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Is Termite Body Size Correlated With Colony Vigor?

by

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ABSTRACT

Folk wisdom among termite researchers holds that the average body size (mass) of workers in a subterranean termite colony (Rhinotermitidae) is associated with the age and/or vigor of the colony. In particular, extremely large individuals are frequently thought to indicate a very old, or senescent, termite colony. However, there are very little data to support this assumption. It is also difficult to understand why subterranean termite colonies of advanced age, with a continuing food supply and supplementary reproductives presumably active in egg production, should be prone to senescence. We present data from 16 years of observations on a *Coptotermes formosanus* Shiraki field colony demonstrating a negative proportional relationship between average individual worker mass and estimated size of the colony foraging population. These results do not explain the phenomenon of senescence, but do suggest that decline in colony population size may be predicted from a measured increase in the average individual mass of workers sampled over a given period of time.

KEYWORDS: *Coptotermes formosanus*, colony demographics, Rhinotermitidae, Isoptera

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1 INTRODUCTION

The published field studies of colony population size and nest parameters largely represent snapshots of different termite colonies at single moments in time due to the need for destructive sampling (Darlington 1984, 1990; Howard et al. 1982; King & Spink 1969), or the time and effort required to conduct mark-release-recapture population estimations (Su et al. 1984, 1993; Su & Scheffrahn 1988; Grace et al. 1989; Grace 1990; Jones 1990; Easey & Holt 1989). As a result, our current knowledge of the developmental cycle of subterranean termite colonies is based upon observations of laboratory colonies (Bess 1970; Higa 1981; Crosland et al. 1994). Su & Tamashiro (1987) determined that the population growth curves of laboratory colonies of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, were best expressed by exponential regressions, and suggested that population growth in field colonies would appear as a logistic curve.

Since subterranean termite colonies maintained in containers in the laboratory never attain the population size of field colonies (Su & Tamashiro 1987) little is known of the mature or declining phases of colony growth. From our own experience in monitoring field colonies of *C. formosanus* (unpublished), and data collected over three years by Su et al. (1991), it is apparent that colony populations can remain fairly stable over several years.

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[1]Results discussed in this conference report have been submitted for publication in a refereed journal.

Termites collected from different colonies have been found to differ in their feeding activity, survival under laboratory conditions, and susceptibility to insecticides (Lenz 1985; Su & La Fage 1984; Tamashiro et al. 1994). Although much of this variability may be attributable to genetic and/or environmental factors, it has been conjectured that advanced age, or senescence, in termite colonies is associated with a reduction in individual vigor (Shimizu 1962; Nakajima et al. 1963).

Shimizu (1962) destructively sampled 14 *C. formosanus* field nests and attempted to classify them by both age and vigor according to the relative number of younger and older workers (or pseudergates) number of eggs, and structure and size of each nest. Based on wet weights, morphological measurements, and chemical analyses of individual workers from these colonies, Shimizu (1962) reported a correlation between worker weight and "vitality" of the nest, with nests containing larger individuals exhibiting less vitality.

Maintenance of long-term field sites at the University of Hawaii afforded us the unique opportunity to (a) plot the declining phase of colony growth through 16 years of observations on a field colony, and (b) examine the relationship of *C. formosanus* colony population size to the average body mass of individuals within the colony.

2 MATERIALS AND METHODS

In early 1976, numerous Douglas-fir (*Pseudotsuga menziezii* [Mirb.] Franco) stakes, each about 4 by 4 by 25 cm, were driven into the soil in the vicinity of the Pope laboratory on the Manoa campus of the University of Hawaii. In September 1976, one of these stakes was found to be infested by *Coptotermes formosanus* Shiraki, and was replaced with a collection trap, as described by Tamashiro et al. (1973). This trap consists of a wooden box (10.2 by 10.2 by 20.4 cm), open on each end, and constructed of two 2.5 by 10.2 by 20.4 cm Douglas-fir boards, and two 2.5 by 5.1 by 20.4 cm boards. The box is placed upright on the soil surface, over the end of the buried wooden stake, and the top capped with a 9.5 by 8.5 by 1.8 cm board. The wood is protected from rainfall by a 19 liter metal can with the bottom removed and a sheet metal cover over the upper end.

Twelve collection traps were installed at the site in fall 1976. Additional traps were installed in succeeding years as stakes were found to be infested, amounting to a total of 42 termite collection traps at this site. Beginning in January 1977, the foraging population of this colony was estimated at irregular intervals, for a total of nine estimates, using a Lincoln Index (simple proportionality) with the mark-release-recapture methodology developed by Lai (1977) and Su et al. (1984). In brief, termites collected in a single trap were separated from wood debris in the laboratory (Tamashiro et al. 1970), fed filter paper impregnated with the oil-soluble dye Sudan Red 7B (= Fat Red 7B) for several days, then counted and released back into the same collection trap in the field. After approximately two weeks, termites were collected from all traps at the site, and the numbers of dyed and undyed individuals recorded. In addition to providing an estimate of the foraging worker (pseudergate) population, recapture of marked individuals in traps distributed throughout the site confirmed that a single colony, designated as "Pope" due to its proximity to the Pope Laboratory, was present at this locale. Methods of studying the foraging distribution and colony size of subterranean termite colonies have been reviewed by Jones (1988) and Grace (1992).

The average wet body mass of individual workers from this colony was determined at irregular intervals by weighing three to five groups of 30 to 50 collected workers. These weights were determined either in conjunction with mark-release-recapture episodes, or in the course of collecting termites from the colony for use in laboratory experiments. By examination of the permanent log book for this site, and cross reference to the records of all experiments performed with individuals from this colony during the 16-year period, we were able to enumerate the pattern of removal and total numbers of termite workers and soldiers removed from the colony during each calendar year. Regressions of population size and individual worker body mass against time were performed with Freelance Graphics for Windows (Lotus Development Corp. 1993).

3 RESULTS AND DISCUSSION

During the first 16 months of observations (January 1977 to April 1978), Lincoln Index estimates of the foraging population ranged from 4.1 to 7.0 million workers, and body mass of individual workers ranged from 2.75 to 2.98 mg (Table 1). Between April and July 1978, however, the estimated population declined drastically to less than 3 million workers. Although construction activity was occurring on this portion of the Manoa campus of the University of Hawaii during this period, we are not able to correlate this population decline with any particular historical event in the vicinity of the termite colony.

By the eleventh year of observations, the colony foraging population had declined to less than 2 million workers; and in the fifteenth year to under 1 million workers (Table 1). Subsequent attempts to estimate the population in late 1993 and 1994 were frustrated by the very small numbers of foragers found in the individual traps, and the small numbers of active traps at the site.

As shown in Figure 1, the size of the foraging population declined exponentially over the 16-year monitoring period ($r^2 = 0.763$, $y = 4.513e^{0.008x}$). The body mass of individual workers, on the other hand, increased exponentially over this same period ($r^2 = 0.888$, $y = 2.684e^{0.004x}$). In the course of the 16-year period, the body mass of an individual worker more than doubled, from under 3 mg to more than 6 mg (Table 1).

Based upon published data from laboratory colonies, Su & Tamashiro (1987) modeled *C. formosanus* colony growth as an exponential function, with a population of 2.5 million individuals achieved within 5 to 8 years. Su & Tamashiro (1987) considered this early period of colony growth to be the intrinsic growth stage of a logistic population growth curve. Our data indicate that the declining stage of colony population growth can also be modeled as an exponential curve (Figure 1). An exponential growth phase of approximately 10 years for the colony described here, consistent with the models constructed by Su & Tamashiro (1987), combined with a 15-year period of exponential population decline provides a minimum estimate of 25 years for the age of this *C. formosanus* colony. However, our observations of other *C. formosanus* colonies over the past two decades (unpublished) indicate that relatively static foraging populations over periods of 10 years or more are not uncommon. Thus, a 10 year growth phase, conservative estimation of a 10 year static phase of minor population oscillations around the environmental carrying capacity, and a 15 year declining phase would increase our minimum colony age estimate to 35 years. Further support for the advanced age of this particular colony is given by recent allozyme studies (J. Wang and J.K. Grace, unpublished) which suggest a high degree of inbreeding which would be consistent with the presence of active supplementary reproductives in the colony.

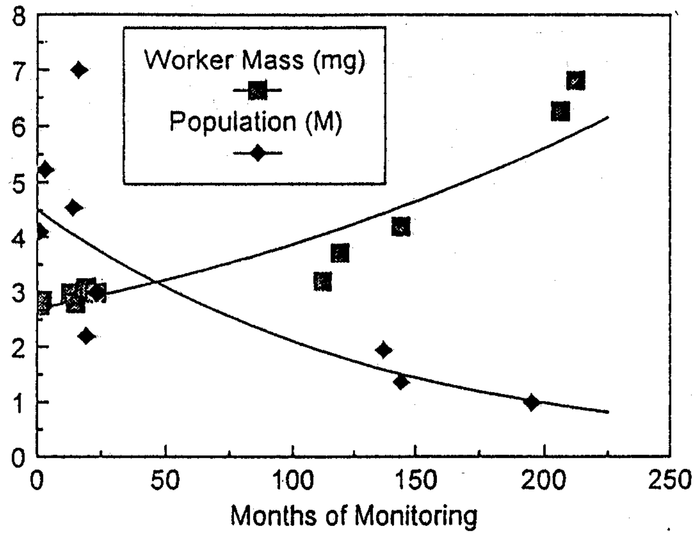

Figure 1. Exponential decrease ($r^2 = 0.763$, $y = 4.513e^{-0.008x}$) in the worker foraging population and increase ($r^2 = 0.888$, $y = 2.684e^{0.004x}$) in the body mass of individual workers in a Formosan subterranean termite colony over 16 years.

Our observations of this colony would appear to generally support Shimizu's (1962) conclusion that older and less "vital" *C. formosanus* colonies contain workers that are larger in body mass than younger and more vigorous colonies. However, we and other researchers (Su & Scheffrahn 1988a, 1988b) have also noted consistent differences over a period of several years in the average mass of individuals from different *C. formosanus* colonies, suggesting that body mass is a function of genetics and/or environment, as well as colony age. Although, given the apparent long life of *C. formosanus* colonies, it is also possible that the differences observed among colonies may indeed be largely attributable to their relative age. Darlington (1991) observed a relationship to that suggested here between dry mass of individual termites and nest population size in *Macrotermes* spp. Interestingly, Waller (unpublished observation, cited in Waller & La Fage 1987) observed that *C. formosanus* individuals kept for several months in the laboratory could increase 30% in biomass. This latter observation could suggest a correlation of body mass with vigor, if not with age.

We are aware that the long-term observations that we report here are fairly unique in the literature and limited to a single *C. formosanus* colony. However, our data demonstrate a close relationship between the increase in worker body mass over time and the decrease in the size of the foraging population. This suggests that observations on individual body mass of termite workers sampled at a single location over a period of several years might allow one to determine the population stage of the colony in the approximate 35 year growth cycle of exponential increase, static growth near the carrying capacity, and subsequent exponential population decrease. Thus, once an increase in individual worker mass is noted, one could estimate the proportional decrease in the colony population as a function of the observed change in individual mass.

It is difficult to understand why a subterranean termite colony with a continuing food supply and supplementary reproductives presumably active in egg production should ever exhibit a pattern of decline. It may be that the relationship of increasing individual body mass to population decline is valid, but that this sequence of events must be triggered by a debilitating (e.g., disease) or catastrophic (e.g., flooding or earth movement) event in the history of the colony. Under such a scenario, termite colonies would enter this final developmental phase at different ages, and colonies existing under extremely favorable or consistent conditions might persist indefinitely.

Table 1. Body mass of individual termite workers, size of foraging population as estimated by mark-release-recapture, and cumulative numbers of workers and soldiers removed from a single *Coptotermes formosanus* field colony over 16 years.

Year	Month	Individual worker mass (mg)	Estimated foraging population	Cumulative no. termites removed[a]	
				Workers	Soldiers
1977	1	2.75	4,104,177		
	2	2.84			
	3		5,228,781		
	9			93,268	4,246
1978	1	2.98			
	2		4,546,631		
	3	2.79			
	4		6,994,100		
	7	3.08	2,197,618		
	11	2.98	2,981,435		
1979	9			103,726	4,996
1980	4			105,402	
1981	2			112,395	5,416
1982	11			173,239	13,933
1983					
1984	12			227,319	21,115
1985	8			455,277	35,164
1986	4	3.20			
	11	3.72		517,227	
1987	12			748,457	42,330
1988	5		1,952,344		
	12	4.21	1,375,258	933,944	54,847
1989	12			1,021,828	63,563
1990	12			1,134,299	71,857
1991	12			1,143,104	72,752
1992	3		994,981		
	12			1,187,324	77,507
1993	2	6.26			
	8	6.81		1,254,059	82,257

[a]Cumulative totals, as of the last month in which termites were removed during each year.

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