

Estimating population density of the Formosan subterranean termite, *Coptotermes formosanus* (Isoptera: Rhinotermitidae) using the effective sampling area of in-ground monitoring stations

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Abstract

The effective sampling area of a monitoring station, α , was calculated for several *Coptotermes formosanus* Shiraki colonies in Broward County, Florida, USA. A simple mark–recapture protocol provided data on termite station catch within a foraging range of a colony. Average recapture probability was 0.005 close to the release point (< 5 m) and declined to 0.0008 at a distance of 51 to 60 m. The relation between the log % termites recaptured was fitted with log distance, to determine $P(x)$, the average proportion of captured termites that started at distance x from the release point. The effective sampling area was estimated by using $P(x)$ and the equation, $\alpha = 2 \pi \int_0^{\infty} x P(x) dx$. Integrating this equation, an average estimate α that ranged from 0.607 to 14.5 m² was obtained. Factors influencing the variation of α among the colonies are discussed. The effective sampling area estimated should be taken as a reliable estimator that translates subterranean termite catches into termite population density.

Introduction

Mark–release–recapture protocols are often used to estimate the population size of subterranean termite colonies because termite foraging sites and galleries are cryptic and almost impossible to discover otherwise. In mark–release–recapture protocols, termites are marked with a dye, released inside an in-ground monitoring station and then recaptured later (Su & Scheffrahn, 1986; Su *et al.*, 1998, 2000; Sajap *et al.*, 2000). The in-ground stations, set in places

where termite activity is previously detected using buried wooden stakes, consist of a plastic collar partially buried in the soil with a wooden block inside where marked termites are recaptured. The proportion of recaptured marked termites collected in the monitoring stations can be used to estimate the size of the population using the Lincoln index (Lincoln, 1930; Southwood, 1975; Begon, 1979). To use this index for estimating population size, the following assumptions need to be satisfied (Southwood, 1975; Begon, 1979): (i) the marker persists in all marked individuals; (ii) the markers do not affect the probability of survival or behavior of marked foragers; (iii) handling has no effect on death or emigration; (iv) all individuals (marked and unmarked) have an equal chance of being caught; and (v)

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the colony population is closed: neither birth, death, emigration nor immigration occur during the sampling period (Southwood, 1975; Begon, 1979).

Several authors (Thorne *et al.*, 1996; Curtis & Waller, 1997; Evans *et al.*, 1998, 1999) have criticized the use of the Lincoln Index for subterranean termites because of violation of some of its assumptions. In spite of the criticisms, none of these authors have postulated an alternative to this index to estimate population size of subterranean termite colonies. In lieu of finding a solution to this problem, the effective sampling area of a trap, (α), was chosen to determine the effectiveness of monitoring stations for subterranean termites to convey ways to estimate the size of the termite population without violating the assumptions required for the Lincoln index. The effective sampling area of a trap is the translation coefficient (α) that represents the area by which the trap catch needs to be divided to obtain an absolute population estimate. Turchin & Odendaal (1996) were the first to use the effective sampling area for multi-funnel baited-pheromone traps to investigate dispersal of southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae), and found that the effective sampling area was ≈ 0.1 ha. Schneider (1999) working with adults of *Heliothis virescens* (Fabricius) (Lepidoptera: Noctuidae), estimated the total density of emerged wild males per hectare based on the average trap catch and the effective sampling area of the trap, the latter estimated to be ~ 20 ha per trap.

Trap efficiency may be influenced by insect biology and population dynamics (age, density, spatial distribution, etc.), location of traps, and environmental factors such as temperature and humidity (Howell, 1974). Therefore, information on how effective a monitoring station is in capturing termites is needed to estimate the size of a foraging termite population. However, no information has

been published on the monitoring station's effective sampling area, α , for capturing subterranean termites.

In this study our objective was to estimate the effective sampling area of monitoring stations used to study the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae).

Materials and methods

Determination of effective sampling area

The effective sampling area of a monitoring station, is the translation coefficient (α) between the population density of termites (number of termites per m^2) marked and released in a monitoring station (M), and the proportion of marked termites captured in other monitoring stations (C). Because, $C = \alpha M$, the unit of α is m^2 . Therefore, the number of captured termites in a monitoring station can be translated into an estimate of absolute population density, or the number of termites per unit area. To estimate α , the effective sampling area of a monitoring station, it is necessary to know the average proportion of captured termites, $P(x)$, that were released at distance x from the release station. If $P(x)$ is known, the effective sampling area can be estimated by

$$\alpha = 2 \pi \int \{ x P(x) \} dx \quad (1)$$

This equation represents the product of two parameters: First, $2 \pi \int x$, represents the area of all possible circles around the release station, that have a radius equivalent to the distance from the monitoring stations to the release point (fig. 1). The second parameter is $P(x)$, the average proportion of marked termites captured in those monitoring stations. To calculate $P(x)$ the relationship between the logarithm of the proportion of recaptured termites and the logarithm of the

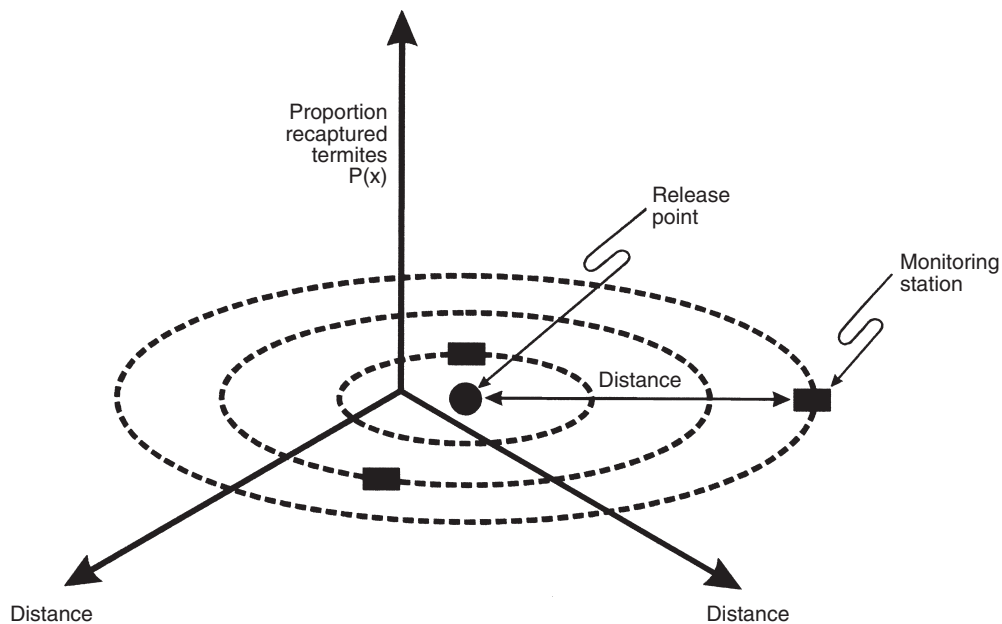


Fig. 1. The effective sampling area (α) can be estimated using the equation, $\alpha = 2 \pi \int \{ x P(x) \} dx$; this represents the product of the area of all possible circles around the release monitoring station (solid circle) that have radii equivalent to the distance from the monitoring stations (solid rectangles) to the release point (solid circle), and $P(x)$, the average proportion of marked termites captured in those monitoring stations.

distance from the monitoring station to the release point was determined. This method for determining absolute population density assumes that the density of marked termites is constant in space, and that the process of trapping averages over time. Furthermore, the method assumes that the effective sampling area can be oblong; and that the derivation is not affected if the termites are distributed in patches (Turchin & Odendaal, 1996).

Monitoring stations

Data from previous mark-recapture studies, using seven colonies of the Formosan subterranean termite, *C. formosanus* were used to calculate α for each colony (fig. 2, Su & Scheffrahn, 1996). These colonies, located in Hallandale, Broward County, Florida, were designated as colonies I, II, III, IV, V, VI and VII. Foraging territories of

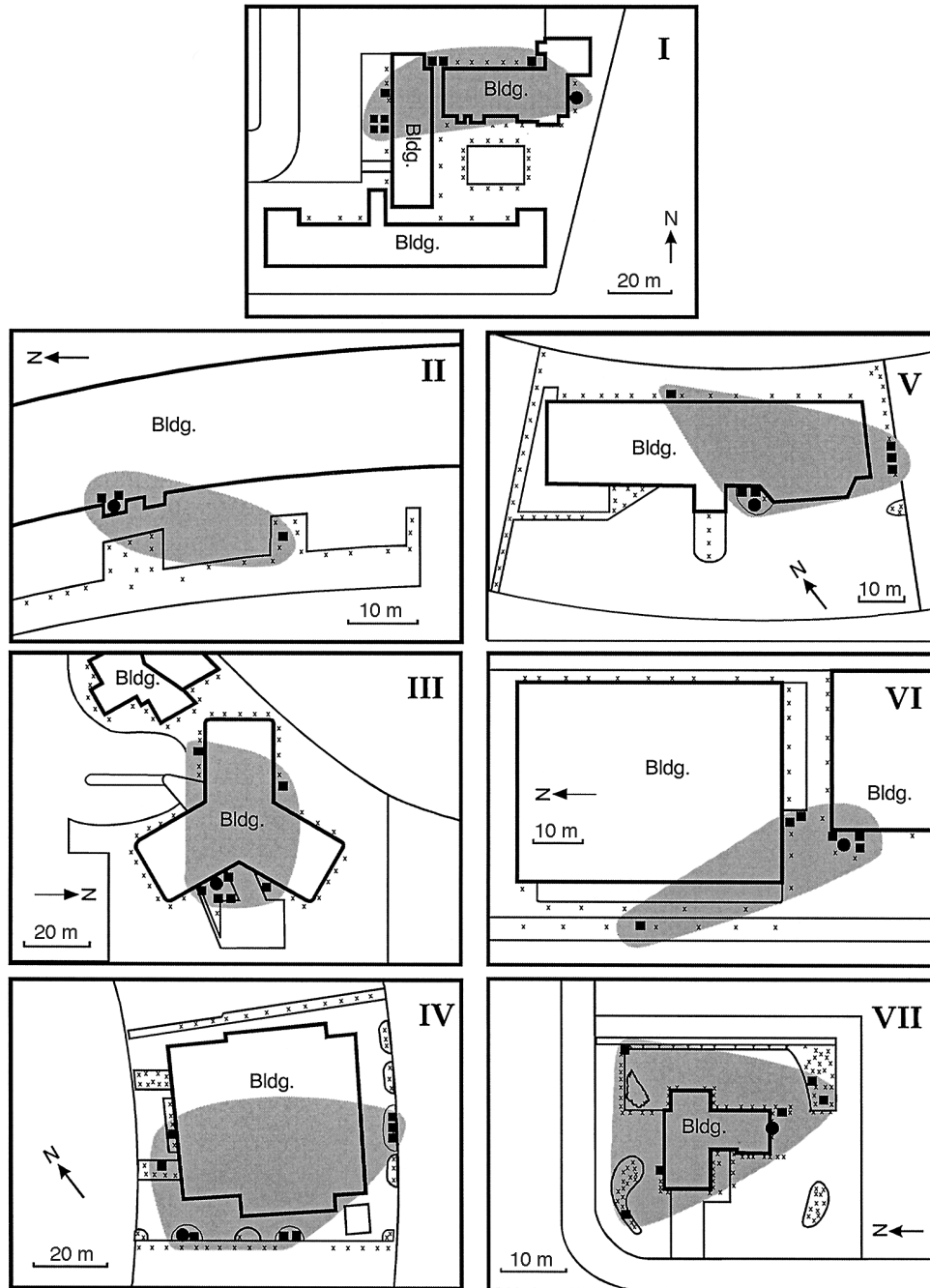


Fig. 2. Estimated foraging territories (shaded areas) of seven *Coptotermes formosanus* colonies from Hallandale, Florida, USA. Survey stakes (X) were used to detect termite activity. Solid circles denote in-ground monitoring stations where termites were released. Solid squares denote in-ground monitoring stations where termites were recaptured.

subterranean termites that inhabit densely populated human urban environments are difficult to discern because nests and foraging mainly occurs under concrete, slabs, and asphalt pavement and within inhabited structures. Therefore, stake surveys were used to detect underground termite activity by partially burying 200 wooden (*Picea* spp.) stakes every 5 m in lawns and planters around buildings attacked by subterranean termites for each colony or site. Only those stakes that were attacked by subterranean termites were replaced by in-ground monitoring stations. These stations were partially buried in the soil and consisted of a plastic collar (17 cm outside diameter, 15 cm high) (Su & Scheffrahn, 1986, 1996), made from polyvinyl chloride (PVC) pipe, placed in a hole surrounding the attacked wooden stake to form a c. 3.4 l underground cavity. A hollow wooden (*Picea* spp.) block was slipped over the stake and the latter was then gently tapped deeper into the soil so the top of the stake stayed below the edge of the pipe. A plastic food-container cover (Eagle Products, New York) was placed over the exposed end of the PVC pipe and covered with soil. When left undisturbed, termites burrow from the attacked stake to the wooden block. The distance between monitoring stations and the release point ranged from 5 to 170 m, and the number of monitoring stations at each site ranged from 12 to 16, depending on the number of stakes attacked by subterranean termites in each site or colony. Infested blocks were collected and brought to the laboratory, and termites separated from the debris by the bridging method described by Tamashiro *et al.* (1973). Mean termite biomass was determined by weighing five groups of ten worker termites. Colony foraging territories were defined as the areas encompassing interconnected stations as determined by the presence of marked termites. During the mark-recapture studies, colonies were not treated with any toxicant. Only after the mark-recapture experiments were finished, colonies were treated with different toxicants. The effect of these toxicants on the long-term population studies of these colonies can be found in Su & Scheffrahn (1996).

Termites collected from monitoring stations from all sites were brought to the laboratory, and marked with Nile Blue (Aldrich Chemical Company, Milwaukee, Wyoming), by forced feeding filter paper stained with 1% (w./w.) Nile Blue for ten days (Su & Scheffrahn, 1996). An average of 4568 marked termites (table 1) were released into the

monitoring station that had the highest termite activity at each site or colony (e.g. the highest density of termites collected). *Coptotermes formosanus* retained the marking for at least 42 days in the laboratory after being stained with 1% dye. Seven days after release, active traps in the vicinity were brought to the laboratory and marked and unmarked termites identified and counted. This time interval was short enough to assure that the marking persisted (Su & Scheffrahn, 1996), that no death, births nor immigration occurred, and to assure that distances between marked and mark-recaptured termites were due to movement from the initial release point to other monitoring stations. Su & Scheffrahn (1996) used two subsequent weekly mark-release and recapture events to estimate the foraging population of these colonies using the weighted mean model (Begon, 1979). In the present investigation, by using only the first mark, release and recapture event, distances between marked and mark-recaptured termites were assured not to be from reintroductions of marked individuals in subsequent mark and recapture events. These simple mark-recapture studies were carried out during the summer (June to August) for all seven colonies because termite activity is highest during these months.

Data analysis

Data from stations at the release point were excluded from the analyses to avoid any bias of the results, because high recapture rates occurred in stations used for releasing marked termites. Numerical solutions to the integrals involved were obtained using MathCAD (1989). A test of homogeneity was performed on the data and a Kruskal-Wallis ANOVA was used to detect differences among the mean values of termites recaptured over distance for each colony. An approximate test of equality of means was used to compare pairs of means for all the experiments (Sokal & Rohlf, 1981).

Results and Discussion

The average proportion of marked individuals of *C. formosanus* recaptured during single mark-release cycles at the seven different colonies, at different distances for the summer season are shown in table 1. Average recapture probability was 0.005 close to the release point (< 5 m) and

Table 1. Per cent recapture at different distances from colonies of *Coptotermes formosanus* in single-release-multiple-recapture experiments.

| Colony | Average no. termites released (± SD) | % Recapture ($\times 10^{-3}$) at distances | | | | | |
|---------|---|---|--------|--------|--------|--------|--------|
| | | < 5 m | < 10 m | < 20 m | < 30 m | < 40 m | < 80 m |
| I | 1420 ± 0 | 2.1 a | 1.2 a | 0.1 a | – | – | – |
| II | 5660 ± 3040 | 2.3 a | – | – | 3.2 a | – | – |
| III | 3130 ± 0 | 0.6 a | 1.1 a | 0.3 a | – | – | 0.6 a |
| IV | 7430 ± 555 | 2.6 a | 1.0 a | 1.5 a | – | – | 0.8 a |
| V | 8960 ± 3320 | 11.1 a | – | 3.2 b | 1.6 b | 1.5 b | 1.7 b |
| VI | 3330 ± 0 | 0.5 a | – | 0.3 a | – | – | 2.1 a |
| VII | 2040 ± 0 | 15.0 a | 3.2 b | – | 4.3 b | – | – |
| Average | 4560 ± 2840 | 5.2 a | 3.0 a | 1.9 a | 2.4 a | 4.1 a | 1.4 a |

Means within the same row followed by different letters are significantly different (Kruskal-Wallis Anova, $P < 0.05$).

Data represent termite releases during the summer season (June, July and August). Recapture rates at the release point were excluded from the analysis.

declined to 0.0008 at a distance of 51 to 60 m. Evans *et al.* (1998) reported recapture rates for *Coptotermes lacteus* (Rhinotermitidae) that were comparable to the recapture rates in the present study. However, for *Reticulitermes* species, recapture rates were ten times higher in other studies (Su *et al.*, 1993; Forschler & Townsend, 1996; Thorne *et al.*, 1996; Tsunoda *et al.*, 1998, 1999; Haverty *et al.*, 2000). For each site, recapture rates were not significantly affected by distance (Kruskal-Wallis ANOVA, $P > 0.05$), with the exception of colonies V and VII. In these colonies, recapture rates were higher in stations located less than 5 m away from the release station than those located at longer distances from the release point (Kruskal-Wallis ANOVA, $P < 0.05$). The relation between the log % termites recaptured was fitted to log distance, to determine $P(x)$, the average proportion of captured marked termites that started at distance x from the release point. The relationship between the proportion recaptured and distance for each site was either:

$$P(x) = 10^{-A-B(\log x)} \text{ or } P(x) = 10^{-A+B(\log x)} \quad (2)$$

(table 2), where A and B are constants for each site evaluated. The effective sampling area (α) was obtained (table 2) by using $P(x)$ in equation 1, and ranged from 0.607 m² for colony I, to 14.5 m² for colony IV. Excluding the colonies with the lowest and highest values of effective sampling area (colonies I and IV), α ranged from 3 to 7 m², which indicates that one trap is needed every 3 to 7 m² to estimate the size of these colonies.

Differences in the effective sampling area between colonies of *C. formosanus* could be greatly influenced by the population size of a colony, which is affected by the age of the colony, environmental conditions, or artificial factors such as control treatments. Control treatments were not used during the mark and recapture events. Furthermore, termite collections were effective during the summer months for all colonies, which may have reduced the possibility of finding differences among colonies due to environmental conditions. Therefore, the values of the effective sampling area should be related to age of the different colonies. The older the colony, the larger the number of workers in the colony, the more workers will be foraging for wood, the higher the probability of catching them (resulting in larger effective sampling areas of monitoring stations), and so fewer monitoring stations will be needed per unit area to estimate the size of the colony or population. As a result, for management purposes, lower numbers of monitoring stations are required to monitor colony IV (one station every 14 m², a large colony with a wide foraging area) compared to other colonies, such as colony I (probably a small young

colony), where monitoring stations are needed every 0.6 m² to estimate the size of this colony. Turchin & Odendaal (1996) also found that several factors influenced the effective sampling area of a trap, such as stand composition, change of seasons and spatial distribution of beetles. The effective sampling area used in this study represents a translation coefficient between station catch and the density of foraging termites inside in-ground tunnels. In other studies, the effective sampling area was based upon trap catch and the density of emerging beetles (Turchin & Odendaal, 1996) or trap catch and density of flying insects (Byers *et al.*, 1989; Schlyter, 1992). The in-ground stations were placed where termites previously intercepted wooden stakes. Therefore, this interception is analogous to intercepting flying insects with aerial traps because the underground tunnels are conveyors of pheromones that elicit recruitment of termites to monitoring stations with wood. In the same way, air acts as a conveyor of pheromones emanating from pheromone traps used to attract beetles or other flying insects in other studies (Byers *et al.*, 1989; Schlyter, 1992; Turchin & Odendaal, 1996). Termites do not detect wood over distance (Puche & Su, 2001a,b). Instead, they find wood by chance and after finding it, recruitment occurs to the specified location. Therefore, the probability of aggregation is the same for any monitoring station with wood, and the possible effect of aggregation on the effective sampling area is negligible for all colonies.

When considering the assumptions of the Lincoln index, several observations need to be taken into account. The markings used in this experiment, persisted more than 42 days (Su & Scheffrahn, 1996) and the termites were recaptured seven days after being marked. Therefore, the assumptions related to the persistence of the marker and the effects of the marking on the probability of survival of marked foragers were satisfied in this study. Furthermore, the apparent criticism of the effect of marking on the catchability of termites seems to be debatable. Several investigators have successfully used the marking technique to study foraging behaviour of subterranean termites (Lai *et al.*, 1983; Su *et al.*, 1983, 1988, 1991, 1993; Grace & Abdally, 1989; Grace, 1990; Jones, 1990; Su, 1994; Sajap *et al.*, 2000). Only a few investigators (Thorne *et al.*, 1996) have failed to succeed in marking and maintaining marked termites alive and the low survivorship has been attributed to an inadequate marking and handling procedure (Su, 2001). Because the recapture rates were not statistically different among stations at various distances (excluding the release point), it appeared that all individuals had an equal chance of being caught. Earlier criticisms for using the Lincoln

Table 2. Relationship between the log proportion of recaptured *Coptotermes formosanus* termites, $P(x)$, and log distance from trap to the release point (x), and effective sampling area of monitoring stations (α) for different colonies during the summer season.

| Colony | Equation | R ² | α (m ²) | Years sampled |
|--------|-------------------------------------|----------------|----------------------------|------------------------|
| I | $\log P(x) = -1.825 - 1.007 \log x$ | 0.342 | 0.607 | 1989 |
| II | $\log P(x) = -2.622 + 0.083 \log x$ | 0.405 | 5.929 | 1990, 1993 |
| III | $\log P(x) = -3.600 + 0.191 \log x$ | 0.580 | 3.312 | 1991 |
| IV | $\log P(x) = -2.622 - 1.189 \log x$ | 1.000 | 14.523 | 1986, 1987 |
| V | $\log P(x) = -1.497 - 0.950 \log x$ | 0.750 | 5.793 | 1986, 1990, 1993, 1995 |
| VI | $\log P(x) = -3.473 + 0.366 \log x$ | 0.364 | 7.498 | 1991 |
| VII | $\log P(x) = -1.845 - 0.602 \log x$ | 0.461 | 6.129 | 1992 |

Data represent termite releases during the summer months (June, July, August).

index model for population estimates of subterranean termites pointed out that one of the assumptions required 'equal mixing' between marked and unmarked individuals (Forschler & Townsend, 1996; Thorne *et al.*, 1996; Evans *et al.*, 1998, 1999). However, 'equal mixing' is not a required assumption and it is not listed in the original mark-recapture protocols (Lincoln, 1930; Begon, 1979). Instead, the 'equal catchability' of marked and unmarked individuals is one of the assumptions of the Lincoln index model (Lincoln, 1930; Begon, 1979). This study results suggest that the 'equal catchability' assumption was not violated for mark-recapture studies with *C. formosanus*. Therefore, the equal catchability of marked and unmarked termites determined in the present study, as well as persistence of the marker and survival of marked foragers, reinforces the belief that the Lincoln index and the effective sampling area are invaluable tools for studying the foraging behaviour and population dynamics of subterranean termites. Furthermore, the effective sampling area can be used as an alternative to the Lincoln index protocols used for estimating the size of foraging populations of subterranean termites.

The effective sampling area estimated in this study, should be taken as a reliable estimator that translates subterranean termite catches from in-ground monitoring stations into foraging termite population density. Alpha may be used to estimate the population size of foraging subterranean termites. If the average catch per station (C) is calculated and then divided by the effective sampling area (α) of that specific colony, its population density can be obtained, i.e. an estimate of the average number of foraging *C. formosanus* per unit area. If the area (A) occupied by the colony can be estimated, then the total foraging population size (N) of each colony can also be estimated using the equation $N = A C / \alpha$. The population size of a foraging colony (N) can be comparable to foraging population estimates using the Lincoln index model, only if the estimated area occupied by the colony (A) is known. The area encompassing interconnected stations, as determined by the presence of marked termites in different monitoring stations, partially represents the estimated area occupied by the colony, because this area only represents the area foraged by termite workers but does not include the area occupied by the underground main nest and connecting galleries. One way to estimate the area occupied by a colony might be to use destructive sampling of the main nest and galleries (Ratcliffe & Greaves, 1940; Greaves, 1962; King & Spink 1969; Inoue *et al.*, 2001) of several colonies of known foraging area (determined by mark-recapture studies), to determine the relationship between colony area (underground galleries and main nest), and the foraging area. This relationship (that should be assumed to be constant for all colonies of a given species), can be translated into an index of 'colony area/foraging area'. This index might then be used in future studies to extrapolate the 'colony area' from the 'foraging area' without destroying the colonies and rendering them available for future investigations. Further studies are needed to determine the area (A) corresponding to α for subterranean termites. The concept of the effective sampling area can be used for quantitative comparisons of subterranean termites or any other cryptic insects in relation to seasonality, age, treatment effects, or to validate other protocols used to estimate population density.

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