 13, 1972, in which *H. aureus* did not forage. Foragers were thus able to make 4.61×10^{10} visits to the surface per ha during the year of simulation. It calculates that this species removed superficial dead wood at the rate of 78.9 kg/ha/yr. This represents 3.7 percent of the standing crop biomass and 17.5 percent of the annual production of superficial dead wood on our research area (2,127 kg/ha and 450 kg/ha/yr, respectively; HAVERTY, 1974). The simulated, annual consumption of individual wood species is presented in Table IV. *H. aureus* fed upon eleven categories of wood, four species of which account for 80.61 percent of all wood consumed in our simulation (kg/ha/yr) : *Opuntia spinosior* (26.0), *Acacia greggii* (13.3), *O. fulgida* (13.1) and *Prosopis juliflora* (11.2).

Our model also emphasizes *Heterotermes'* role in selectively removing wood from the ecosystem. Two (*O. spinosior* and *O. fulgida*) of the five dominant wood species (the above plus *Cercidium floridum*) were consumed by *H. aureus* at a rate equal to or greater than that of the over all average (Table IV). Although substantial quantities of *A. greggii* and *P. juliflora* are consumed, this is only a small proportion of the standing crop of each species (2.10 and 3.11 percent,

TABLE IV. — Simulated annual consumption of twelve categories of wood, by *Heterotermes aureus*, and percentage of dead wood standing crop biomass consumed (annually).

TABELLE IV. — Simulierter jährlicher Verzehr von 12 Holzkategorien durch *Heterotermes aureus* und % der jährlich verzehrten stehenden toten Biomasse.

Wood species	Annual consumption (kg/ha/yr)	% Annual consumption of standing crop
Acacia greggii	13.3	2.1
Celtis pallida	5.6	32.8
Cercidium floridum	2.3	1.7
Ephedra trifurca	3.5	43.1
Gutierrezia sarothrae	0.5	6.6
Opuntia engelmannii	1.6	15.9
Opuntia fulgida	13.1	3.7
Opuntia spinosior	26.0	8.3
O. fulgida & spinosior, joints	1.1	0.4
Prosopis juliflora	11.2	3.1
Other woods	0.8	11.4
All woods, average	78.9	3.7

respectively; HAVERTY, 1974). The larger portion of the latter two wood species is probably consumed by other soil dwelling termites, *Gnathamitermes perplexus* (Banks), *Paraneotermes simplicicornis* (Banks) and *Amitermes* spp., which allocate a substantial portion of their foraging activities to these two woods (HAVERTY and NUTTING, unpublished).

Of the remaining, less abundant species of wood, *H. aureus* appears to exert extreme pressure on both *Celtis pallida* and *Ephedra trifurca.* Since *Celtis* is highly preferred and attacked almost exclusively by *H. aureus,* one would expect a heavy impact on this species. *Ephedra,* on the other hand, is less preferred and attacked as often by *G. perplexus* as by *H. aureus* (HAVERTY and NUTTING, unpublished). It is curious then, that the model predicts such a high annual consumption of this wood. The average, temperature-dependent consumption rate of *E. trifurca* may be much too high.

DISCUSSION

Wood or food consumption by termites may be measured directly by weight differences of food offered for a given period of time (NUTTING *et al.,* 1973; see below). However, if direct measurement is not practical, indirect estimates of consumption can be derived through two types of simulation. The first requires a detailed knowledge of the species energy budget and population parameters (JOSENS, 1973). If maintenance and production energy requirements are known for a population of a certain size, it should be possible to predict, *a posteriori,* the amount of food it would need to consume in order to meet its energy requirements under given environmental conditions (HADLEY, 1972). The second approach requires a knowledge of population parameters and behavioral res-

ponses under known environmental conditions. Wood consumption is predicted *a priori* by coupling population numbers or foraging sorties with temperature-dependent, species-specific food consumption rates as we have done here.

We have determined the number of termite foragers attacking a food source per unit time as the product of two temperature-dependent functions : the size of the surface foraging force and the rate at which it turns over. DE BRUYN and DE BRUIN (1972) have used the same type of logic in developing a model to determine the number of *Formica polyctena* Först. captured in pitfall traps (N_t). This number is the product of two factors : $N_t = (P_t)\ (V_t)$ where P_t is the number of ants present at a given temperature and V_t is their velocity at this temperature.

We have assigned *H. aureus* foraging biomass proportionately among the wood species (or categories) on the basis of carefully determined preferences (Table II). The resulting partitioned foraging biomasses are then coupled with specific, temperature-dependent wood consumption rates which were determined in laboratory tests (HAVERTY and NUTTING, 1974). In this simulation of ant food consumption BARONI-URBANI (1972) assigned all foragers of a particular species to the most preferred food. If this food was being utilized by another ant species or otherwise not available, foragers were then assigned the next most preferred food and so on. However, we do not believe that this is a realistic way to assign termite foragers among wood species (food). Long-term simulation over large areas requires a model to describe and utilize average behavior (WATT, 1962). Even though *H. aureus* prefers certain woods it does utilize almost all sources of woody plant material.

By direct measurement paper (essentially pure cellulose) consumption by *H. aureus* in the field was shown to be at least 19.5 kg/ha/yr and possibly as much as 33.9 (NUTTING *et al.*, 1973). Our simulation estimate of annual wood consumption by *H. aureus* (78.9 kg/ha/yr) is, therefore, of a reasonable order of magnitude and considerably less than the annual accumulation (450 kg/ha/yr; HAVERTY, 1974). Certain parameters used in the model are undoubtedly contributing to the over- or under-estimation of consumption, and should be refined.

We believe our foraging population figures are good since our periodic visual estimates were verified against actual counts, and the relationships between foraging intensity and environmental factors are quite good ($R^2 = .612$, $\alpha = .01$; HAVERTY *et al.*, 1974). However forager speed may be excessive since it was determined for horizontal and not vertical movement, and does not allow for any inefficiency. Many students of social insects have noted that these insects spend a good deal of their time idle (WILSON, 1971). Such considerations might easily cause over-estimation of the forager turnover rate.

Wood consumption rates determined in the laboratory are probably lower than they would be in the field. This is because termites in laboratory test groups have few nest mates to feed and, since they do not appear to store wood, they consume only what they need for themselves. Therefore, in our model, any over-estimation of wood consumption due to an excessive turnover rate,

might tend to balance the under-estimation caused by low consumption rates.

Termites may have a considerable role in the removal and recycling of plant material in an ecosystem. The effect of termite grazing can be so great that whole areas are denuded of grass (COATON, 1951; WATSON and GAY, 1970). BASSON (1972) conservatively estimated that *Hodotermes mossambicus* (Hagen) removed 274 kg/ha/yr from veld in South Africa. NEL (1970), in a different area, calculated that the same species removed only 14.6 kg/ha/yr or one percent of the total production of dry material. BODINE (1973) estimated that *Gnathamitermes tubiformans* (Buckley) removed 360 kg of grass/ha/yr from rangeland or 12 percent of the net primary productivity. LEE and WOOD (1971) estimated that *Nasutitermes exitiosus* (Hill), which feeds on sound wood, consumed 116 kg/ha/yr or 16.6 percent of the annual production of superficial dead wood (700 kg/ha/yr) in a dry sclerophyll forest in Australia. Both BODINE (1973) and LEE and WOOD (1971) used consumption rates determined at one temperature to predict annual consumption of grass or wood.

Our simulated estimate of the effect of *H. aureus* on the fallen dead wood in a desert grassland is comparable to that of *N. exitiosus* in Australia. Each species apparently processed an almost equivalent proportion (17.5 and 16.6 percent, respectively) of the annual accumulation of fallen sticks and logs. The impact of *Heterotermes* on wood removal is greatest in its selective pressures exerted on certain species of wood, notably *Opuntia spinosior* and *O. fulgida.*

Heterotermes aureus is only one of four important soil dwelling termites on the Santa Rita Experimental Range. The other three species have host preferences (*Acacia greggii, Cercidium floridum* and grasses) which complement those of *H. aureus.* Since termite micro-organisms have recently been shown to fix atmospheric nitrogen (BREZNAK *et al.*, 1973; BENEMANN, 1973), a logical and eventual extension of our model would be to include other termite species and to determine their nitrogen and energy budgets. By doing this we might eventually ascertain how each or all function(s) to increase the fertility of the soil by the addition of available nitrogen compounds and the production of numerous alates as food for a variety of predators.

This first attempt at simulating wood consumption by one subterranean termite species has given results of a reasonable order of magnitude. We will continue to exercise the model to determine its sensitivity to long term variation in environmental parameters. However, our model answers the question « how much wood can *H. aureus* consume or remove from the ecosystem per unit area per unit time ? » and suggests that this species is an important component of the desert grassland ecosystem.

REFERENCES

BARONI-URBANI (C.), 1972. — An example of the usefulness of simulation techniques in ecological researches : the study on food consumption of a large ant community. *Ekol. Pol., 20,* 33-42.

BASSON (N. C. J.), 1972. — Beskadiging van natuurlike wieveld in die Noord-Vrystaat deur die grasdraer-termiet, *Hodotermes mossambicus* (Hagen). *Phytophylactica, 4,* 67-72.

BENEMANN (J. R.), 1973. — Nitrogen fixation in termites. *Science, 181,* 164-165.

BODINE (M. C.), 1973. — The impact of the termite *Gnathamitermes tubiformans* on rangeland herbage dynamics. *M.S. Thesis, Texas Tech. Univ.,* Lubbock, Texas, U.S.A., 39 p.

BREZNAK (J. A.), BRILL (W. J.), MERTINS (J. W.) and COPPEL (H. C.), 1973. — Nitrogen fixation in termites. *Nature, 244,* 577-580.

COATON (W. G. H.), 1951. — The snouted harvester termite; natural mortality as an aid to chemical control. *Farm. S. Afr., 26,* 263-267.

DE BRUYN (G. J.) and DE BRUIN (M. K.), 1972. — The diurnal rhythm in a population of *Formica polyctena* Först. *Ekol. Pol., 20,* 117-127.

HADLEY (M.), 1972. — Perspectives in productivity studies, with special reference to some social insect populations. *Ekol. Pol., 20,* 173-184.

HAVERTY (M. I.), 1974. — The significance of the subterranean termite, *Heterotermes aureus* (Snyder), as a detritivore in a desert grassland ecosystem. *Ph.D. Dissertation, The University of Arizona,* Tucson, Arizona, U.S.A., 89 p.

HAVERTY (M. I.) and NUTTING (W. L.), 1974. — Natural-wood consumption rates and survival of a dry-wood and a subterranean termite at constant temperatures. *Ann. Entomol. Soc. Amer., 67,* 153-157.

HAVERTY (M. I.), LAFAGE (J. P.) and NUTTING (W. L.), 1974. — Seasonal activity and environmental control of foraging of the subterranean termite, *Heterotermes aureus* (Snyder), in a desert grassland. *Life Sciences, 15,* 1091-1101.

JOSENS (G.), 1973. — Observations sur les bilans énergétiques dans deux populations de termites a Lamto (Côte d'Ivoire). *Ann. Soc. Roy. Zool. Bel., 103,* 169-176.

LAFAGE (J. P.), NUTTING (W. L.) and HAVERTY (M. I.), 1973. — Desert subterranean termites : A method for studying foraging behavior. *Environ. Entomol., 2,* 954-956.

LEE (K. E.) and WOOD (T. G.), 1971. — Termites and Soils. *Academic Press* Publ., New York. 25 p.

NEL (J. J. C.), 1970. — Aspekte van die gedrag van die werkers van die grasdraertermiet, *Hodotermes mossambicus* (Hagen). in die veld. *J. Entomol. Soc. S. Afr., 33,* 23-24.

NUTTING (W. L.), 1968. — Termites in Arizona. *Prog. Agric. Arizona* (U.S.A.), *20,* 8-9.

NUTTING (W. L.), HAVERTY (M. I.) and LAFAGE (J. P.), 1973. — Foraging behaviour of two species of subterranean termites in the Sonoran Desert of Arizona. *Proc. 7th Internat. Congr., Internat. Union for the Study of Social Insects,* London, Sept. 10-15, 298-301.

SANDS (W. A.), 1972. — Problems in attempting to sample tropical subterranean termite populations. *Ekol. Pol., 20,* 23-31.

SKAIFE (S. H.), 1955. — Dwellers in Darkness, *Longmans Green,* Publ., London, 134 p.

WATSON (J. A. L.) and GAY (F. J.), 1970. — The role of grass-eating termites in the degradation of a mulga ecosystem. *Search, 1,* 43.

WATT (K. E. F.), 1962. — Use of mathematics in population ecology. *Annual Rev. Entomol., 7,* 243-260.

WILSON (E. O.), 1971. — The Insect Societies. *Belknap Press of Harvard Univ. Press,* Publ., Cambridge, Mass., 548 p.