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NUMERICAL AND BIOMASS CASTE PROPORTIONS IN COLONIES OF THE TERMITES *NASUTITERMES CORNIGER* AND *N. EPHRATAE* (ISOPTERA ; TERMITIDAE)

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SUMMARY

Caste ratios among monogynous *N. corniger* colonies are less variable (higher correlation coefficients and lower variances) than among polygynous colonies. Polygynous colony caste proportions are more constant than for queenless colonies.

Correlation coefficients are not significantly different between numerical and biomass neuter caste ratios (large workers : small workers ; total worker population : soldiers) in *N. corniger* or *N. ephratae.*

The intraspecific range of both numerical and biomass percentages of soldiers, small workers, and large workers is large in *N. corniger* and *N. ephratae.*

Numerical and biomass percentage of soldiers, small workers, and large workers were all significantly different between monogynous *N. corniger* and monogynous *N. ephratae* colonies. Mean individual weights of soldiers, large workers, and small workers did not differ between species.

Single queen *N. corniger* colonies tend to have a higher ratio of the number of small workers : large workers and the number of soldiers : workers, and a lower proportion of presoldiers : soldiers than do monogynous *N. ephratae* nest.

Polygynous *N. corniger* colonies have a statistically larger ratio of number of larvae : number of workers, and a higher number of presoldiers : soldiers than do single queen colonies. These all suggest differences in growth rate related to single versus multiple queens. Monogynous and polygynous nests have significantly higher ratios of larvae : workers than do queenless colonies.

In both numerical and biomass analyses of various *N. corniger* caste ratios, correlation coefficients were highest in comparisons between the total number or dry weight of all workers vs soldiers.

Mean individual dry weights of large and small workers in queenless *N. corniger* colonies are significantly higher than in queenright colonies. This may be because the queenless colony population is aging without generating more young so fewer individuals are in the early worker instars.

ZUSAMMENFASSUNG

Zahlen- und Gewichtsverhältnisse der Kasten in Termitenkolonien der Arten Nasutitermes corniger und N. ephratae (Isoptera ; Termitidae)

Die numerischen Proportionen der Kasten sind bei monogynen *N.c.* Kolonien weniger variabel (höherer Korrelationskoeffizient und niedrigere Abweichung) als bei polygynen Kolonien. Polygyne Kolonien sind konstanter in ihren Kasten-Proportionen als Kolonien ohne Königinnen.

Die Korrelationskoeffizienten von Mengen- und Gewichtsverhältnissen unter den sterilen Kasten (grosse Arbeiter : kleine Arbeiter ; gesamte Arbeiter Population : Soldaten) sind weder bei *N.c.* noch bei *N.e.* signifikant verschieden.

Sowohl bei *N.c.* wie auch bei *N.e.* findet man eine weite innerartliche Verteilung von proportionalen Anteilen von Soldaten, kleinen Arbeitern, und grossen Arbeitern.

Der zahlen- und gewichtsmässige Anteil der Soldaten, kleinen und grossen Arbeitern, war zwischen monogynen *N.c.* Kolonien und monogynen *N.e.* Kolonien signifikant unterschiedlich. Das mittlere Gewicht von Soldaten, grossen Arbeitern und kleinen Arbeitern war nicht unterschiedlich zwischen den beiden Arten.

In monogynen *N.c.* Kolonien ist gewöhnlich das Zahlenverhältnis zwischen kleinen Arbeitern : grossen Arbeitern, und Soldaten : Arbeitern grösser, dagegen ist das Verhältnis zwischen Prä-Soldaten : Soldaten kleiner als bei monogynen *N.e.* Kolonien.

Polygyne *N.c.* Kolonien haben ein statistisch grösseres Zahlenverhältnis von Larven : Arbeitern, und Prä-Soldaten : Soldaten, als monogyne Kolonien. Dies alles lässt vermuten, dass monogyne und polygyne Kolonien unterschiedliche Wachstumsraten haben.

Bei der Analyse der Zahlen- und Gewichtsverhältnisse verschiedener *N.c.* Kasten waren die Korrelationskoeffizienten am höchsten beim Vergleich von Gesamtzahl oder Trockengewicht der Arbeiter versus Gesamtzahl oder Trockengewicht von Soldaten.

Das durchschnittliche Trocken gewicht grosser und kleiner Arbeiter in königinlosen Kolonien war signifikant höher als in Kolonien mit Königin. Dies ist wahrscheinlich deshalb so, weil die Population der königinlosen Kolonie älter wird, ohne mehr Jungtiere zu produziern, sodass weniger Anfangsstadien von Arbeitern zu finden sind.

INTRODUCTION

Castes are the functional infrastructure of social insect colonies : they enable a colony to accomplish tasks " concurrently instead of sequentially " (OSTER and WILSON, 1978 p. 10) and they facilitate specialization in division of labor. Data on caste proportions within field colonies, and on the natural range of variation of these ratios, are fundamental to understanding the ecological, behavioral, physiological, and reproductive dynamics of species. In studies of termites, complete dissections of entire nests have proven the most reliable method for quantitatively assessing colony composition and caste ratios. This paper presents numerical and biomass caste ratio results of dissections of 112 *Nasutitermes corniger* and 32 *N. ephratae* arboreal carton nests in the Republic of Panama (number of larvae, presoldiers, soldiers, and workers are included in this treatment ; data on alate production is presented in THORNE, 1983). Population patterns of caste ratios are compared using principal axis correlation analysis to examine inter- and intraspecific caste ratios and their variance. Such colony analyses provide data on ergonomic investment in each caste and on the range of variation in such investment among colonies. The data are also used to determine if external metric characteristics of *Nasutitermes* nests (such as weight or volume) could be used as correlates of colony population size, and thus serve as an index to estimate population size of field colonies.

METHODS

Entire *N. corniger* (Motschulsky) and *N. ephratae* (Holmgren) arboreal nests were collected from areas of young second growth on the Gigante Peninsula and Frijoles Island near Barro Colorado Island (BCI; 9°09' N, 79° 51' W), Republic of Panama. Both species occur in lowland forests and areas of second growth throughout much of Middle America and parts of South America (THORNE, 1980). Collections were made April-July 1979; October 1979 - January 1980; March - July 1980; and April and November 1981. Colonies were collected between 7 a.m. and 11 a.m. The carton nests were excised from host trees (wood encompassed by the nest included in the sample), placed in thick plastic bags, and transported to the Smithsonian Tropical Research Institute's laboratory on BCI. Colonies were refrigerated for 24-48 hours to inactivate the termites. Nests were then sequentially shaved and shaken, allowing termites to fall from the exposed galleries. Most individuals fell readily, but if the nest interior was moist some clung to damp walls. Estimates of the percentage of the population retrieved (normally above 90 %) accounted for such remaining individuals.

All termites removed from a colony were mixed in a large bowl. Total volume was determined and three random 5 ml subsamples were drawn for analysis. Each subsample, containing 400-900 individuals depending on amount of nest debris, was sorted and counted by caste. Total colony size and caste proportions were estimated from the subsample counts, with standard deviations consistently less than 10 % of the estimate, and usually below 6 %. This technique does not account for foragers (mature soldiers and workers) outside the nest at the time of collection.

Dry weights of all castes were taken after $\leqslant$ 72 hours in a drying oven. " Average " dry weight for a colony's soldier, for example was determined by weighing 30-50 dry soldiers and dividing the cumulative weight by number of individuals. This gives no measure of intra-colony variation in soldier weight. Queen live (fresh) weights were taken immediately after primary reproductives were removed from the royal chamber.

Nest volumes were based on the volume of an ellipsoid. The volume of trunks or branches going through the nest were subtracted to yield nest volume. Nest weights were determined by weighing the nests in their plastic bags after collection, weighing wood inclusions after removal by dissection, and then subtracting the weight of the wood from the initial weight. Nest weight is thus a measure of nest carton weight plus the comparably insignificant weight of the housed termites (normally less than 10 % of the total).

Principal axis correlation analysis is appropriate for caste ratios because the procedure does not assume that one of the two axes is measured without error, and it does not assume that one axis varies independently of the other. The least squares fit of a linar regrssion, however, must be used to compare two (*t* test) or more (analysis of covariance) relationships statistically. (One can also examine overlap or nonoverlap of

95 % confidence limits on the slope of the principal axis correlation. In most cases, this result and the result of the regression analysis are in agreement).

Caste relationships are given separately for monogynous ($N = 46$), polygynous ($N = 25$), and queenless (empty queen cell, $N = 42$) *N. corniger* colonies. Queen absence indicates a declining colony, possibly capable of requeening if alate brood are developing. At the time of collection, however, such colonies have unreplenished cohorts of immatures and lack any royal influence over control of caste ratios. Queenless *N. ephratae* colonies were relatively rare in this sampling (7 of 39 colonies), so only data from monogynous nests are presented. No polygynous *N. ephratae* colonies were found in this study, although literature accounts, museum specimens, and unpublished observations document their existence (Becker, 1961, Mathews, 1977 ; specimens of Zetek & Molino, U.S. National Museum ; H. Jacobson, pers. comm.).

RESULTS

Caste Proportions

The mean numerical and biomass percentages of soldiers, large workers and small workers in the neuter population of monogynous, polygynous and queenless *N. corniger*, and monogynous *N. ephratae* colonies, are shown in *figure 1.* Not surprisingly, numerical caste proportions for all groups are significantly different ($p < 0.001$) from biomass percentages. All caste proportions are significantly different ($p < 0.001$) between monygynous *N. corniger* and *N. ephratae* colonies. Among *N. corniger* colonies the only significant difference among groups of different queen status is that monogynous colonies have a significantly higher ($p < 0.05$) mean numerical percentage of soldiers than do polygynous colonies.

The mean numerical percentage of larvae found in *N. corniger* colonies (based on arcsine transformed data) was as follows : monogynous $\bar{x} = 19.6$ % (max. S.D. = 32.9 ; min. S.D. = 90) ; polygynous $\bar{x} = 23.8$ % (max. S.D. = 35.3 ; min. S.D. = 14.0) ; queenless $\bar{x} = 2.5$ % (max. S.D. = 10.7 ; min. S.D. = 0). The mean for monogynous *N. ephratae* colonies was $\bar{x} = 23.5$ % (max. S.D. = 34.1 ; min. S.D. = 14.4). (Because termites are hemimetabolous, all immatures should technically be called nymphs, but worker/soldier immatures are termed " larvae " by Isopterists to distinguish them from fertile-line pre-alate " nymphs " (Noirot, 1969).) Monogynous *N. ephratae* and polygynous *N. corniger* colonies have a statistically higher ($p < 0.01$) numerical percentage of larvae than do monogynous *N. corniger* societies. Predictably, queenless *N. corniger* colonies house a lower numerical percentage of larvae than do queenright conspecific nests ($p < 0.001$).

Nest Measurements as Correlates of Colony Population Size

In the field, *Nasutitermes* nest volume is a more convenient measurement than nest weight, which ultimately requires removal of the colony from its host tree. The principal axis lines listed in *table I* show that while the

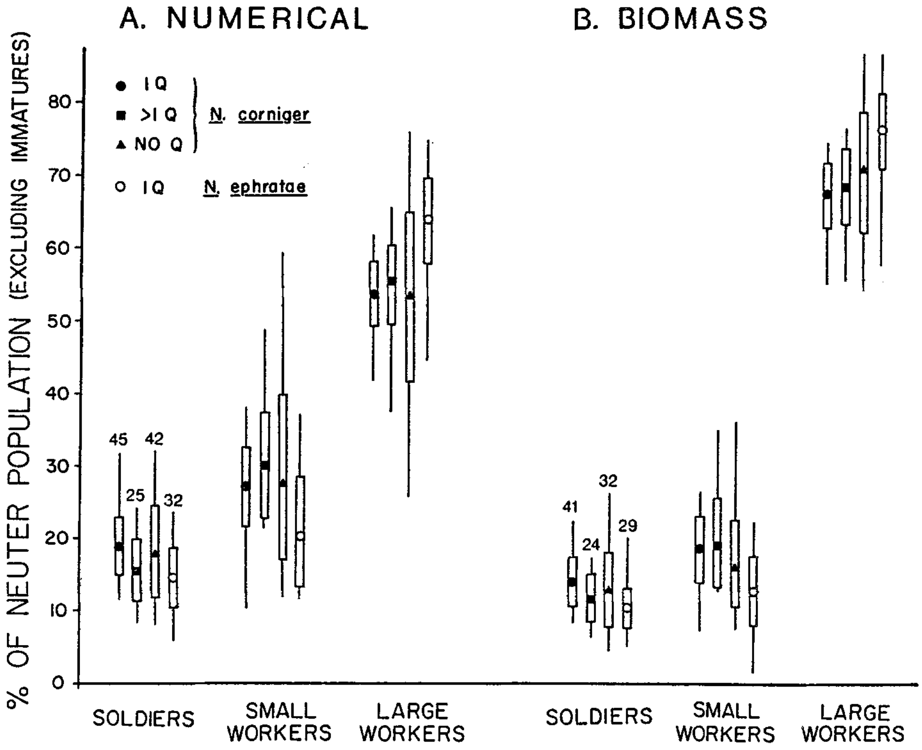

Fig. 1. — Numerical and biomass caste proportions in monogynous, polygynous and queenless *N. corniger* and monogynous *N. ephrataè* colonies. Means (calculated from arcsine transformed data) are indicated by symbols, open bars show standard deviation, and lines span the range. Sample sizes for numerical and biomass analyses are given above the soldier bars in each category. Statistical differences among groups are summarized in the text.

Abb. 1. — Die numerischen und Biomasse Kasten Proportionen bei monogynen, polygynen und Königinnen-losen *N. corniger* und monogynen *N. ephratae* Kolonien. Die Mittelwerte (errechnet durch *arcus sinus* transformierte Daten) sind durch Symbole angedeutet, die offenen Rechtecke Zeigen die Standard Abweichung, und die Linien messes die Verteilungsbreite. Gesamtmengen für numerische und Biomasse Analysen sind in jeder Einheit über den Soldaten Strich angegeben. Statistische Unterschiede zwishen den Gruppen sind im Text zusammengefast.

correlation between nest weight or volume and neuter population size is high ($0.78 \leqslant r \leqslant 0.87$) for both species, there is considerable scatter around the best fit line (see 95 % confidence limits on r and on the slope). Nest population projections based on that equation will be subject to error (usually less than or equal to a factor of 2), but depending on the desired use might give sufficient accuracy. An analysis of covariance among re-

Table I. — Numerical caste ratios : Principal Axis Correlations and Comparisons.

Tabelle I. — Zahlenverhältnisse der Kasten : Korrelationen und Vergleiche.

Abcissa	Ordinate	Species and queen number		Principal axis correlation line	r	95 % Confidence limits on r	95 % Confidence limits on slope	Significant differences in regression lines (ns comparisons not listed)
Nest Weight (kilos)	Neuter Population Size (including larvae) (x 10^5)	*N. corniger*	1 Q	y = 36,900x + 45,400	0.85	0.73 ; 0.91	31,262 ; 44,972	1 Q *N. corniger* vs > 1 Q *N. corniger* *** (E)
			> 1 Q	y = 73,900x — 25,600	0.83	0.63 ; 0.91	58,409 ; 100,600	
		N. ephratae	1 Q	y = 47,000x + 18,700	0.85	0.88 ; 0.97	38,556 ; 60,379	
Nest Volume (x 10^4 cm^3)	Neuter Population Size (including larvae) (x 10^5)	*N. corniger*	1 Q	y = 18x + 27,500	0.87	0.76 ; 0.92	15.53 ; 21.73	1 Q *N. corniger* vs > 1 Q *N. corniger* *** (E)
			> 1 Q	y = 33x — 43,700	0.86	0.70 ; 0.93	26.63 ; 42.32	
		N. ephratae	1 Q	y = 21x + 17,800	0.78	0.57 ; 0.88	16.11 ; 28.83	
Number of Large Workers (x 10^5)	Number of Small Workers (x 10^5)	*N. corniger*	1 Q	y = .49x + 1,440	0.93	0.87 ; 0.96	0.44 ; 0.55	1 Q *N. corniger* vs NO Q *N. corniger* *** (S)
			> 1 Q	y = .46x + 7,510	0.90	0.77 ; 0.95	0.38 ; 0.56	> 1 Q *N. corniger* vs NO Q *N. corniger* *** (S,E)
			NO Q	y = .28x + 11,300	0.71	0.51 ; 0.83	0.20 ; 0.36	
		N. ephratae	1 Q	y = .35x — 332	0.83	0.64 ; 0.90	0.26 ; 0.43	1 Q *N. corniger* vs 1 Q *N. ephratae* *** (E)
Total Number of Workers (x 10^5)	Number of larvae (x 10^5)	*N. corniger*	1 Q	y = .22x + 9850	0.80	0.67 ; 0.88	0.18 ; 0.27	1 Q *N. corniger* vs > 1 Q *N. corniger* *** (S) * (E)
			> 1 Q	y = .52x — 19,500	0.77	0.53 ; 0.88	0.36 ; 0.71	1 Q *N. corniger* vs NO Q *N. corniger* * (S) *** (E)
			NO Q	y = .09x — 730	0.45	0.17 ; 0.65	0.04 ; 0.14	> 1 Q *N. corniger* vs NO Q *N. corniger* *** (S,E)
		N. ephratae	1 Q	y = .22x + 12,500	0.73	0.51 ; 0.85	0.15 ; 0.85	

Total Number of Workers (x 10^5)	Number of Soldiers (x 10^4)	*N. corniger*	1 Q	$y = .20x + 2{,}520$	0.97	0,94 ; 0.98	0,18 ; 0.21	1 Q *N. corniger* vs 1 Q *N. ephratae* *** (E)
			> 1 Q	$y = .20x - 2{,}320$	0.91	0.79 ; 0.95	0.16 ; 0.23	
			NO Q	$y = .22x + 1{,}000$	0.82	0.68 ; 0.89	0.18 ; 0.27	
		N. ephratae	1 Q	$y = .14x + 2{,}280$	0.86	0.72 ; 0.92	0.11 ; 0.17	
Number of Soldiers (x 10^4)	Number of Presoldiers (x 10^3)	*N. corniger*	1 Q	$y = .095x - 120$	0.77	0.61 ; 0.86	0.07 ; 0.18	1 Q *N. corniger* vs > 1 Q *N. corniger* ** (E)
			> 1 Q	$y = .78x + 1{,}880$	0.66	0.35 ; 0.82	0.04 ; 0.11	
		N. ephratae	1 Q	$y = .224x + 495$	0.78	0.57 ; 0.88	0.16 ; 0.29	1 Q *N. corniger* vs 1 Q *N. ephratae* *** (E)
Queen Fresh Weight (g)	Neuter Population Size (including larvae) (x 10^5)	*N. corniger*	1 Q	$y = (15.8x - 2.03) \times 10^5$	0.77	0.16 ; 0.86	1.3×10^6 2.1×10^6	ns
		N. ephratae	1 Q	$y = (14.1x - 1.19) \times 10^5$	0.82	0.64 ; 0.90	1.1×10^6 1.9×10^6	
Queen Fresh Weight (g)	Number of larvae (x 10^4)	*N. corniger*	1 Q	$y = (35.4x - 5.02) \times 10^4$	0.65	0.43 ; 0.78	2.6×10^5 5.4×10^5	ns
		N. ephratae	1 Q	$y = (29.8x - 2.38) \times 10^4$	0.78	0.57 ; 0.88	2.3×10^5 4.2×10^5	

Legend : ns = not significant ; * = significant $p < 0.05$; ** = significant $p < 0.01$; *** = significant $p < 0.001$. (S) = slopes of regression lines are significantly different ; (E) = elevations of regression lines are significantly different.

gression lines shows that polygynous colonies have a higher population size per kilogram or cm^3 of nest material than do monogynous colonies. This is indicative of their faster population growth rate (THORNE, 1984).

WIEGERT and COLEMAN (1970) suggest that because gas exchange within a termite nest takes place across the nest surface, the population size of a nest should be related to nest surface area rather than to nest volume or weight. They generalize the shape of *Nasutitermes costalis* arboreal nests, and suggest that surface area increases as the 0.67 power of nest volume. Principal axis correlations between this estimate of nest surface area and population size in the present study do not significantly change either the correlation cœfficients or the range on their 95 % confidence limits.

Intra- and Interspecific Comparisons of Numerical Caste Proportions

Principal axis correlation lines of various caste ratios (number of large versus number of small workers, number of workers vs number of larvæ, number of workers vs number of soldiers, and number of soldiers vs number of presoldiers) are listed in *table I* along with intra-and interspecific comparisons (analyses of covariance based on regression lines) of each ratio.

Queenless *N. corniger* colonies tend to have a higher ratio of large workers (vestigial females) : small workers (vestigial males) than that found in queenright colonies. Monogynous *N. corniger* nests have a lower ratio of large workers : small workers than do monogynous *N. ephratae* colonies (regressions are significantly different in elevation). Both castes forage, tend reproductives, nurse immatures, feed soldiers, groom nestmates, and repair nest carton. Fine-scale polyethism studies describing tasks performed by each caste have not been conducted on these species.

The relationship between the total number of workers in a colony sum of large workers + small workers) and the number of larvae is important because immature termites are dependent on workers for food and care. Among *N. corniger* colonies, polygynous nests have the lowest average worker : larvae ratio. They also have the greatest number of larvae per colony (THORNE, 1984). No significant differences in slope or elevation are indicated by an analysis of covariance between monogynous *N. corniger* and *N. ephratae* cases.

The ratio of workers : soldiers in *N. corniger* colonies appears fairly precise (high r, especially in queened colonies), and regression lines do not differ among 1 Q, > 1 Q, and NO Q colonies. On average, monogynous *N. corniger* nests contain a higher ratio of soldiers : workers than do monogynous *N. ephratae* colonies.

Presoldiers are immatures in the ultimate stage before becoming functional, sclerotized soldiers (NOIROT, 1969). If colonies are constantly replenishing their soldier ranks, then the number of developing presoldiers should be a uniform proportion of the total soldier population. While the correlation between number of mature and immature soldiers is positive ($0.66 \leqslant r \leqslant 0.78$), there is considerable variance for both *N. corniger* and *N. ephratae.* This suggests that soldier production may be somewhat episodic with mature individuals added in pulses rather than continuously. On average, polygynous *N. corniger* and monogynous *N. ephratae* colonies have a higher ratio of presoldiers : mature soldiers than do monogynous *N. corniger* societies.

Because physogastric termite queens are egg-laying specialists with virtually all of their biomass devoted to gonad, one predicts and finds a high correlation between queen wet weight and number of eggs found in the colony at the time of dissection ($r = 0.85$, $N = 41$) for monogynous *N. corniger.* A fairly high correlation cœfficient is also found between queen wet weight and the total neuter population size (including larvae) within a colony *(table I).* No interspecific differences in slope or elevation of monogynous regression lines are exposed by a *t* test. The correlations weaken slightly between queen wet weight and the number of larvae in a colony. Again, no differences are shown when comparing monogynous *N. corniger* and *N. ephratae* cases.

Table II. — Individual soldier, large worker, and small worker dry weights.

Tabelle II. — Die Trockengewichte der individuellen Soldaten, groped Arbeiterinnen und und kleiner Arbeiterinnen.

			Mean[a] individual soldier Dry weight ($x10^{-4}g$)		Mean[a] individual large worker Dry weight ($x10^{-4}g$)		Mean[a] individual small worker Dry weight ($x10^{-4}g$)
N. corniger	1 Q	(41)	$\bar{x} = 35 \pm 7$ $r = 23 — 55$	(41)	$\bar{x} = 60 \pm 10$ $r = 43 — 87$	(41)	$\bar{x} = 32 \pm 5$ $r = 22 — 49$
	> 1 Q	(24)	$\bar{x} = 33 \pm 5$ $r = 23 — 55$	(24)	$\bar{x} = 56 \pm 8$ $r = 37 — 68$	(24)	$\bar{x} = 30 \pm 4$ $r = 23 — 37$
	NO Q	(35)	$\bar{x} = 38 \pm 7$ $r = 27 — 55$	(34)	$\bar{x} = 65 \pm 11$ $r = 49 — 110$	(32)	$\bar{x} = 34 \pm 5$ $r = 25 — 46$
N. ephratae	1 Q	(29)	$\bar{x} = 36 \pm 5$ $r = 26 — 44$	(29)	$\bar{x} = 60 \pm 9$ $r = 44 — 76$	(29)	$\bar{x} = 31 \pm 4$ $r = 21 — 38$

a Mean ± S.D. is mean for all colonies of " average " individual dry weights as described in Methods. Sample size (number of colonies) is given in parentheses. r = range.

Worker and Soldier Dry Weights

"Average" large worker, small worker, and soldier individual dry weights (see Methods) in monogynous, polygynous and queenless *N. corniger* colonies, and in monogynous *N. ephratae* colonies are listed in *table II.* There is a large range of weights (sizes) within all castes : average individual weights within a given caste can differ by a factor of 2 or more among colonies. There are no significant intra- or interspecific differences in caste weights, except that queenless *N. corniger* colonies have higher mean large and small worker weights than those found in mono- or polygynous conspecifics (determined by an analysis of variance followed by a Student-Newman Keuls multiple comparison test). This may be because in colonies with a reduced number of juveniles, a higher proportion of the worker population is in later instars. Later instars have greater pigmentation, heavier sclerotization, and slightly larger head capsules and body sizes. Soldiers do not molt once they enter the mature soldier stadium, so it is expected that they do not show this pattern of higher average weight in queenless colonies.

Polygynous *N. corniger* colonies have lower mean large worker, small worker, and soldier weights than monogynous and queenless conspecifics, although the difference with this sample size is not statistically significant. This pattern suggests, however, that polygynous colonies are younger (skewed toward younger worker instars ; small soldiers) (see THORNE, 1982, 1984).

Biomass Caste Ratios

Principal axis correlation lines of two biomass caste ratios (weight of all large workers in a colony versus weight of small workers, and weight of all workers versus weight of soldiers) are listed in *table III.* Correlation cœfficients for these relationships are high among queened *N. corniger* and *N. ephratae* colonies, and similar to the comparable correlation coefficients from the numerical caste ratio analysis *(table I).* Among monogynous and polygynous *N. corniger* colonies, 95 % confidence bands around r and the slope of the principal axis are narrow, indicating a tight relationship between abcissa and ordinate. Queenless *N. corniger* and monogynous *N. ephratae* caste ratios are more variable. Polygynous *N. corniger* colonies have a larger biomass investment in small workers relative to large workers than do queenless colonies. Similarly, monogynous *N. corniger* societies have a higher small worker : large worker biomass investment than do monogynous *N. ephratae nests.* Monogynous *N. corniger* colonies have a larger soldier : worker investment than do either polygynous or queenless colonies, but show no significant difference from the monogynous *N. ephratae* soldier : worker investment pattern.

Table III. — Biomass caste ratios : Principal axis correlations and comparisons.

Tabelle III. — Gewichtsverhältnisse der Kasten : Korrelationen und Vergleiche.

Abcissa	Ordinate	Species and queen number		Principal axis Correlation line	r	95 % Confidence limits on r	95 % Confidence limits on slope	Significant differences in regression lines (ns comparisons not listed)
Dry weight of large workers (g)	Dry weight of small workers (g)	*N. corniger*	1 Q	y = .25x + 0.92	0.93	0.86 ; 0.96	0.22 ; 0.28	1 Q *N. corniger* vs NO Q *N. corniger* ** (S)
			> 1 Q	y = .23x + 3.27	0.89	0.74 ; 0.94	0.18 ; 0.28	> 1 Q *N. corniger* *vs NO Q N. corniger* ** (S,E)
			NO Q	y = .14x + 4.25	0.65	0.37 ; 0.80	0.08 ; 0.20	
		N. ephratae	1 Q	y = .21x — 1.25	0.83	0.65 ; 0.91	0.16 ; 0.26	1 Q *N. corniger* vs 1 Q *N. ephratae* *** (E)
Dry weight of all workers (LW + SW) (g)	Dry weight of soldiers (g)	*N. corniger*	1 Q	y = .15x + 0.78	0.96	0.92 ; 0.98	0.13 ; 0.16	1 Q *N. corniger* vs > 1 Q *N. corniger* * (E)
			> 1 Q	y = .14x — 1.23	0.92	0.80 ; 0.96	0.12 ; 0.17	1 Q *N. corniger* vs 1 Q *N. ephratae* *** (E)
			NO Q	y = .14x + 0.65	0.76	0.57 ; 0.88	0.10 ; 0.18	
		N. ephratae	1 Q	y = .09x + 1.32	0.80	0.59 ; 0.89	0.06 ; 0.11	

DISCUSSION

Single queen *N. corniger* colonies tend to have a higher ratio of the number of small : large workers, a higher ratio of soldiers : workers, and a lower proportion of presoldiers : soldiers then do monogynous *N. ephratae* nests.

Among monogynous, polygynous, and queenless *N. corniger* colonies, significant differences in numerical caste ratios are probably associated with differences in colony growth rates. Polygynous colonies have a higher neuter population size relative to a given nest weight or volume than do monogynous conspecifics. Polygynous colonies also house a higher ratio of larvae : workers, and a higher ratio of presoldiers : soldiers than do single queen colonies. These differences suggest differences in colony growth rate related to single versus multiple queens (see THORNE, 1982, 1984). Predictably, both monogynous and polygynous colonies have significantly higher ratios of larvae : workers than do queenless nests. The number of workers (LW + SW) : number of soldiers is unlikely to depend on colony growth rate and is statistically equivalent in all three cases.

The one intraspecific *N. corniger* difference which cannot be directly attributed to queen number is the relationship between number of large and small workers, differing in slope between monogynous and queenless colonies, and in slope and elevation between polygynous and queenless colonies. This difference in large and small worker proportions may suggest a separation in nursing tasks between the two castes.

Queen number appears to be an important parameter influencing *N. corniger* caste ratios, but intraspecific variance in caste ratios in other species has been attributed to a number of sources. BOUILLON (1964, 3 spp. of *Apicotermes*) and NUTTING (1970, *Pterotermes occidentis* and *Marginitermes hubbardi*) report a decreased percentage of soldiers with increased colony size ; HAVERTY (1979, *Coptotermes formosanus*) and HAVERTY & HOWARD (1981, *Reticulitermes flavipes* and *R. virginicus*) found reduced proportions of soldiers in small experimental groups. Authors suggest that caste proportions differ depending on colony age in *Zootermopsis angusticollis* and *Z. nevadensis* (CASTLE, 1934), *Incisitermes minor* (HARVEY, 1934), *Cubitermes severus* (BODOT, 1969), *Cubitermes subcrenulatus* (BODOT, 1970) and in *Macrotermes bellicosus* (COLLINS, 1981). Ratios of the castes present in portions of a nest may change with a diurnal periodicity, as reported in *Trinervitermes ebenerianus* (= *T. geminatus*) (SANDS, 1965). The *N. corniger* and *N. ephratae* data presented in this paper were analyzed for seasonal fluctuations, but none were apparent (the current small sample size should be augmented for a thorough examination of seasonal variation).

Sampling Techniques and Data Analysis

Comparison of data from different studies is difficult because the methodology of caste ratio sampling and analysis varies markedly. The ideal, albeit virtually impossible, technique for obtaining accurate caste proportion data would be to capture and count every individual from a large number of colonies, all collected at the same time on the same day. Species with small colony sizes and relatively discrete nest and foraging boundaries are more suitable for precise counts than are termites with large population sizes, diffuse nests, and/or wide-ranging foraging habits. (However, see Wood *et al.*, 1977 who describe a soil core technique for sampling diffuse nests of soil dwelling termites. They report that with their technique, all parts of the nests (including foraging areas) have the same probability of being sampled).

It is not feasible to count each individual in a large colony, particularly since it is desirable to get population and caste proportion estimates from as many colonies as possible. Population subsampling techniques are thus important, and should be examined critically to assure accurate results. Many estimates are based on partial sampling of termitaria (by removing a section of nest material or by taking a core subsample). Termites in the removed portion are sorted and counted, and that fractional census is used to extrapolate total colony size and composition. For some species such techniques may be valid, but one must determine that the subsamples are not biased by compartmentalized occupancy within the nest (e.g. most immatures positioned close to the royal cell), or by caste-specific responses to the pre-sampling disturbance (e.g. workers scurry away while soldiers rush towards the site of sawing or banging vibrations cause by subsampling equipment).

The technique used in this study, volumetric subsampling from a removed, homogenized nest population assures fair population and caste ratio estimates of termites within the termitaria, but excludes counts of the foraging population. Retrieving foragers from a field *Nasutitermes* colony is virtually impossible because of their extensive gallery network, around-the-clock foraging activity, and the inconvenience that few remain at wood bait blocks placed in the vicinity of a removed nest. Although entire colony population estimates, including foragers, would be preferable, data reported here are useful for comparative purposes.

Biological Implications of Intraspecific Variance in Caste Proportions

Biologists are interested in social insect colony caste ratios for two major reasons : (1) to assess the population structure of a termite species and project its abundance and/or consumption in a community (e.g. Baroni-Urbani *et al*, 1978 ; Collins, 1981), or (2) to explore the ergonomics of allocating among labor specialists : are caste proportions fixed, or are there intra- or interpopulation differences in caste ratios which might reflect different seasonal or microhabitat demands on individual colonies (e.g. HAVERTY, 1977, 1979 ; OSTER & WILSON, 1978 ; HOWARD & HAVERTY, 1981) ? Measures of intraspecific variance in caste proportions are fundamental for both purposes. Caste ratio analyses must therefore be evaluated critically. Tables of raw data listing the number of individuals in each caste are of little help to readers who must make their own calculations of caste percentages or ratios. Reports of the percentage of soldiers or workers found in a given species must be accompanied by the number of colonies sampled, and by the standard deviation and range around the mean proportion. Caste ratio correlation analyses should not use obviously dependent axes, such as total neuter population size (including soldiers) versus number of soldiers. Correlation lines and cœfficients must be reported and interpreted with their confidence limits.

Even when statistics describing variance are available, scientists face the difficult judgement of deciding how much variance in a species' caste proportions categorizes it as plastic instead of fixed. HAVERTY (1977) reviews mean numerical soldier percentages, and their ranges when available. The range span (in percentage points) is greater than or equal to the mean soldier percentage in 24 of the 33 species for which both mean and range are listed. In the present study, both the numerical and biomass percentage of soldiers range over 20 percentage points in *N. corniger*, and the ranges for the percentage of small and large workers are even greater *(fig. 1)*. All principal axis correlation coefficients listed in *tables I* and *III* are highly significant, but the 95 % confidence limits on r and on the slope of the principal axis line show that the variance can be considerable. If investigators are interested in caste proportion data to estimate the number of workers per hectare, for example, and then project consumption, they might view a mean with a standard deviation spanning 10 percentage points as sufficiently tight to yield a reasonable projection of species consumption. Researchers studying intraspecific patterns of ergonomics and caste investment might interpret those same data as highly variable.

Biologists interested in whether social insect colony caste ratios are genetically fixed or set in response to environmental conditions should begin by studying individual lab or field colonies over time (e.g. HAVERTY, 1979 ; HOWARD & HAVERTY, 1981, JOHNSTON & WILSON, 1984). This requires a nondestructive, accurate sampling technique. If ratios are genetically determined, a colony will maintain its caste proportions despite environmental perturbation. Variation in caste ratios among colonies does not rule out a genetic influence : it may simply be a polymorphic trait or suite of traits varying within the population. Most likely, a genetic mechanism fixing caste proportions and a regulatory system dependent on tracking environmental conditions would involve some type of a feedback loop. There will be a time lag between " recognition " that a particular caste is understaffed and recruitment to fill those ranks. These continual lags mean that destructive field sampling, eclipsing colonies during one time window, cannot be used to determine whether intraspecific or intracolony caste proportions are fixed. Field studies are important, however, in assessing the range of plasticity in caste proportions within a population or species.

CONCLUSIONS

Data presented here demonstrate intraspecific variability in numerical caste ratios among field colonies of Panamanian *N. corniger* and *N. ephratae.* Correlations between nest characteristics and population size, and among some caste ratios are high, but the variance can also be large. Queen status of the nest is important, yet remains unknown unless the colony is dissected. Although sampling error may contribute to estimates of variance, a lack of precise, static caste proportions is not surprising. Colony size, age, proximity to resources, individual history, season, and vulnerability to predators could all simultaneously affect caste composition. Further, there is no reason to expect that ergonomic constraints are so uniform and severe as to regulate caste proportions precisely and statistically within a species. Deviations around a " basic " ratio probably enable colonies to function with approximately equal productivity and success. This problem may be amenable to experimental approaches in future investigations.

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