Relationship of Individual Worker Mass and Population Decline in a Formosan Subterranean Termite Colony (Isoptera: Rhinotermitidae)

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ABSTRACT Current knowledge of the developmental cycle of subterranean termite (Isoptera: Rhinotermitidae) colonies is primarily based on observations of colonies maintained in laboratory containers. Because-laboratory-reared colonies never attain the population size of field colonies, little is known of the mature or declining phases of colony growth. In a unique long-term study we report 16 yr of observations on the estimated population size and wet mass of individual termites collected from a *Coptotermes formosanus* Shiraki field colony in Hawaii. During this period, the mean wet body mass of individual foraging workers more than doubled, from <3 mg to >6 mg, while the estimated colony foraging population declined exponentially. The size of the colony foraging population (y) was negatively related to individual worker body mass (x) by a power equation of the form $y = 37.136x^{-2.109}$. These data support the conclusion that older or less vigorous *C. formosanus* colonies contain workers that are larger in body mass than younger colonies, although other genetic and environmental variables also may influence observed variation in individual mass among termite colonies. Given a baseline estimate of colony foraging population, the subsequent proportional decrease in the population of this *C. formosanus* colony (y) could be predicted from the proportional increase in individual wet mass (x), as expressed by $y = 36.402x^{0.169}$.

KEY WORDS *Coptotermes formosanus*, termite population model

FEW, IF ANY, long-term field studies of the population dynamics of termite (Isoptera) colonies have been conducted. 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 (King and Spink 1969; Howard et al. 1982; Darlington 1984, 1990), or the time and effort required to conduct mark–release–recapture population estimations (Su et al. 1984, 1993; Su and Scheffrahn 1988; Easey and Holt 1989; Grace et al. 1989; Grace 1990; Jones 1990). Field studies of subterranean termite (Rhinotermitidae) species that lack an above-ground mound or other well-defined nest structure are particularly challenging.

Current knowledge of the developmental cycle of subterranean termite colonies is based on observations of laboratory colonies (Bess 1970, Higa 1981, Crosland et al. 1994). Su and 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 they suggested that population growth in field colonies followed a logistic curve.

Because subterranean termite colonies maintained in containers in the laboratory never attain the population size of field colonies (Su and 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 data), and data collected over 3 yr by Su et al. (1991), colony populations apparently can remain fairly stable over several years.

Termites collected from different colonies have been found to differ in their feeding activity (Su and La Fage 1984), survival under laboratory conditions (Lenz 1985), and susceptibility to insecticides (Tamashiro et al. 1994). Although much of this variability may be attributable to genetic or environmental factors, or both, it has been conjectured that advanced age, or senescence, in termite colonies is associated with reduced vigor of individuals (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 mass, morphological measurements, and chemical analyses of individual workers from these colonies, Shimizu (1962) reported a negative correlation between worker mass and vitality of the nest, with nests containing larger individuals exhibiting less vitality.

The current study afforded an unique opportunity to plot the declining phase of colony growth through 16 yr of observations of a field colony, and examine the relationship of *C. formosanus* colony population size to the average body mass of foraging individuals.

Materials and Methods

In the summer of 1976, numerous Douglas-fir, *Pseudotsuga menziezii* (Mirb.) Franco, stakes, each ≈25 by 4 by 4 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, 1 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 between September and December 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 9 estimates, using a Lincoln index mark–release–recapture technique (Begon 1979) with methodology for termites 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. 1973), fed filter paper impregnated with the oil-soluble dye Sudan Red 7B (=Fat Red 7B) for several days, then dyed workers (pseudergates) were counted and released back into the same collection trap in the field. After ≈2 wk, termites were collected from all traps at the site, and the numbers of dyed and undyed workers recorded. In addition to allowing an estimate of the foraging worker population, recapture of marked individuals in traps distributed throughout the site confirmed that a single colony was present near the Pope laboratory.

The population of foraging workers was estimated using the Lincoln index (Begon 1979). This is a simple proportionality in which the proportion of marked workers recaptured in a random sample of foragers is considered to be equivalent to the total proportion of marked workers in the entire foraging population. This method was also used by Lai (1977), Esenther (1980), and Su et al. (1984) to estimate termite colony foraging populations. Since the Lincoln index relies on a single recapture of marked termites, the estimate provided may be less precise than estimates based on the multiple recapture methods later described by Su and Scheffrahn (1988) and Grace et al. (1989). 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 foraging workers from this colony was determined at irregular intervals by weighing 3–5 groups of 30–50 workers, subsampled randomly from active trap collections. These weights were determined either in conjunction with mark–release–recapture episodes or in the course of collecting termites for use in laboratory experiments, and were taken immediately after the termites were removed from the field. In each instance, the principal purpose of the collection was to obtain a large number of living termites, rather than to assess individual morphological parameters. Thus, the dry body mass of dead and desiccated termites was not measured, although dry mass would be expected to be less susceptible than wet mass to environmental and seasonal variation. 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-yr 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 foraging population size and individual worker wet body mass against time, population size against individual mass, and the change in population size against the change in individual mass were performed with Freelance Graphics (Lotus Development 1993). For the latter regression, mass and population estimates made during the first 16 mo of the study were averaged, as were those during months 19–23. Later estimates of body mass and population size were correlated by their temporal proximity to each other.

Results and Discussion

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

Although no estimates were made for a 10-yr interval, by the 11th yr of observations, the colony foraging population had declined to <2 million workers; and in the 15th yr to <1 million workers (Table 1). Subsequent attempts to estimate the population in late 1993 and 1994 were frustrated

Table 1. Mean wet body mass of individual foraging termite workers, size of foraging population as estimated by Lincoln index mark–release–recapture methodology, and cumulative numbers of workers and soldiers removed from a single *C. formosanus* field colony over 16 yr

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

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

by the small numbers of foragers found in the individual traps, and the small numbers of active traps at the site.

As shown in Fig. 1, the size of the foraging population declined exponentially over the 16-yr monitoring period ($r^2 = 0.763$, $y = 4.513e^{-0.008x}$). The mean wet mass of individual foraging workers, however, increased exponentially over this same period ($r^2 = 0.888$, $y = 2.684e^{0.004x}$). In the course of the 16-yr period, the mean wet body mass of individual foragers more than doubled, from <3 mg to >6 mg (Table 1). An increasing proportion of later instar workers in the foraging population would certainly contribute to such an effect, although this may not be sufficient to explain the magnitude of the observed mass increase.

Based on published data from laboratory colonies, Su and Tamashiro (1987) modeled *C. formosanus* colony growth as an exponential function, with a population of 2.5 million individuals achieved within 5–8 yr. Su and 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

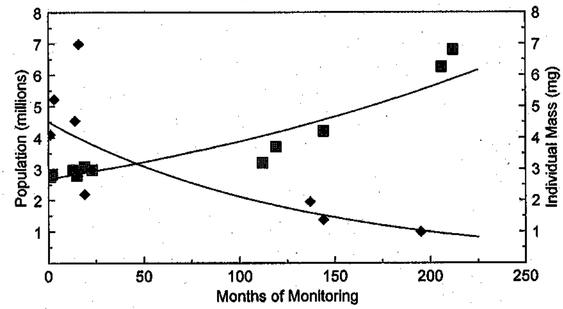

Fig. 1. Exponential decrease ($r^2 = 0.763$, $y = 4.513e^{-0.008x}$) in the worker foraging population and increase ($r^2 = 0.888$, $y = 2.684e^{0.004x}$) in the wet body mass of individual foraging workers in a Formosan subterranean termite colony over 16 yr. Worker foraging population, millions, indicated by black diamonds. Worker wet mass, mg, indicated by shaded squares.

stage of colony population growth can also be modeled as an exponential curve (Fig. 1). An exponential growth phase of ≈10 yr for the colony described here, consistent with the models constructed by Su and Tamashiro (1987), combined with a 15-yr period of exponential population decline provides a minimum estimate of 25 yr for the age of this *C. formosanus* colony. However, our observations of other *C. formosanus* colonies over the past 2 decades (unpublished data) indicate that relatively static foraging populations over periods of 10 yr or more are not uncommon. Thus, a 10-yr growth phase, conservative estimation of a 10-yr static phase of minor population oscillations around the environmental carrying capacity, and a 15-yr declining phase would increase our minimum colony age estimate to 35 yr. Further support for the advanced age of this particular colony is given by recent allozyme studies (J. Wang and J. K. Grace, unpublished data) that suggest a high degree of inbreeding consistent with the presence of active neotenic reproductives in the colony.

The size of the colony foraging population was negatively related to individual worker wet body mass ($r^2 = 0.773$) by a power equation of the form $y = 37.136x^{-2.109}$ (Fig. 2). This would appear to

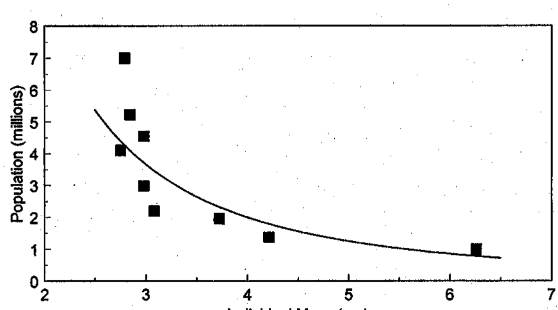

Fig. 2. Relationship of termite colony foraging population to average individual *C. formosanus* foraging worker wet body mass ($r^2 = 0.773$, $y = 37.136x^{-2.109}$).

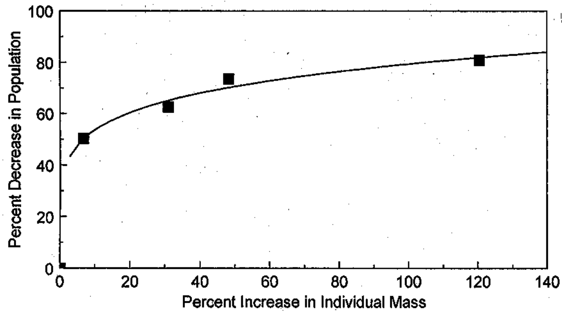

Fig. 3. Relationship of the proportional decrease in *C. formosanus* colony foraging population over a 16-yr period to the proportional increase in the average foraging worker wet body mass (r^2 = 0.969, $y = 36.402x^{0.169}$).

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 and Scheffrahn 1988a, 1988b) have also noted consistent differences extending over periods of several years in the average mass of foragers collected from different *C. formosanus* colonies, suggesting that body mass is a function of genetics or environment, or both, 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) also fit a power regression to the relationship between dry mass of individual termites and nest population size in *Macrotermes* spp. Interestingly, D. A. Waller (observation cited in Waller and La Fage 1987) observed that *C. formosanus* individuals that are kept for several months in the laboratory could increase 30% in biomass. This latter observation suggests again a correlation of body mass with vigor, if not with age.

Given that genetic and possibly environmental variation exists among *C. formosanus* colonies in the average individual wet mass of workers from those colonies, we would not suggest that one could estimate the colony population simply by weighing a sample of workers. We are also aware that the long-term observations that we report here are unique in the literature and limited to a single *C. formosanus* colony. However, our data (Fig. 3) demonstrate a strong relationship between the proportional increase in average worker wet body mass over time and the proportional decrease in the size of the foraging population (r^2 = 0.969, $y = 36.402x^{0.169}$). This suggests that observations on individual body mass of foraging 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-yr growth cycle of exponential increase, static growth near the carrying capacity, and subsequent exponential population decrease.

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