

and untreated controls. Turtles entered compartments treated with Galveston solution more often ($P \leq 0.05$) than those that were untreated or treated with Padre solution (Table 1). They entered Padre solution compartments less often than untreated compartments, but the total time spent in Padre solution and Galveston solution compartments was similar. Entries in Padre solution compartments were low because turtles stayed much longer in this solution when they did enter. Total time spent in both Padre and Galveston solution compartments was greater but not statistically different than that for untreated compartments. When turtles entered Galveston solution compartments they did not stay there longer than if they had entered untreated compartments. We interpret the high number of entries in Galveston solution to be a result of the animals' unrewarded appetitive behavior or search for a releasing stimulus (9). We suggest that the high amount of time spent per entry in Padre solution indicates a rewarded appetitive behavior or drive-reducing consummatory act.

From the behavior exhibited by these ridley turtles, one might predict that they would move (migrate?) in the direction of Padre Island when they detect olfactants emanating from the artificial imprinting area. In our test situation, however, we suggest that turtles accepted Padre solution as a substitute for a more appropriate releasing stimulus such as food, possibly because they were imprinted to Padre Island. In nature one would expect the threshold of the migratory drive to the nesting beach to be higher than thresholds for an appropriate juvenile behavior such as feeding. This would result in juvenile behaviors having priority over migratory behavior. In reproductive adults, one might predict that the threshold of the migratory drive would be lowered. The fact that nesting beaches are often far from feeding areas suggests that migration becomes a higher priority than feeding in reproductive turtles. Also, the observation that estrogen-treated turtles eat less suggests that these threshold changes have a physiological basis (10).

Our results suggest that Kemp's ridley turtles, artificially imprinted to Padre Island, are behaviorally imprinted to the chemosensory environment of Padre Island. This is the only experimental evidence that sea turtles might imprint and that artificial imprinting may be a valid conservation practice. The best proof for imprinting would be the establishment of a new population by artificially imprinting hatchlings to a novel beach. Such

Table 1. Mean (\pm standard error of the mean) total entries and time spent in Padre solution (P), Galveston solution (G), and untreated (C) compartments for the 12 turtles.

Com-part-ment	Number of entries	Time spent (seconds)
P	10.89 \pm 2.84	1290.0 \pm 474.0
G	21.2 \pm 8.32	1176.0 \pm 336.0
C	17.25 \pm 8.38	642.0 \pm 300.0
C	18.2 \pm 10.46	756.0 \pm 426.0

phenomena as long times to maturity (15 to 45 years in *Chelonia mydas*), temperature-dependent sex differentiation, and nearly insurmountable tagging limitations were not anticipated when this work started in the 1950's (1, 4). Thus, laboratory experimentation to evaluate the imprinting question may be the only viable approach to the problem. In fact, failure to establish new nesting populations through artificial imprinting techniques would not disprove the possibility that turtles imprint to their natal beach. Artificial imprinting techniques currently used for conservation may be inappropriate or incomplete to behaviorally imprint turtles. Until more is known about the timing and stimulus requirements of a possible imprinting mechanism, the methods used to artificially imprint turtles must be considered to be experimental.

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5. Solutions to be pumped into the behavior monitoring tank (4) (Fig. 1) were prepared from samples by washing 1 kg of sand with 1 liter of seawater. A sufficient volume of seawater was then added to bring the total volume to 4 liters. Equal volume (1143 ml) of synthetic seawater at concentrations appropriate to equilibrate the salinity of the solutions to each other and the monitoring tank water were then added to facilitate mixing. Because equal volumes of water were added to each sample, concentrations of possible olfactants in the two samples did not change in relation to each other.
6. In a previous experiment only total entries and total time spent in compartments were reported (4). Because entries and time spent were not independent variables in our investigations, it was important not only to consider these two variables, but also to consider the length of time an animal spent each time it entered a compartment.
7. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1981); total entries and total time spent were analyzed with a two-factor (compartment by solution) log likelihood ratio test. This test was designed for analyzing discrete variables. Because time was continuous, total time spent was transformed by dividing by 600 seconds. This was established by a runs test of independence to be a discrete unit of time in the animals' response. A nested-factorial analysis of variance on data on time spent per entry was used to account for individual and compartment variation. There was a significant treatment-solution effect [$F(3) = 2.64$, $P \leq 0.05$]. Also, data on time spent per entry were further analyzed with a Tukey's test ($P \leq 0.01$) on treatment-solution means. Data on time spent per entry underwent arcsin transformations to meet the homogeneity assumption of analysis of variance.
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Termites and Atmospheric Gas Production

Zimmerman *et al.* (1) reported that termites are a potential source of large quantities of atmospheric methane, carbon dioxide, and hydrogen. We do not question their laboratory experiments, but we are critical of their extrapolations of gas emission (calculated from food consumption) to a global scale. Our appraisal of the available data indicates

that gas emission by termites was overestimated by at least one order of magnitude.

Gnathamitermes perplexus Banks (Termitinae) should not be used as the sole representative of the very variable family Termitidae, which constitutes two-thirds of all termites. The subfamily Macrotermitinae (fungus-growing ter-

mites) was not considered, yet these are the dominant termites in many ecosystems of the Ethiopian and Indo-Malayan regions. Most of their digestion is performed externally by a mutualistic fungus that aerobically metabolizes five to six times as much material as do the termites and their gut flora (2). The combs are unlikely to produce methane (even though the termite gut microbes may do so), and attempts at global estimates should await the study of fungus growers. Soil-feeding termites, which occur in all tropical regions except Australasia (3) and are often very abundant (4, 5), were also not studied or considered. Their energy source is not plant material but degraded soil organic matter, and therefore, if methane is produced, it is likely to be in much smaller amounts. One soil feeder, *Cubitermes*, is known not to produce hydrogen (6).

The global extrapolations were based on published estimates of food consumption and termite populations. These data were misinterpreted by Zimmerman *et al.* in their table 2. They state that four of the ratios of material consumed to net primary productivity (NPP) "agree fairly well" with values reported in the literature. The apparent similarity of the percentages—for example, a calculated value of 41 percent compared to a field value of 30 for tropical moist forest—derives from the fact that they are in no case percentages of the same units. In this example, the field result of 30 percent refers to leaf litter production only, not NPP. Zimmerman *et al.*'s calculated annual consumption (given only as a percentage) of 623 g/m² greatly exceeds the field value of 189. Similarly, for wet savanna, dry savanna, and temperate grassland the calculated and field values differ markedly, being 613 and 192, 116 and 12.5 and 300 and 41 g/m², respectively.

The overestimates are attributable to Zimmerman *et al.*'s calculation of an average annual consumption of 140 mg per individual termite on the basis of laboratory estimates of consumption by various species [table 4.1 in (7)] of which the majority were large species and not Termitidae. Since consumption is related to body weight these are unrepresentative of field populations, which are dominated by Termitidae. We recalculated global consumption rates on the basis of termite biomass and a daily consumption rate of 30 mg per gram of termite, derived from field estimates (Table 1) (7, 8). Further corrections were made for soil-feeding termites and for the fact that in many cases the population figures quoted by Zimmerman *et al.* are nearer

Table 1. Termite global biomass consumption, reconstructed after table 2 of Zimmerman *et al.*

Ecological region	Area (10 ¹² m ²)	Termite populations (8)		Annual consumption (g/m ²)	Annual consumption for ecological region (10 ¹⁵ g)		
		Number per square meter	Grams per square meter		Calculated from column 5	Corrected for average populations and soil feeders	Estimates by Zimmerman <i>et al.</i>
Tropical wet forest	4.6	1000	11.0	120.5	0.55	0.37*	0.6
Tropical moist forest	6.1	4450	11.2†	122.6	0.75	0.23‡	3.8
Tropical dry forest	7.8	3163	8.0	87.6	0.68	0.30‡	3.4
Temperate	12.0	600	3.0	32.9	0.39	0.01§	1.0
Wood/shrub land	8.5	431	0.8	8.7	0.07	0.01§	0.5
Wet savanna	14.2	4402	11.1	121.5	1.73	1.09¶	8.7
Dry savanna	4.3	861	1.7	18.6	0.08	0.33¶	0.5
Temperate grassland	9.0	2139	5.2	56.9	0.51	0.01§	2.7
Cultivated land	11.9	2813	7.8	85.4	0.97	0.44**	4.7
Desert scrub	18.0	229	1.0	10.9	0.20	0.20††	0.6
Clearing burning	6.8	6825	18.9	207.0	1.40	0.37‡‡	6.5
Total	103.2				7.33	3.36	33.0

*Thirty-three percent of the termites are soil feeders. †Calculated from an estimated individual termite weight of 2.53 mg. ‡Maxima are 4450 and 3163 termites per square meter; average population is 2000 per square meter [biomass, 5.0 g/m², based on an individual weight of 2.53 mg calculated from table 9 in (5)], excluding upper montane forest. Soil feeders are estimated at a minimum of 30 percent [range, 6.5 to 90 percent (5)]. §The latitudinal limits of termite distribution are approximately 45°S and 45°N (3). Zimmerman *et al.* extrapolated from a single population estimate for these regions to the global area, notwithstanding the fact that termites occur in less than 1.0 percent of these regions. ||Calculated from a weight of 1.9 mg for individual *Heterotermes aureus* [table 4.1 in (7)]. ¶The maximum population is 4402 termites per square meter, and 861 per square meter is the population for wet savanna created by forest clearing; other data [table 9.5 in (8)] indicate an average population of 3000 per square meter (biomass, 7.6 g/m²). Soil feeders are estimated at 7.7 percent [table 9.8 in (8)]. **Cultivated land is derived from both forest and savanna; figures of 1553 termites per square meter (1.7 g/m²) from former savanna [table 9.5 in (8)] and 1151 per square meter (5.3 g/m²) from former forest [table 6 in (5)] give an average of 1352 per square meter (3.5 g/m²). Soil feeders are ignored, as they rarely survive cultivation. ††The quoted figure is for Sahel savanna, which is likely to have higher populations than many areas of desert scrub. ‡‡The quoted figure is for land under long-term cultivation. Areas under industrial and fuel wood production are likely to have termite populations similar to that of tropical dry forest without soil feeders (2000 per square meter; 5.0 g/m²) (no population data are available).

to maxima than averages. Even our averages are probably too high. Certain widely distributed tropical soils support very few termites (3), and we know of several localities and vegetation formations where termites are rare or absent (9).

The contention that human activities increase the density of termites is unsubstantiated on a global scale. The only data from rain forest show a reduction in the number of species in cleared dipterocarp forest in Sarawak (10). Clearing and cultivation reduced termite populations in Nigerian forest (5) and Japanese woodland (11). The only documented increase in abundance, for savanna woodland in Nigeria (12), was entirely due to a fungus-growing termite, *Microtermes*, which is unlikely to produce methane from its combs. Cultivated lands and regions of clearing and burning contributed approximately 34 percent of the methane emission in Zimmerman *et al.*'s calculations.

Our calculations (Table 1) show that their consumption estimates should be reduced by a factor of at least 4 and by 10 when soil-feeding termites and near-average rather than near-maximum popula-

tions are considered. Since no allowance has been made for aerobic digestion on fungus combs by Macrotermitinae or for the fact that actual average populations are certainly lower than the figures we used, the global consumption of 3.36×10^{15} g should be reduced by yet another factor.

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Collins and Wood assert that our estimates of potential trace gas production by termites (1) were too high and that there is no evidence to support our speculation that human activities lead to increased termite populations. We will show that our estimates were conservative.

Collins and Wood correctly note that four literature values for litter consumption by termites in our table 2 (1) represent the percentage of litter consumed in each ecosystem. Those numbers, however, were not used in any calculations and were only one of two ways we used to indicate that our calculated values for consumption were reasonable [note 33 in (1)]. In stable ecosystems the net primary productivity (NPP) is equal to the production of dead organic material. Since overall primary consumption is small and inefficient, NPP should about equal total litter production (2). Our estimates were based on trace gas production efficiencies, an average consumption rate, and literature values for population densities.

The field values for litter consumption quoted by Collins and Wood are underestimates, since they do not include consumption by all termite species present or consumption of large branches, dead tree trunks, soil organic matter, or belowground biomass (3–5). In addition, the field sampling techniques used may alter termite behavior and affect consumption estimates (4). Collins and Wood contend that our consumption rate of 140 mg per termite per year is much too high and say that a value of 30 mg per gram of termite per day is more reasonable. We believe that a global average consumption figure of 30 mg/g per day is low. However (assuming the authors are using milligrams of dry weight consumed per gram of termite fresh weight per day), a termite fresh weight of 12.7 mg makes the two figures equivalent. Higher consumption rates would lower this “average” termite size. Fresh weights for individual termites range from about 0.5 mg to over 100 mg (4, 6). Many ecologically important species of *Cubitermes* and *Macrotermes* have individuals weighing at least 10 mg (4). An average weight of about 11 mg was reported for

all species sampled in the riverine forests of Central Africa (4).

Collins and Wood propose their table 1 as a correction for our overestimates. There are four major differences between their table 1 and our table 2:

1) They assume a global average consumption of 30 mg/g per day as a basis for their calculation of CH₄ production. This value is unrealistically low. It should at least be corrected for areas where Macrotermitinae are dominant. Literature values for consumption by these termites are as high as 560 mg/g per day (3).

2) They arbitrarily assume that soil feeders are low CH₄ producers. Recent measurements show that soil feeders have the highest weight specific CH₄ production and CH₄/CO₂ emission ratio of any termite group measured (7).

3) They change some termite densities to correct for alleged overestimates. They state that values we used, 4450 and 3163 termites per square meter, are maximum values and that the average value should be 2000 termites per square meter, and they cite Wood and Sands (4). However, according to Wood and Sands (pp. 266–267), “maximum populations (4450 per m²) in rainforest were recorded by Strickland (1944) from soil cores only 7.5 cm deep which would probably sample less than half of the subterranean population and exclude mound-building and arboreal-nesting species.” Thus the values we used were very conservative. In fact, a population of 15,000 termites per square meter has been reported for a single species (4).

4) They assume that CH₄ emissions would be lower for Macrotermitinae because of the metabolism of their fungus combs. Actual measurements on intact colonies of *Macrotermes* in East Africa show high CH₄ emission rates. Although metabolism of the fungus comb does result in higher CO₂ production rates for in situ colonies than for nonfungus growers, total consumption by Macrotermitinae is much larger (4, 8). Energy balance considerations (4, 9) and our in situ measurements of total colony respiration (7) cast doubt on the universal applicability of the fungus/termite metabolism ratios of 5/1 or 6/1 that they quote.

Finally, Collins and Wood state that human activities tend to decrease termite populations. Although the matter needs much more study, the literature clearly does not support their contention. Although the number of species tends to decrease, the populations of the few species able to exploit man-modified niches

increase dramatically (10). Termites are reported as pests of virtually every crop grown in the tropics (11). Some authors have proposed a mechanism to explain the increase in the density of termites (5, 12). The studies cited by Collins and Wood were not designed to correlate changes in termite densities with changes in land use.

In our report we did not claim to present the definitive answers about trace gas production by termites. We attempted to estimate trace gas production potential. Research has continued and we now have much more data (7, 13). We still believe that our original estimates were conservative.

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