Refuse to Refuge: Dry Season Use and Modification of Cattle Dung by Subterranean Termites in Guanacaste, Costa Rica[1]

Kevin A. Gould[2]

373 Newins-Ziegler Hall, School of Forest Resources and Conservation, University of Florida, Gainesville, Florida 32611, U.S.A.

Jeffrey E. Herrick

USDA-ARS Jornada Experimental Range, P.O. Box 30003, MSC 3JER, NMSU, Las Cruces, New Mexico 88003-8003, U.S.A.

and

Humberto Lezama

Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica

ABSTRACT

Baits and soil cores were used to quantify temporal variation in the use of cattle dung by two species of subterranean termites, *Amitermes beaumonti* Banks and *Hoplotermes* sp. nov. (hereafter referred to by genus), during the 1991 dry season in Guanacaste, Costa Rica. The densities of termite foragers of both species were evaluated in cattle dung patches (baits), in the soil beneath each patch (litter, 0–3.5 cm, and 3.5–7 cm), and in the same layers from adjacent dung-free control sites. Dung patch and control plots were sampled 3, 10, 60, or 110 days after 1450-ml dung patches were deposited on the pasture. *Amitermes* foragers were abundant in 3-, 10-, 60-, and 110-day-old dung patch plots with a mean (median) ± SD of 100 (59) ± 120 individuals/bait plot, and only 8 (3) ± 11 individuals/control plot. *Hoplotermes* foragers were less abundant, with a mean of 22 (0) ± 87 individuals in dung patch plots and 2 (0) ± 9 in control plots. *Hoplotermes* was most abundant in the surface litter under 10-day-old dung patches, where an average of 39 (0) ± 105 individuals were found. In association with dung patches, *Amitermes* density was highest inside or directly beneath the dung patch and lowest in the 3.5- to 7.0-cm microsite. In control areas, however, *Amitermes* was most abundant in the 3.5- to 7.0-cm microsite. *Amitermes* and *Hoplotermes* were found in 35 and 9 of the 54 control plots, respectively. We believe that the high termite densities associated with cattle dung patches can be explained by the energetic and microclimatic requirements of the termites and the physical structure of the dung. Although neither species of termite is a mound builder, these termites use specialized behaviors to exploit and modify dung patches such that foragers have access to concentrated food resources and partial protection from the dry climate and from their invertebrate predators.

RESUMEN

Cebos de excremento de vaca y muestras de suelo fueron usados para cuantificar la variación temporal en el uso de excremento de vaca por dos especies de termitas subterráneas, *Amitermes beaumonti* Banks y *Hoplotermes* sp. nov. (desde aquí referidas por el género), durante la temporada seca de 1991 en Guanacaste, Costa Rica. Se evaluaron las densidades de termitas forrajeras de las dos especies, en los parches de excremento (cebos), en las capas del suelo bajo cada excremento, (superficie, 0–3.5 cm, y 3.5–7.0 cm), y en las mismas capas en sitios adyacentes libres de excremento (controles). Tanto los parches de excremento como los controles fueron muestreados 3-, 10-, 60-, o 110-días después de que los cebos de 1450 ml fueron puestos en el potrero. Los individuos forrajeros de *Amitermes* fueron más abundantes en parcelas de excremento de 3, 10, 60, y 110 días con un promedio (mediana) ± desviacion estandard de 100 (59) ± 120 individuos por parcela, mientras las parcelas control tuvieron solo 8 (3) ± 11 individuos por parcela. Individuos forrajeros de *Hoplotermes* fueron menos abundantes con un promedio de 22 (0) ± 87 individuos en las parcelas de excremento y 2 (0) ± 9 en las parcelas control. *Hoplotermes* fué mas abundantes en la materia orgánica superficial debajo de los parches de excremento de 10 días, donde se encontró un promedio de 39 (0) ± 105 individuos por parcela. En los parches de excremento la densidad de *Amitermes* fué más alta dentro y directamente debajo de estos y más baja entre 3.5 y 7.0 cm. En los controles, sin embargo, *Amitermes* fué más abundante en el suelo entre 3.5 y 7.0 cm. Se encontraron individuos de *Amitermes* y *Hoplotermes* en 35 y 9 de los 54 sitios controles, respectivamente. Estas altas densidades de termitas asociadas con el excremento de vaca pueden obedecer a los requerimientos energéticos y microclimaticos de las termitas y la estructura física del excremento. A pesar de que ninguna

[2] Corresponding author, E-mail: kgould@ufl.edu

de estas dos especies es constructora de montículos, estas termitas presentan comportamientos especializados para maximizar y modificar los parches de excremento de tal manera que los individuos forrajeros tengan acceso a recursos más concentrados de alimento y una protección parcial contra el clima e invertebrados depredadores de termitas.

SUBTERRANEAN TERMITES ARE AMONG THE LEAST KNOWN, yet potentially most important, soil macroinvertebrates in many areas of the seasonally dry tropics (Lee & Wood 1971, Sands 1972). They appear to play a key role as decomposers during the dry season when few other soil macroinvertebrates are active. Historically, investigators have focused on mound building termites despite the fact that "subterranean termites of tropical savannas . . . are at least as numerous and ecologically significant" (Sands 1972). Because of the inaccessibility of subterranean termites to researchers, only foraging individuals can be sampled effectively (Sands 1972).

Herrick and Lal (1995) quantified changes in soil physical properties associated with the decomposition of cattle dung at Hacienda La Pacifica, Guanacaste, Costa Rica, but little is known of the biology of the invertebrates that appear to be responsible for these changes. In other seasonally dry tropical ecosystems, dung is consumed primarily by coprophagous beetles during the wet season and by termites during the dry season, (*e.g.*, Coe 1977). Soil dwelling termites are the primary decomposers of dung in the Chihuahuan desert, with dung beetles playing a minor role during wet periods (Whitford *et al.* 1982). Although Janzen (1983a) described extensive wet season dung beetle activity in Guanacaste pastures, he found that cattle dung is untouched by decomposers during the dry season (Janzen 1983b). Herrick and Lal (1996) found that decomposition rates for cattle dung deposited at the beginning of the dry season were nearly 50 percent of those recorded during the wet season. Based on these data and rough estimates of total Coleoptera and termite densities, they attributed the dry season dung removal to termite activity.

We hypothesized that near-surface, dry season termite activity in Guanacaste pastures is concentrated around cattle dung patches. This study was designed to describe the spatial and temporal patterns of soil termite activity with respect to dung deposited during the dry season and to interpret these patterns in relation to exogenous environmental factors that control termite behavior, and termite responses to these factors.

MATERIALS AND METHODS

SITE DESCRIPTION.—This study was conducted during the dry season (December 1990–May 1991) at Hacienda La Pacifica, a cattle farm and ecotourism site, 5 km north of Cañas, Guanacaste (10°28'36"N, 85°9'14"W; 50 m elev.). During the dry season, only ten percent of the 1220 mm annual precipitation normally occurs (Hagnauer 1993). The slope at the study site was one to three percent and the soil was classified as a Typic Argiustoll. A complete description of the climatic and edaphic conditions at the site can be found in Herrick and Lal (1995).

Typical of pastures in the seasonally dry, Pacific coastal regions of Central America, the study site is dominated by *Hyparrhenia rufa*, a low quality pasture grass introduced from Africa (Daubenmire 1972, Vargas & Fonseca 1989). The site was cleared first at the turn of the century and again in 1965. Before it was converted to nonirrigated cattle pasture in 1970, it was planted (briefly) with cotton, sorghum, and rice.

Cattle were excluded from the 0.5-ha experimental area beginning November 1989. The pasture was cut to a height of 10 cm with a machete immediately prior to the first experimental dung deposition in December 1989. Cut grass was removed by hand raking.

Within the study area, we divided a 20- × 30-m grid into 576 0.8- × 0.8-m plots in which dung patch baits were eventually deposited. The plots were arranged in double rows 1.6 m wide by 20 m long, and were bordered by a path 0.9 m wide. We excluded plots with obviously compacted soil or that contained a dung fragment or a shrub with basal stem diameter > 5 mm. Pairs of adjacent plots were mapped as a block and one plot in each block was selected randomly as a treatment. Finally, each block was randomly assigned a date when a dung-patch bait was to be deposited and a second date when the dung was to be collected along with all associated samples (including controls). On 19 December 1990, cattle were inadvertently permitted to enter the site and deposit additional "alternate baits." Affected plots were excluded from the experiment.

TABLE 1. *Dates shown are the second of three evenly spaced dates from nine-day dung deposition and collection schedules. Nine paired dung patch and control plots were sampled at each collection.*

Deposition month	3-day collection	10-day collection	60-day collection	110-day collection	Additional collections
December (16/12/1990)	—	—	18/2	7/4	17/4 120-day collection of dung and litter only between 0500 and 0700
February (5/2/1991)	8/2	15/2	9/4	—	9/4 60-day collection in Herrick and Lal's experimental area
March (20/3/1991)	—	23/3	—	—	23/3 10-day collection between 0130 and 0630

DUNG DEPOSITION.—Fresh dairy-cow dung was collected 2 km from the study site in a cement corral within one hour of deposition. Water was added to the dung until 1450 ml of dung dropped from a plastic pitcher held 40 cm above the ground produced a standard-sized patch: *ca* 20 cm in diameter and 6–7 cm high. Dung deposited in December and February contained 13.4 (SD = 0.5, $N = 18$) and 14.3 (SD = 1.1, $N = 9$) percent dry matter by weight, respectively. Percent dry matter content data were not collected for the March deposition. Although the depositions had significantly different dry matter contents (Wilcoxon rank sums test: $Z = 2.08$, $P = 0.04$), the difference is probably biologically unimportant. Experimental dung patches were deposited at the study site on each of three days over a nine-day period in December, February, and March (Table 1).

COLLECTION OF DUNG AND SOIL SAMPLES.—Samples from nine treatment and control plots were collected 60 and 110 days after the December deposition; 3, 10, and 60 days after the February deposition; and 10 days after the March deposition (Table 1). The final column of Table 1 describes the three additional collections made to further examine temporal and spatial variation in termite foraging activity. The additional December and March collections were made to describe any temporal bias that may have resulted from the diurnal collection of termites. The additional collection in February was made to examine any differences in termite forager populations between the experimental area used in this study and the nearby area where Herrick and Lal (1995, 1996) collected microclimate and soil property data.

Between 0800 and 1500 h, macroinvertebrate samples were collected from the following microsites: dung, litter, and 0- to 3.5-cm and 3.5- to 7.0-cm soil samples. Soil and surface litter samples were

circular, 15 cm in diameter, and centered on the approximate center point of the dung patch or control plot. A subsample for moisture analysis was taken also from each of the soil samples using a sharpened metal cylinder (diam. = 5.5 cm). The remaining 75 percent of the volume of each dung patch and 90 percent of each soil or surface debris sample was searched for invertebrates. The macroinvertebrate counts were corrected to account for the soil volume that was removed for the moisture samples. All soil and dung samples were stored in plastic bags in an insulated cooler after sampling. The surface litter microsite could not be collected from the 60- and 110-day-old dung patch sites because the termites virtually eliminated all litter and replaced it with a column of masticated soil. Soil surfaces were cleaned using a battery-operated portable vacuum with hose attachment, and all macropores > 2 mm diameter and depth were counted. Macropore counts were made at the surface after the litter was collected, and then at 3.5- and 7.0-cm depths after soil samples were removed. (Macropores are airspaces in soil created by either biotic or abiotic processes).

PROCESSING OF DUNG AND SOIL SAMPLES.—Dry dung and soil samples with high proportions of dry grass were hand sorted. Termites and dung beetles were removed from soil and wet dung, respectively, by flotation (Holter 1979). The soil sample or dung was mixed with water and stirred briefly. Then the water surface was searched for floating beetles and termites until one minute passed without finding an invertebrate. Calibration of the flotation technique was accomplished by adding known numbers of termites to 700 g of termite-free soil samples. Eighty-four percent (SD = 10%) of the termites were recovered ($N = 13$ trials, 25 termites/trial).

ANALYSIS.—Dung and soil gravimetric moisture

contents were calculated as a percent of dry weight for samples dried at 70°C. The 0- to 3.5-cm and the 3.5- to 7.0-cm soil samples were assumed to provide independent estimates of termite abundance; however, the disturbance caused by the collection of the 0- to 3.5-cm sample must have affected the numbers of termites recovered from the 3.5- to 7.0-cm sample. Nevertheless, we believe that the effect was minimal. Termite abundance was characterized in relation to four factors: deposition month, collection day, treatment, and microsite. "Deposition month" refers to the month when the dung patches were deposited in the experimental area; "collection day" refers to the number of days that passed between the deposition of the dung patch and the sampling date; "treatment" refers to the presence or absence of dung in the plot; and "microsite" refers to the specific soil, litter, or dung sample. On the basis of the data collected, we estimated the density of termite foragers per hectare to a depth of 7 cm in the pasture. All data analyses were conducted with JMP 3.2 (SAS Institute 1997).

RESULTS

IDENTIFICATION OF TERMITES AND DUNG BEETLES.— *Hoplotermes* sp. nov. and *A. beaumonti* were the principal termite species encountered. Both species were found exploiting dung on other irrigated and nonirrigated pastures at Hacienda La Pacifica and several other nearby pastures. *Hoplotermes* sp. nov. is a new species with greatest similarity to *H. amplus*, which was first described by Light (1933) from western Mexico. A set of 50 *Hoplotermes* individuals weighed 0.295 g wet and 0.094 g dry, while the 50 *Amitermes* individuals weighed only 0.093 g wet and 0.025 g dry. Two other termite species, *Heterotermes convexinotatus* (Snyder) and *Coptotermes crassus* Snyder were found in < 5 percent of dung plots. Reference collections of *Hoplotermes*, identified by the late M. S. Collins, can be found at the National Museum of Natural History, Washington, D. C., and Museo de Insectos at the Universidad de Costa Rica in San Pedro.

Histeridae spp. and *Ateanius* sp. were the two principal beetle taxa present in the dung during the dry season. Both taxa are relatively small compared to the other species common in the study area during the wet season (Janzen 1983a). Body length was *ca* 5.5 mm for *Ateanius* spp. and *ca* 2.5 mm for Histeridae spp. A reference collection of beetles was identified by B. C. Ratcliffe of the University of Nebraska State Museum. Ants, centipedes, spi-

TABLE 2.   *Presence of* Amitermes *and* Hoplotermes *in control and dung patch plots (N = 54 blocks).*

	Dung patch	Control
Amitermes	52	35
Hoplotermes	13	9
Spp. of either genus	52	36

ders, beetle larvae, and maggots sometimes were encountered in dung and soil samples, but were not counted.

PRESENCE OF FORAGING TERMITES.—We found termites in 52 of the 54 dung patch plots and 36 of the 54 controls plots (Table 2). *Amitermes* foragers were abundant in 3-, 10-, 60-, and 110-day-old dung plots with a mean (median) ± SD of 100 (59) ± 120 individuals/dung plot, and only 8 (3) ± 11 individuals/control plot. *Hoplotermes* foragers were less abundant, with a mean of 22 (0) ± 87 individuals in dung plots and 2 (0) ± 9 in control plots. Although *Hoplotermes* was encountered less frequently than *Amitermes*, the number of sites in which both species were found together was significantly greater than would be expected by chance (Pearson chi-square test: $\chi^2 = 3.9$, $P < 0.05$, $N = 54$). Of the 22 sites in which *Hoplotermes* occurred, 21 also contained *Amitermes*. However, restricting the analysis to the 10-day-old dung patches in which *Hoplotermes* was most abundant, there was no significant positive or negative association between the two species at the microsite level (Pearson chi-square test: $\chi^2 = 2.23$, $P > 0.05$ for all microsites; $N = 18$ dung patch plots). Nevertheless, when *Amitermes* and *Hoplotermes* foragers came into contact during sampling, they attacked each other with their mandibles.

TERMITE AND DUNG BEETLE ABUNDANCE ASSOCIATED WITH DUNG PATCHES OF DIFFERENT AGES.—Multiple regression analysis showed that collection day (df = 1, $P = 0.06$), treatment (df = 1, $P = 0.0001$), and microsite (df = 3, $P = 0.003$) were significantly related to a ranked score of termite density, whereas deposition month was not (df = 2, $P = 0.83$). Therefore, throughout the analysis, data from all three deposition months have been combined.

Amitermes was significantly more abundant in association with dung patches than in control microsites for all four collection dates, (Wilcoxon rank sums test: $Z > 16$, $P < 0.05$; Fig. 1), and was found at peak numbers associated with both
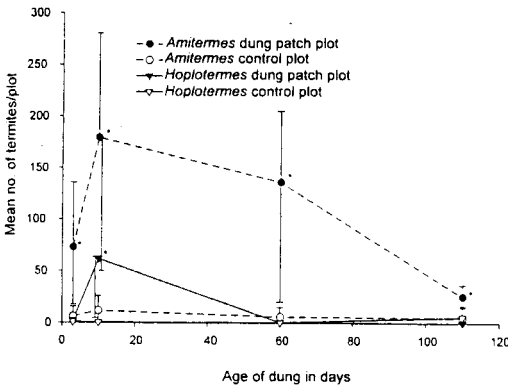
FIGURE 1.   Mean termite densities associated with four dry season collections of dung patches and controls. Upper and lower quartiles are shown. Significant differences between control and dung patch termite counts are indicated with asterisks (paired Wilcoxon rank sums test, $Z > 16$, $P < 0.05$).
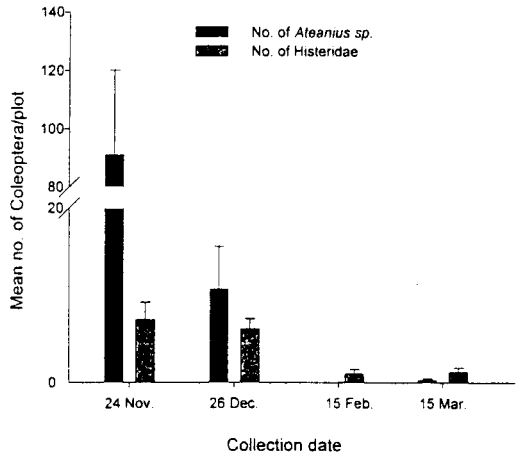

FIGURE 2.   *Ateanius* sp. and Histeridae (family) density associated with 10- to 14-day-old dung patches. SE bars are shown. The approximate beginning of the dry season was 15 December. Soil was collected to a depth of 7 cm below each patch ($N = 9$ dung patches/sampling date.

10- and 60-day-old dung. In contrast, *Hoplotermes* was found primarily in the surface litter under 10-day-old dung, where an average (median) ± SD of 39 (0) ± 105 individuals was determined. For all collection dates, *Amitermes* was significantly more abundant than *Hoplotermes* (Wilcoxon rank sums test: $Z > 3.2$, $P < 0.003$; Fig. 1). A linear regression of the number of termites per control soil core versus the (julian) collection date indicated that the number of termites foraging near the surface remained stable during the five months of the dry season sampled (*Hoplotermes*: $R^2 = 0.019$, $P > 0.3$, $N = 54$ soil cores; *Amitermes*: $R^2 = 0.008$, $P > 0.52$, $N = 54$ soil cores).

Ateanius sp. and histerid dung beetles were extracted from 10-day-old dung and soil on three occasions between December and April and from 14-day-old dung patches in November (Fig. 2). These beetle species were more abundant at the end of the wet season (November to mid-December)

than during the dry season. In fact, during March and April, no *Ateanius* sp. were active in fresh dung, even in nearby pastures. The *Ateanius* sp. sampled in March and April were found exclusively in the soil under 60- and 110-day-old dung that had been deposited in December.

TERMITE ABUNDANCE ASSOCIATED WITH DIFFERENT COLLECTION TIMES.—There was no significant difference between the abundance of foraging termites in 10-day nocturnal and diurnal collections in March (Table 3). On the other hand, dawn collections of 120-day-old dung and litter contained far more foraging *Amitermes* than did daylight collections of 110-day-old dung patches (dawn collection [$\bar{x} \pm$ SE {M}]: 534 ± 288 {7}; daylight collection: 26 ± 7 {9}. No *Hoplotermes* were present in the 110- or 120-day-old dung patches. For the pur-

TABLE 3.   *Nocturnal versus diurnal termite abundance associated with 10-day-old dung patches. A set of nine paired dung and control plots was collected during the day and another set was collected during the night.*

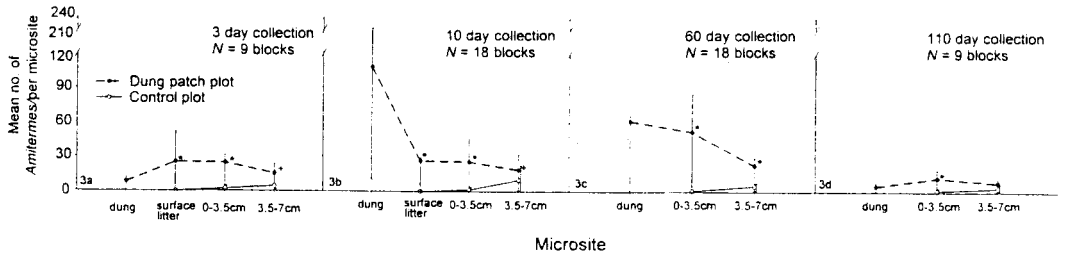|	Diurnal mean density (median) ± SE	Nocturnal/dawn mean density (median) ± SE	Wilcoxon rank sums test statistic	*P*-value
Amitermes				
Dung patch	137.6 (60) ± 45.6	183.7 (140) ± 57.7	6.5	0.75
Control	9 (3) ± 4.4	7.7 (2) ± 4.3	2	0.41
Hoplotermes				
Dung patch	32.8 (0) ± 31.2	95.3 (19) ± 46.0	7	0.81
Control	0 (0) ± 0	0 (0) ± 0	—	—

FIGURE 3a–d.   Abundance and spatial distribution of *Amitermes* 3, 10, 60, and 110 days after dung deposition. Upper and lower quartiles are shown. Significant differences of $P < 0.05$ between control and dung patch counts are indicated with "*"; differences with $P < 0.1$ are indicated with "+" (paired Wilcoxon rank sums test).

poses of this experiment, we assumed that termite activity in 110- and 120-day-old patches was comparable.

TERMITE ABUNDANCE ASSOCIATED WITH THE DUNG PATCH AND THREE DIFFERENT SOIL MICROSITES.—*Hoplotermes* was found predominantly in surface litter and the bottom third of 10-day-old dung patches. When groups of 50 or more foragers were found in the surface litter under the dung patch, they were accompanied by 1 to 4 soldiers. *Hoplotermes* foragers created a 3- to 5-mm-deep irregular chamber beneath the dung, in addition to tunnels leading to deeper chambers.

Under dung patches, more *Amitermes* were found in the 0- to 3.5-cm soil microsite than in the 3.5- to 7.0-cm microsite (Wilcoxon rank sums test: $Z = 1.97$, $P < 0.05$, $N = 54$; Fig. 3a–d). The pattern of greater *Amitermes* densities close to the surface was reversed in the control samples. No
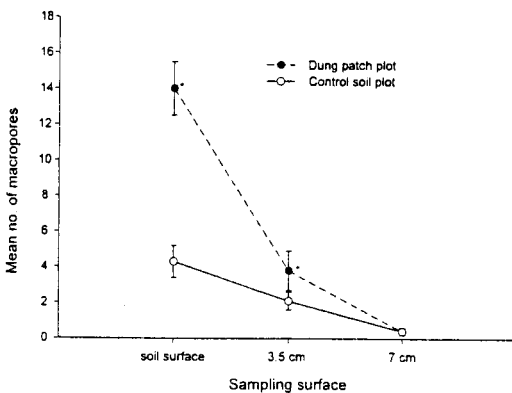

FIGURE 4.   Macropore density in soil below 60-day-old dung patches. SE bars are shown. Significant differences of $P < 0.05$ between control and dung patch densities are indicated with "*"; differences with $P < 0.1$ are indicated with "+" (paired *t*-test, $N = 18$).

Amitermes were ever found in the control surface litter, even at night. Taking all control samples together, significantly higher termite densities were found in the 3.5- to 7.0-cm soil sample than in the 0- to 3.5-cm sample (Wilcoxon rank sums test: $Z = 2.49$, $P < 0.05$, $N = 54$). In the 3- and 110-day collections, the microsite with the lowest mean number of foragers was the dung pat itself, while in the 10- and 60-day collections, the dung patch contained the highest mean numbers of foragers (Fig. 3a–d).

PHYSICAL CHANGES IN SOIL AND DUNG ASSOCIATED WITH TERMITE ACTIVITY.—We compared termite behavior and abundance with soil property data collected by Herrick and Lal (1995). We believe that comparisons between the two sites are justified because termite densities did not differ significantly between the two sites (Wilcoxon rank sums test, dung patch plots: $Z = 1.1$, control plots: $Z = 0.5$, $P > 0.05$, $N = 9$).

As foraging termites exploited the dung patch, they created tunnels that led from the soil into the drying dung. Consistent with this observation, the number of macropores observed at the surface and at 3.5 cm under 60-day-old dung patches was significantly higher than in the corresponding strata in adjacent control sites (paired *t*-tests: $8.0 \geq t \geq 1.54$, $0.07 \geq P \geq 0.0001$, $N = 18$). At 7 cm depth, there was no treatment effect on macropore abundance (paired *t*-test: $t = 0$, $P = 0.5$, $N = 18$; Fig. 4). The termites lined their tunnels with a mixture of soil and their own fecal material. In fact, they brought so much soil into the dung patch that the mean dry weight of nine patches collected after 110 days ($\bar{x} \pm SD$ [N]: 317 g $\pm$ 59 [9]) was 1.5 times greater than the mean weight of patches collected after three days (205 g $\pm$ 32 [9]).

Gravimetric moisture content of the soil 0–7 cm under dung patch baits remained significantly
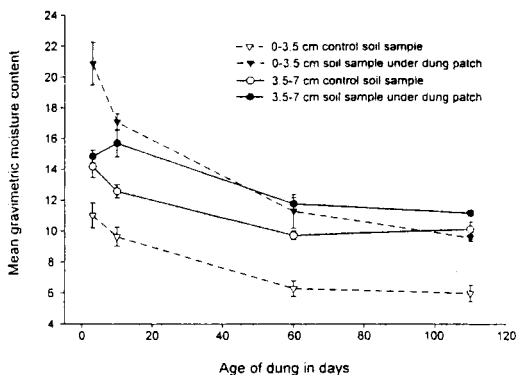
FIGURE 5.   Gravimetric moisture content of soil samples associated with four dry season collections of dung patches and controls from the December deposition. SE bars are shown. All treatment and corresponding controls were significantly different (paired *t*-test: $t > 2.5$, $P < 0.02$, $N = 6$–9) except for the 3-day collection of the 3.5- to 7-cm soil sample ($t = 1.72$, $P < 0.09$, $N = 6$).

higher than that in the corresponding control soil samples (paired *t*-test: $t = 2.5$, $P < 0.02$, $N = 33$ blocks; Fig. 5). Notably, even 110 days after the dung was deposited, the soil samples 3.5–7.0 cm under the dung had significantly higher moisture contents than the corresponding control soil samples.

When *Amitermes* and *Hoplotermes* use dung patches, they typically seal the edges of the patch to the ground using the same mixture of fecal material and soil used to line their tunnels. In part, this seal is formed without termite action as the dung patch dries. Small chips of horse dung that are quite common in the same pastures rarely attract termite foragers, while large piles of horse dung, which seal more easily to the ground, are commonly exploited. When dung patches are overturned by the hooves of grazing cattle, *Ectatomma* sp. ants begin to prey upon termite workers within minutes. Dung patches that were closely monitored after they had been disturbed were all resealed to the ground by termites. These data were confirmed by numerous observations under a range of conditions, although recolonization was not always observed immediately after disturbance.

CALCULATING TERMITE ABUNDANCE AND BIOMASS.—We relied on nine assumptions to make our estimate of the density and biomass of *Amitermes* foragers per hectare (to a depth of 7 cm) in the agroecosystem: (1) 150 foragers are associated with 0-to10-day-old dung patches; (2) 180 foragers are associated with 11- to 60-day-old dung patches; (3)

55 foragers are associated with 60+-day-old dung patches; (4) dung patches are used by termites for 9 months (Herrick & Lal 1996); (5) stocking rate at Hacienda la Pacifica is 2 animal units/ha; (6) each animal unit produces 10 dung patches/day (Herrick & Lal 1996); (7) the average dung patch is 25 cm in diameter; (8) wet and dry weights of individual foragers are 0.00186 and 0.0005 g, respectively; and (9) the density of termites in all areas not covered by dung patches less than nine months old (97% of pasture) is 1,849,899 individuals/ha and 3 foragers/plot (extrapolated from the median density of *Amitermes* in control soil samples).

The numbers of foragers associated with dung patches were calculated based on the median numbers of termites collected from the dung and soil samples. The density of termites was assumed to remain constant under the entire dung patch, although only the soil under the center of the patch was sampled. The estimated density, wet weight, and dry weight of *Amitermes* foragers was 2,218,239 individuals/ha, 4,126 g/ha, and 1,109.1 g/ha, respectively. According to the model, 20 percent of foraging *Amitermes* are found associated with cattle dung patches. We made no estimate of *Hoplotermes* density because we felt that there were insufficient data to make a meaningful estimate.

DISCUSSION

ESTIMATES OF FORAGING TERMITE ABUNDANCE.—In Guanacaste pastures during the dry season, subterranean termites are abundant around cattle dung patches. *Amitermes* density calculated in this study is comparable to published estimates for other subterranean termite species in Neotropical arid ecosystems. (*Gnathamitermes tubiformans* and *Amitermes wheeleri*: 12,000,000 foragers/ha, Johnson & Whitford 1975; *Gnathamitermes perplexus*: 705,200 foragers/ha, LaFage *et al.* 1976; *Heterotermes aureus*: 4,309,132 foragers/ha, Haverty *et al.* 1975). In tropical savannas and pastures worldwide, measurements of total termite biomass (based on fresh weight) vary between 0.96 and 11.1 g/m^2 (reviewed in Sanderson 1996). Even if *Hoplotermes* biomass had been calculated, our estimate for total termite biomass would have been lower than 0.96 g/m^2. Our estimate might have been somewhat higher if not for three methodological biases. First, the termite search technique detected only 84 percent of termites contained in soil samples. Second, the density of foragers associated with older dung patches may peak at dawn, but samples were col-

lected during the day when foragers are less abundant. Third, termites were sampled only to a depth of 7 cm, even though termite activity was noted deeper in the soil. On the other hand, our density estimate should be more precise than estimates that are based only on randomly taken soil samples, because we accounted for some of the aggregated spatial distribution of foragers (Martius 1994).

Amitermes was present in dung patch plots of varying ages, and in many control plots, whereas *Hoplotermes* was, for the most part, restricted to 10-day-old dung patches. The lack of evidence for competitive exclusion at the microsite level despite obvious interspecific aggression suggests the existence of a species separation mechanism at a relatively fine spatial scale. This result is surprising given than other researchers have found that termite colonies defend both large and small food resources (*e.g.,* coconut trees [Leponce *et al.* 1997] and toilet paper rolls [Jones & Trosset 1991]).

REFUSE TO REFUGE: DUNG PATCH USE AND MODIFI-
CATION BY SUBTERRANEAN TERMITES WITH POTENTIAL
APPLICATIONS TO RESTORATION ECOLOGY.—Mound building permits certain species of termites to live in habitats that they could not otherwise tolerate. Benefits accrued by termites as a result of mound building include regulation of humidity and temperature, partial protection from predators, and access to cached food supplies. In contrast, foraging activity of subterranean termites is thought to be exogenously controlled by temperature, moisture, and other environmental factors (Collins *et al.* 1973; Haverty *et al.* 1974; LaFage *et al.* 1976; Ueckert *et al.* 1976; Buxton 1981; Salman *et al.* 1988; Delaplane *et al.* 1991; Smith & Rust 1993; 1994; Davis & Kamble 1994). Wilson (1971) wrote that "[l]ike the soil dwelling ants, the primitive termites. ... rely heavily on the natural insulating properties of their nest materials and their ability to move from chamber to chamber as local conditions demand. ... " Although *Amitermes* and *Hoplotermes* clearly benefit from "natural insulating properties" of dung patches, these termites also modify the patches, further improving the microclimatic conditions in chambers where they consume dung.

Macroinvertebrate activity generally is believed to reduce moisture content (in dung) by increasing aeration (Wilson 1971); however, a combination of termite-derived structural modifications to the soil and dung patch and natural physical processes, may elevate gravimetric moisture content in the soil below the dung patch relative to the drier soils of the surrounding pasture. Termite tunnels connect the dung to deeper soils where humidity is always higher than at the soil surface. These tunnels may increase near-surface soil moisture by increasing nocturnal movement of water vapor and reducing evaporation. This hypothesis is supported by the dramatic increase in macroporosity associated with decomposition (Herrick & Lal 1995) and the reduction in diurnal soil surface temperatures beneath the dung patches (Herrick 1993). In addition to reducing soil surface temperatures, the dung patch increases resistance to evaporation at the soil surface by providing a much denser barrier to vapor flow than the thin layer of leaf litter found in control sites. Termites are also known to humidify their nests by bringing water up from moist deep soils (Lee & Wood 1971). This behavior also could help to account for the differences between the moisture content of the dung patch and that of the control plots. Incidentally, the seal that the termites help to construct between the dung patch and the pasture is a barrier to some invertebrate predators.

The modified dung patch has a limited capacity to buffer termite foragers from the harsh climate. For example, *Amitermes* activity remained roughly constant in 10-day-old patches throughout the day and night, while in the oldest patches (>110 d), many more termites were found at dawn than during day time collections. This pattern suggests that exogenous control of termite activity, possibly by moisture limitation, is more important around older dung patches than around younger patches. On the other hand, neither termite species ever was found foraging within fresh dung, suggesting that both species have an upper, as well as a lower, moisture threshold. The greater abundance of *Amitermes* individuals in the deeper (and wetter) control soil-microsites also suggests that moisture availability affects the spatial distribution of this species. During the wet season, of course, termite foraging behavior may change dramatically in response to greater moisture availability and to competition by dung beetles (Janzen 1983a, Herrick & Lal 1996).

The dung patch modifications that are created, both by these subterranean termites and by the physical effects of decomposition, permit the termites to survive in an environment that they could not otherwise tolerate. This finding is of special interest, because researchers historically have focused on microhabitat manipulation by mound building termites, but not by subterranean termites.

Herrick *et al.* (1997) argued that adding biosolids (including manure) to degraded pastures

could increase macroporosity and infiltration by promoting termite activity. This study found that the net effect of decomposition may depend on the size, structure, and soil surface contact of individual dung fragments, and on the behavior of termites in the dung and soil. The interaction between dung structure and form and termite behavior should be considered together with effects of other decomposer groups, including fungi, in ecologically based pasture restoration programs.

AN EVOLUTIONARY PERSPECTIVE ON DUNG PATCH MODIFICATION.—Janzen and Martin (1982) have suggested that past interactions between existing species and extinct Pleistocene megafauna have left an evolutionary residue in the "leaves and bones" of contemporary Costa Rican flora and fauna. Furthermore, they proposed that cattle introduced to Central America by the Spanish > 400 years ago now are functioning as ecological surrogates for the Pleistocene megafauna. Janzen (1983a) reasoned that the absence of dry season consumers of cattle dung in Santa Rosa National Park indicated a vacant niche; he theorized that during the Pleistocene there were dry season dung beetles that consumed megafaunal dung. This research suggest that if more dry season dung beetles existed during the Pleistocene, they probably shared manure with subterranean termites.

Dung modification by termites occurs in Australia (Ferrar & Watson 1970, Whitford et al. 1992), India (Veeresh & Belavadi 1986), and the southwestern United States–northern Mexico region (Whitford et al. 1982). Ferrar and Watson (1970) observed the same patterns of dung use by termites described in this study. Veeresh and Belavadi (1986) and Whitford et al. (1992) found that termites not only tunnel into dung from below but also create earthen sheeting over dung patches and other food sources as they consume them. We also encountered these sheaths during later stages of dung decomposition in Costa Rica. These resource use patterns may be an evolutionary precursor to mound building by termites.

ACKNOWLEDGMENTS

LITERATURE CITED

BUXTON, R. 1981. Changes in composition and activities of termite communities in relation to changing rainfall. Oecologia 51: 371–378.

COE, M. 1977. The role of termites in the removal of elephant dung in the Tsavo (East) National Park Kenya. East Afr. Wildl. J. 15: 49–55.

COLLINS, M. S., M. I. HAVERTY, J. P. LAFAGE, AND W. L. NUTTING. 1973. High temperature tolerance in two species of subterranean termites from the Sonoran Desert in Arizona. Environ. Entomol. 2: 1122–1123.

DAUBENMIRE, R. 1972. Ecology of *Hyparrhenia rufa* (Nees) in derived savanna in northwestern Costa Rica. J. Appl. Ecol. 9: 11–23.

DAVIS, R. W., AND S. T. KAMBLE. 1994. Low temperature effects on survival of the eastern subterranean termite (Isoptera: Rhinotermitidae). Environ. Entomol. 23: 1211–1214.

DELAPLANE, K. S., A. M. SAXTON, AND J. P. LAFAGE. 1991. Foraging phenology of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in Lousiana. Am. Midl. Nat. 125: 222–230.

FERRAR, P., AND J. WATSON. 1970. Termites (Isoptera) associated with dung in Australia. J. Aust. Entomol. Soc. 9: 100–102.

HAGNAUER, W. 1993. El sistema agroecologico de Guanacaste: oportunidades y desafios para la agricultura y el turismo. *In* Modernización de la agricultura y turismo con desafio ecologico: los desafios para Cañas, Guanacaste. IICA, San Jose, Costa Rica.

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

———, W. L. NUTTING, AND J. P. LAFAGE. 1975. Density of colonies and spatial distribution of foraging territories of the desert subterranean termite, *Heterotermes aureus* (Snyder). Environ. Entomol. 4: 105–109.

HERRICK, J. E. 1993. Restoration of tropical pasture ecosystems and the role of cattle dung patches. Ph.D. dissertation. Ohio State University, Columbus, Ohio.

———, K. M. HAVSTAD, AND D. P. COFFIN. 1997. Rethinking remediation technologies for desertified landscapes. J. Soil Water Conserv. 52: 220–225.

————, AND R. LAL. 1995. Evolution of soil physical properties during dung decomposition in a tropical pasture. Soil Sci. Soc. Am. J. 59: 908–912.

————, AND ————. 1996. Dung decomposition and pedoturbation in a seasonally dry tropical pasture. Biol. Fertil. Soils 23: 177–181.

HOLTER, P. 1979. Effects of dung beetles (*Aphodius* spp.) and earthworms on the disappearance of cattle dung. Oikos 32: 393–402.

JANZEN, D. H. 1983a. Seasonal changes in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture. Oikos. 41: 274–283.

————. 1983b. Insects. *In* D. H. Janzen (Ed.). Costa Rican natural history, pp. 619–645. University of Chicago Press, Chicago, Illinois.

————, AND P. S. MARTIN. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science 215: 19–27.

JOHNSON, K. A., AND W. G. WHITFORD. 1975. Foraging ecology and relative importance of subterranean termites in a Chihuahuan Desert ecosystem. Environ. Entomol. 4: 66–70.

JONES, S. C., AND M. W. TROSSET. 1991. Interference competition in desert subterranean termites. Entomol. Exp. Appl. 61: 83–90.

LAFAGE, J. P., M. I. HAVERTY, AND W. L. NUTTING. 1976. Environmental factors correlated with the foraging behavior of a desert subterranean termite, *Gnathamitermes perplexus* (Banks) (Isoptera: Termitidae). Sociobiology 2: 155–169.

LEE, K. E., AND T. G. WOOD. 1971. Termites and soils. Academic Press, New York, New York. 251 pp.

LEPONCE, M., Y. ROISIN, AND J. M. PASTEELS. 1997. Structure and dynamics of the arboreal termite community in New Guinean coconut plantations. Biotropica 29: 193–203.

LIGHT, K. E. 1933. Termites of western Mexico. Univ. Calif. Publ.Entomol. 6: 79–164.

MARTIUS, C. 1994. Diversity and ecology of termites in Amazonian forests. Pedobiolia 38: 407–428.

SALMAN, A. G., M. A. MORSY, AND A. A. SAYED. 1988. Foraging activity of the sand termite *Psammotermes hybostoma* in the New Valley, Egypt. J. Arid Environ. 15: 175–177.

SANDERSON, M. G. 1996. Biomass of termites and their emissions of methane and carbon dioxide: a global database. Global Biogeochem. Cycles 10: 543–557.

SANDS, W. A. 1972. Problems in attempting to sample tropical subterranean termite populations. Ekol. Pol. 20: 28–31.

SAS INSTITUTE. 1997. JMP 3.2. Duxbery Press, Boston, Massachusetts.

SMITH, J., AND M. K. RUST. 1993. Influence of temperature on tunneling, feeding rates, and oxygen requirements of the western subterranean termite, *Reticulitermes hesperus* (Isoptera: Rhinotermitidae). Sociobiology 21: 225–236.

————, AND ————. 1994. Temperature preference of the western subterranean termite, *Reticulitermes hesperus* Banks. J. Arid Environ. 28: 313–323.

UECKERT, N. D., M. C. BODINE, AND B. M. SPEARS. 1976. Population density and biomass of the desert termite *Gnathamitermes tubiformans* (Isoptera Termitidae) in a shortgrass prairie: relationship to temperature and moisture. Ecology 57: 1273–1280.

VARGAS, E., AND H. FONSECA. 1989. Contenido mineral y proteico de forrajes para rumiantes en pastoreo en Costa Rica. Universidad de Costa Rica, San Jose, Costa Rica. 215 pp.

VEERESH, G. K., AND V. V. BELAVADI. 1986. Influence of termite foraging on the fertility status of the soil. Soil Biol. Ecol. 6: 53–56.

WHITFORD, W. G., J. A. LUDWIG, AND J. C. NOBLE. 1992. The importance of subterranean termites in semi-arid ecosystems in south-eastern Australia. J Arid Environ. 22: 87–91.

WHITFORD, W. G., Y. STEINBERGER, AND G. ETTERSHANK. 1982. Contributions of subterranean termites to the "economy" of Chihuahuan desert Ecosystems. Oecologia 55: 292–302.

WILSON, E. O. 1971. The insect societies. Belknap Press of Harvard University Press, Cambridge, Massachusetts. 548 pp.