

SOME STATISTICAL OBSERVATIONS ON TERMITES,
MAINLY BASED ON THE WORK OF THE LATE
MR G. D. HAVILAND.

By ERNEST WARREN, D.Sc. Lond.

(1) In the year 1906 Mr A. E. Haviland of Estcourt, Natal, kindly placed at my disposal the collections and notes of the late Mr G. D. Haviland. The latter had made a special study of the termites of Natal and of the Malay Archipelago, and he published a valuable paper on these insects in the *Linnean Society's Journal*, Vol. XXVI. p. 358 *et seq.*, 1897. The notes include some interesting observations on the life-histories of the Natal species of termites, and also a large series of measurements made on one particular species, *Termes natalensis* Haviland. The general biological observations, which appear to be unrecorded, are being incorporated in a short paper which is about to be published in the *Annals of the Natal Government Museum*, while in the present paper the measurements will be briefly dealt with. For the elucidation of some doubtful points, Mr Haviland's observations have been supplemented by some fresh measurements on *Termes natalensis* and also on other species.

As is well known, termites are social insects with an economy bearing some resemblance to that of ants and social bees and wasps. The nature of the inhabitants of a termite-nest varies according to the species and to the season of the year at which examination is made. If a nest of *T. natalensis* be examined in the spring (September) the following different castes may be found: (1) a single *queen* and a single *king*, these are the only sexually mature forms that occur; (2) *soldiers* of two sizes, asexual; (3) *workers* of two sizes, asexual; (4) *winged males* and *females*, not sexually mature; (5) *young or immature members* of castes (2), (3) and (4).

In some species there are several queens and kings in the nest, and the soldiers and workers may be of one size only, or the soldiers may be absent altogether.

In ants and bees the workers (and soldiers, when they occur) are sterile females; while in the termites it appears that both the soldiers and workers are abortive individuals of either sex. There is also evidence for believing that the ultimate

fate of the young on hatching is not predetermined, but depends on the subsequent treatment they receive at the hands of the workers. According to this view any given individual on hatching from the eggs may, in the case of *T. natalensis* for example, develop into any one of five distinct forms or castes, which in no way grade into one another, viz. two forms of soldiers, two forms of workers and the winged sexual form. It is certainly most difficult to form a conception on any theory of heredity as to the means by which hereditary characters could be inherited by such a plastic and modifiable organism as the newly hatched young of a termite.

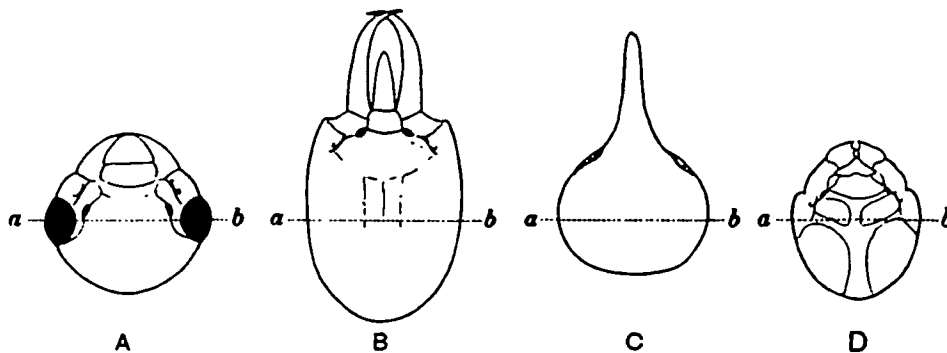
After the first rains the winged sexual forms swarm out of the nest and copulate in the air; they seldom or never appear to return to the parent nest. A pair may succeed in founding a new nest, and will ultimately become the queen and king.

The nest of *T. natalensis* is slow in growing, and it remains inhabited for many years. The same queen and king undoubtedly live for a number of years, and in some species (including *T. natalensis*) it is not known how they are replaced, should they die or an accident befall them.

(2) The Measurements.

The measurements were made only on what appeared to be *adult* members of the different castes, except in the case of the winged imagos, when on one occasion nymphs with wing-rudimenta were measured. An individual was regarded as *adult* when the exoskeleton of the head was firm and had assumed the characteristic yellow or brown colour. This point is, of course, of considerable importance as there is no sharply marked metamorphosis among termites.

In any case, whether of soldiers, workers or winged imagos, the same dimension was chosen for measurement, viz. the maximum breadth of the head (*ab* in figure below). Owing to the varying configuration of the head in the different castes and species, this dimension in certain cases passes through the compound lateral eyes;



Heads of various castes, viewed from above, showing the line of measurement (*a b*).

- | | |
|----------------------------------------------|----------------------------------------------|
| A. Imago, <i>Termes natalensis</i> . | B. Small Soldier, <i>Termes natalensis</i> . |
| C. Large Soldier, <i>Termes trinervius</i> . | D. Worker, <i>Termes trinervius</i> . |

and when such occurs it was found that the measurement could be more conveniently and accurately taken if the breadths of the eyes were included in the dimension. It is certain that the inclusion of the eyes in such cases has no appreciable effect on the results, as the correlation of the size of head and eyes is exceedingly close; and the eyes being partially sunk in the exoskeleton complete the contour of the head. It should be noticed that the dimensions taken of the different castes are not perfectly homologous, for some soldiers are blind and others have curiously shaped heads; but they are as nearly homologous as the nature of the case admits, and they may all be regarded as closely comparable measurements.

The measurement of the selected dimension may be made with sufficient accuracy on account of the comparatively rigid nature of the exoskeleton of the head. Length or breadth measurements of the abdomen would have been quite unreliable.

The specimens were in all cases preserved in alcohol.

The method of measurement adopted by Mr Haviland is not recorded in his notes; but I have no hesitation in accepting his data as thoroughly trustworthy. The method which I found most satisfactory was to examine the specimen under an 'aa' or 'AA' Zeiss objective with a camera lucida, and to mark off the dimension on a slip of paper. The termite was flooded with spirit on a slide, and orientated by means of a small piece of glass placed above it. The slip of paper was referred to a scale made with the camera from a stage-micrometer (divided into $\frac{1}{10}$ and $\frac{1}{100}$ mm.) viewed under the same magnification, and the absolute dimension could thus be read off. One or two small series measured by Mr Haviland were re-measured by my method and the results were in close accord.

The measurements of *Termes natalensis* will be first dealt with, and subsequently a comparative review of some of the Natal species of termites will be made.

(3) *Termes natalensis* Haviland.

As we have already seen a colony of this species consists of one queen and king, numerous soldiers of two sizes and workers of two sizes, also immature young or larvæ, and at certain seasons nymphs of males and females, which on becoming winged leave the nest as a swarm.

In the accompanying table the means, standard deviations and coefficients of variation $\left(\frac{\text{Standard Deviation}}{\text{Mean}} \times 100 \right)$ of a considerable number of different colonies are shown. The measurements refer chiefly to the soldiers and the workers: where the material was available the queen and king were measured, and in nest No. "653" one hundred male and one hundred female nymphs with wing-rudiments were measured (see Table VIII.).

The nests are arranged in the table according to the season of the year at which the material was collected, beginning with November.

TABLE I.
Termes Natalensis.
Unit=0.01 mm.

Date of Collection	No. of Nest	Royalty		LARGE SOLDIERS				SMALL SOLDIERS				LARGE WORKERS				SMALL WORKERS			
		Queen	King	No.	Mean	S. D.	O. of V.	No.	Mean	S. D.	O. of V.	No.	Mean	S. D.	O. of V.	No.	Mean	S. D.	O. of V.
Nov. 7	668	—	—	—	—	—	—	100	227.3	10.20	4.49	86	214.2	5.99	2.79	—	—	—	—
Jan. 18		—	—	3	456.3	—	—	100	233.2	7.61	3.26	86	213.9	7.22	3.37	10	143.4	—	—
Mar. 16		—	—	—	—	—	—	100	237.5	7.40	3.12	89	222.5	4.79	2.15	—	—	—	—
May 16		—	—	3	425.0	—	—	100	237.3	6.91	2.91	100	235.2	7.69	3.23	54	166.7	6.93	4.42
Aug. 23	670	—	—	—	—	—	—	100	231.8	8.23	3.55	100	226.9	4.68	2.06	—	—	—	—
Nov. 11		—	—	4	428.0	—	—	100	247.9	7.05	2.84	100	231.5	7.44	3.22	45	160.3	4.41	2.75
Jan. 18		—	—	46	422.4	13.98	3.31	200	260.3	7.11	2.73	100	246.3	6.07	2.46	—	—	—	—
Mar. 16		—	—	7	441.1	—	—	200	261.3	6.07	2.32	72	248.5	5.45	2.19	—	—	—	—
May 17	672	—	—	1	434.0	—	—	100	255.7	6.84	2.71	100	247.7	7.02	2.83	14	161.6	—	—
Aug. 25		—	—	5	437.8	—	—	100	237.7	9.23	3.88	100	233.4	6.40	2.74	43	155.4	3.60	2.25
Nov. 12		—	—	14	410.6	—	—	100	240.4	13.28	5.52	100	235.9	10.13	4.29	—	—	—	—
Jan. 12		—	—	12	412.0	—	—	100	245.7	7.89	3.21	100	234.4	5.10	2.18	—	—	—	—
Mar. 17	674	—	—	15	413.7	—	—	100	245.2	6.32	2.68	100	239.4	4.88	1.96	100	167.9	3.62	2.29
May 18		—	—	23	412.0	9.89	2.40	100	239.6	8.78	3.63	100	236.4	5.78	2.44	76	164.6	3.28	2.12
Aug. 28		—	—	8	409.7	—	—	100	227.9	8.48	3.72	100	226.9	5.09	2.24	—	—	—	—
Nov. 16		—	—	7	424.6	—	—	100	244.7	7.09	2.90	92	234.9	5.73	2.44	4	158.0	—	—
Jan. 18	676	—	—	3	421.5	—	—	100	238.8	7.28	3.05	100	230.0	5.82	2.53	4	152.3	—	—
Mar. 17		—	—	10	417.0	—	—	100	251.5	7.08	2.82	100	243.6	4.64	1.91	57	162.2	3.59	2.27
May 20		—	—	—	—	—	—	100	244.5	6.93	2.83	100	242.3	4.83	2.03	38	164.1	2.70	1.75
Aug. 29		—	—	—	—	—	—	100	231.2	7.47	3.23	100	230.2	6.33	2.75	27	150.4	3.02	2.01
Nov. 16	678	—	—	19	419.1	—	—	197	245.6	7.40	3.01	100	236.0	5.65	2.39	68	161.0	4.78	2.97
Jan. 18		—	—	22	415.0	—	—	100	262.6	7.02	2.67	100	247.8	5.96	2.40	5	162.2	—	—
Mar. 17		—	—	7	417.6	—	—	100	263.3	6.84	2.86	100	253.9	4.64	1.83	25	167.9	3.62	2.33
May 29		—	—	3	438.6	—	—	88	246.7	6.84	2.91	100	246.1	5.30	2.15	22	155.3	—	—
Aug. 29	—	—	—	27	429.0	14.55	3.39	100	241.0	6.88	2.86	100	236.0	7.31	3.10	42	166.4	3.04	1.94

Aug. 20 {	620	361.1	—	37	458.8	14.76	3.23	300	270.7	12.57	4.64	600	255.4	9.99	3.91	—	18	165.8	—	—
May 23 {	621	—	—	34	458.2	16.13	3.52	848	271.3	7.24	2.67	33	262.5	5.07	1.93	—	36	156.4	3.33	2.13
Nov. 12 {	630	—	—	187	423.7	12.94	3.05	1100	239.0	8.36	3.50	200	238.5	5.40	2.26	—	4	159.0	—	—
June 3 {	631	—	—	27	431.1	13.20	3.08	1000	243.6	6.59	2.70	32	248.0	5.12	2.06	—	—	—	—	—
Nov. ...	676	—	—	10	459.0	—	—	100	220.5	6.91	3.01	74	231.9	6.03	2.60	—	—	—	—	—
Nov. ...	677	—	—	10	421.6	—	—	100	245.4	6.52	2.68	86	240.5	6.85	2.85	—	—	162.4	—	—
Nov. ...	678	—	—	—	—	—	—	100	241.6	7.31	2.98	80	233.6	5.18	2.32	—	45	160.0	3.85	2.40
Nov. ...	679	—	—	6	450.2	—	—	100	233.1	7.72	3.31	100	232.4	4.46	1.92	—	—	—	—	—
Apr. ...	681	361	absent	219	456.1	12.83	2.61	1600	277.3	7.35	2.65	268	270.9	5.06	1.87	—	—	—	—	—
May 23	682	361.1	—	34	458.2	16.13	3.52	848	271.3	7.24	2.67	33	262.5	5.07	1.93	—	18	165.8	—	—
May 16	686	—	—	3	425.0	—	—	100	237.3	6.90	2.91	100	225.2	7.59	3.23	—	54	156.7	6.93	4.42
May 17	670	—	—	—	—	—	—	100	255.7	6.94	2.71	100	247.7	7.02	2.83	—	14	161.6	—	—
May 18	672	—	—	23	412.0	9.89	2.40	100	239.6	8.78	3.66	100	236.4	5.78	2.45	—	76	154.0	3.28	2.12
May 28	674	—	—	—	—	—	—	100	244.5	6.93	2.83	100	242.3	4.93	2.03	—	38	164.1	2.70	1.75
May 29	675	—	—	3	438.6	—	—	98	248.7	6.94	2.91	100	246.1	5.20	2.15	—	22	155.3	—	—
June 3	630	—	—	27	431.1	13.20	3.08	1000	243.8	6.58	2.70	32	248.0	5.12	2.06	—	4	159.0	—	—
June ...	634	—	—	100	408.5	10.46	2.66	100	233.3	7.76	3.33	—	—	—	—	—	—	—	—	—
June ...	637	368	—	30	429.2	12.02	2.80	200	247.8	6.50	2.62	36	247.8	6.97	2.81	—	65	160.4	4.01	2.80
June 20	641	—	—	34	424.7	10.31	2.43	200	242.8	5.92	2.44	49	249.1	5.23	2.10	—	2	161.0	—	—
June 22	643	—	—	46	424.4	11.78	2.78	100	245.0	6.30	2.57	—	—	—	—	—	—	—	—	—
June 28	648	—	—	94	453.2	12.72	2.81	100	266.6	7.39	2.77	—	—	—	—	—	—	—	—	—
June ...	649	—	—	26	450.5	11.63	2.63	300	255.0	6.94	2.72	86	249.6	7.36	2.95	—	34	158.9	5.12	3.22
June 28	651	352	—	88	445.6	13.18	2.98	200	262.8	7.18	2.73	63	266.9	4.46	1.73	—	—	—	—	—
June 30	652	373	—	55	468.6	22.64	4.82	200	280.2	9.32	3.33	57	271.6	4.70	1.73	—	3	169.7	—	—
June ...	653	369	—	213	456.1	15.31	3.36	1100	267.7	9.50	3.55	1100	262.7	8.41	3.20	—	1100	168.5	5.35	3.18
Aug. 9	654	354	—	38	430.6	16.72	3.84	500	229.5	6.92	3.02	200	230.7	5.88	2.55	—	35	150.0	3.44	2.29
Aug. 25	657	367	—	34	424.2	12.61	2.80	100	221.7	9.36	4.22	100	233.7	8.97	3.80	—	47	149.0	3.10	2.08
Sept. 20	658	363	—	8	446.2	—	—	500	235.1	6.54	2.78	500	235.1	6.10	2.40	—	14	154.4	—	—
Sept. 23	660	366	—	55	438.1	10.98	2.51	200	231.7	13.33	5.72	100	227.6	7.36	3.24	—	15	155.4	—	—
Sept. 26	661	—	—	22	420.5	—	—	100	227.6	6.37	2.80	100	224.9	5.13	2.28	—	16	161.5	—	—
Sept. ...	662	—	—	82	413.8	13.92	3.36	100	225.8	5.74	2.54	100	227.5	6.32	2.78	—	100	154.5	3.01	1.95
Oct. 4	665	362	—	179	418.3	16.66	3.98	100	241.6	7.46	3.09	100	234.9	5.38	2.29	—	100	159.1	5.51	3.47
Oct. 5	666	366	—	84	421.4	14.11	3.35	100	232.4	6.23	2.68	100	232.6	5.38	2.32	—	100	156.6	3.72	2.38
Oct. 25	667	367	—	88	439.3	15.46	3.55	300	235.5	6.47	2.76	100	227.4	4.38	1.93	—	12	154.5	—	—

[Probable errors of means about .7 and of standard deviations about .5 for 100 cases. Ed.]

(4) *Seasonal Variation.*

Material obtained from the *same* nest at different months exhibited variation in the means and standard deviations. In the first part of Table I. are given the records of seven nests from which material had been collected at different seasons, generally Nov., Jan., Mar., May and August. A comparison of the figures will show that as a rule the mean was lowest and the standard deviation greatest when the material was taken in November, while generally the mean was highest and the standard deviation smallest in the month of March.

In the following table (Table II.) are given the arithmetic means of the means, standard deviations and the coefficients of variation of samples (varying from 72 to 200 in number) of small soldiers and large workers taken from five nests "668," "670," "672," "674," "675" (see Table I.) in the months mentioned above.

TABLE II.
Termes Natalensis.

Month of Collecting	MEANS OF THE FIVE NESTS					
	Small Soldiers			Large Workers		
	Mean	Standard Deviation	Coefficient of Variation	Mean	Standard Deviation	Coefficient of Variation
November ...	241.2*	9.00*	3.75	230.5*	6.99*	3.03
January ...	248.1	7.38	2.99	234.5	6.03	2.59
March ...	251.8	6.56	2.62	241.6	4.84	2.01
May ...	245.2	7.30	3.00	241.5	6.12	2.54
August ...	233.9	8.06	3.45	230.7	5.96	2.58

* Unit = .01 mm.

This seasonal variation probably arises from two causes at least; (1) the elimination of the physically unfit, (2) post "adult" growth. With reference to the first cause it may be noticed that it is very probable that more individuals arrive at maturity from August to November, that is during the first rains, than at other seasons, and therefore the stunted adults will be more abundant during this period, with the result that the mean would be lowered and the standard deviation would be raised. By the time that March arrives the small and weakly individuals of the nest are likely to have died, and consequently the mean will be raised and the standard deviation will be diminished. The second, and perhaps more potent influence, is that the so-called "adults" appear to grow to a certain extent even after their exoskeleton has become hard and yellow. In the following table (Table III.) the frequencies for six nests are given for small soldiers and large workers mostly collected in November and March.

Termes Natalensis.
Material collected from six nests during November, March and June.

Scale. Unit = 0.08 mm.	SMALL SOLDIERS						LARGE WORKERS					
	630		668		670		678		674		676	
	Nov.	June	Nov.	Mar.	Nov.	Mar.	Nov.	Mar.	Nov.	Mar.	Nov.	Mar.
197-199	—	—	—	—	—	—	—	—	—	—	—	—
200-208	—	—	—	—	—	—	—	—	—	—	—	—
203-205	—	—	—	—	—	—	—	—	—	—	—	—
206-208	—	—	—	—	—	—	—	—	—	—	—	—
209-211	—	—	—	—	—	—	—	—	—	—	—	—
212-214	—	—	—	—	—	—	—	—	—	—	—	—
215-217	—	—	—	—	—	—	—	—	—	—	—	—
218-220	—	—	—	—	—	—	—	—	—	—	—	—
221-223	—	—	—	—	—	—	—	—	—	—	—	—
224-226	—	—	—	—	—	—	—	—	—	—	—	—
227-229	—	—	—	—	—	—	—	—	—	—	—	—
230-232	—	—	—	—	—	—	—	—	—	—	—	—
233-235	—	—	—	—	—	—	—	—	—	—	—	—
236-238	—	—	—	—	—	—	—	—	—	—	—	—
239-241	—	—	—	—	—	—	—	—	—	—	—	—
242-244	—	—	—	—	—	—	—	—	—	—	—	—
245-247	—	—	—	—	—	—	—	—	—	—	—	—
248-250	—	—	—	—	—	—	—	—	—	—	—	—
251-253	—	—	—	—	—	—	—	—	—	—	—	—
254-256	—	—	—	—	—	—	—	—	—	—	—	—
257-259	—	—	—	—	—	—	—	—	—	—	—	—
260-262	—	—	—	—	—	—	—	—	—	—	—	—
263-265	—	—	—	—	—	—	—	—	—	—	—	—
266-268	—	—	—	—	—	—	—	—	—	—	—	—
269-271	—	—	—	—	—	—	—	—	—	—	—	—
272-274	—	—	—	—	—	—	—	—	—	—	—	—
275-277	—	—	—	—	—	—	—	—	—	—	—	—
278-280	—	—	—	—	—	—	—	—	—	—	—	—
Totals	1100	1000	100	100	100	900	100	100	100	100	100	100

A careful comparison of these frequencies will, I think, lead to the opinion that both of the suggested causes have a share in producing the seasonal variation. The apparent elimination of the small and unfit is best shown in nests "630" and "672" for both the small soldiers and large workers.

(5) *Ratios and Variation of the different Castes.*

Having thus noted the presence of a seasonal variability in a single nest, we may pass to the variability exhibited by a series of colonies. It would, of course, have been preferable to have avoided the disturbing element of the seasonal variation by collecting all material at one season of the year; but this was not done as the presence of a seasonal variation was not suspected.

In the following table (Table IV.) are given the arithmetical means of the means, standard deviations and coefficients of variation of the four castes in a number of nests (see Table I.).

TABLE IV. *Means.*

Caste	Number of Nests*	Mean	Number of Nests †	Standard Deviation	Coefficient of Variation
Large Soldiers ...	23	434.01‡	20	13.64‡	3.12
Small Soldiers ...	30	245.00	30	7.37	3.02
Large Workers ...	27	242.21	27	5.94	2.46
Small Workers ...	19	156.90	12	4.17	2.65
Male Nymphs ...	1	300.05	1	4.71	1.57

There is no overlapping of the large soldiers and small soldiers or of the large workers and small workers; in other words, there was never any question whether any individual should be classed amongst the "large" or "small" series.

With reference to the particular dimension measured there is overlapping between the small soldiers and large workers; but the soldiers and workers are totally distinct in general structure and shape.

Ratios.

$$\frac{\text{Mean of Small Soldiers}}{\text{Mean of Large Soldiers}} \times 100 = \frac{245.001}{434.013} \times 100 = 56.4,$$

and

$$\frac{\text{Mean of Small Workers}}{\text{Mean of Large Workers}} \times 100 = \frac{156.901}{242.206} \times 100 = 64.8.$$

Thus, in the proportion in size that occurs between the "large" and "small" classes, the soldiers and workers approach each other; the "small" class being more than half the size of the "large" class.

$$\frac{\text{Mean of Large Workers}}{\text{Mean of Large Soldiers}} \times 100 = \frac{242.206}{434.013} \times 100 = 55.8,$$

and

$$\frac{\text{Mean of Small Workers}}{\text{Mean of Small Soldiers}} \times 100 = \frac{156.901}{245.001} \times 100 = 64.0.$$

* Nests from which less than 10 individuals were available are here excluded.

† Only nests from which more than 23 individuals were available are included.

‡ Unit=0.01 mm.

Thus it will be seen that the workers are more than double the size of the soldiers of the similarly sized class.

The variability of the soldiers, as measured by the coefficient of variation, is greater than that of the workers, the ratios being :

$$\frac{\text{Coefficient of Large Workers}}{\text{Coefficient of Large Soldiers}} \times 100 = \frac{2.461}{3.123} \times 100 = 78.8,$$

$$\frac{\text{Coefficient of Small Workers}}{\text{Coefficient of Small Soldiers}} \times 100 = \frac{2.647}{3.022} \times 100 = 87.6,$$

that is the workers are about 0.8 times as variable as the soldiers.

(6) *General Variability of the sexual and asexual Castes.*

The average coefficient of variation for the four castes is 2.8: it is thus seen that the general variability of these termite-castes is distinctly small. The nymphs of the winged sexual forms appear to exhibit extraordinarily little variation. In the case of 100 male and 100 female nymphs (Table VIII. nest "653") the coefficients were only 1.57 and 1.60 respectively. Unfortunately there is no available material for ascertaining the variability of the adult sexual form before leaving the nest in the species *natalensis*; but, as will be seen later, small series of winged imago have been measured in some of the other species, and there is a general tendency towards a low variability.

It has been remarked that there appears to be good evidence for supposing that the young which hatch from the eggs are all alike, and that by special feeding, or by some manipulation by the workers, any one of the five castes may be produced. From this it would be expected that the variability exhibited by all the castes would be about the same; but it has been shown above that the workers are less variable than the soldiers, and that the asexual castes generally are much less variable than the sexual castes. In this connexion, it should be remembered that the individuals in a nest are all produced from one queen and king. The difference in the variability of the castes must therefore be referred to differences in food or other environmental conditions, since they all have a common parentage, and are presumably all alike on hatching.

Thus, the tendency to vary is induced or modified by the special food or manipulation received, and the influences necessary for the production of a soldier or worker lead to greater variability than those for the formation of a sexual imago. It appears that either sex may be converted into either soldiers or workers, the potential sex having no effect on the ultimate destiny of the individual. It is clear that the environment has an overwhelming effect on these organisms, it influences the variability and decides on the bodily shape and structure of the developing insect.

(7) *Comparison of the Constants of a Family with those of the Population.*

Of small soldiers, random samples from 30 nests were measured. The sizes of the samples were most disproportionate, ranging from 100 to 1600. On adding

all together there is obtained a population of 8497 individuals derived from 30 different nests.

The constants are: Mean 251.8, Standard Deviation 19.86, Coefficient of Variation 7.89.

The distribution of the frequencies is irregular, and the polygon shows a well-marked double peak. The cause of this is chiefly attributable to the great disproportion of the size of the samples, and the consequent undue influence of one or two individual nests. To avoid this disturbing effect, random samples of 100 individuals from each of the 30 nests were taken. In this way there results a population of 3000 (Table V.), and the constants are: Mean 243.5, Standard Deviation 17.08, Coefficient of Variation 7.02. The distribution of the frequencies is much less irregular than in the former case, and the polygon is consequently much smoother.

The coefficient of variation of the population of 3000 is thus 7.02 as compared with the mean value of 3.02 for the families. In other words the variability of the family of small soldiers is about 43% of that for the population. The variability of the population compared with the fraternal variability is much higher than was expected, judging from the value obtained from certain breeding experiments with a moth, *S. clathrata*, conducted several years ago at University College, London. The cause would appear to be attributable to the great effect of the environment on the means and variabilities of the different castes of a nest.

(8) *Correlation of the Means.*

The correlation between the means of the small soldiers and large workers has been determined in the case of the 27 nests entered in Table I. The correlation-surface is shown in the following table. The calculated constants are: mean of means of small soldiers, 244.3 units, standard deviation, 15.29; large workers, 241.4 units and 13.04 respectively.

Correlation coefficient = .953, probable error \pm .012.

For the calculation of the correlation between the large soldiers and small soldiers only 20 nests were available.

The constants are: Large soldiers, mean of means, 435.5 units, standard deviation, 16.9; small soldiers, 247.3 units and 17.14 respectively.

Coefficient of correlation = .831, probable error = \pm .046.

Since the probable error is so considerable, there is no reason for supposing that the correlation between the large and small soldiers differs appreciably from that between the small soldiers and the large workers, which we found to be $.953 \pm .012$. It may be assumed that the correlation of the means between any two castes is about .9. It is curious that the correlation between similar castes (large and small soldiers) does not appear to be greater than that between dissimilar castes (small soldiers and large workers).

TABLE VI.

Termes Natalensis Haviland.

Correlation of the Means of Small Soldiers and Large Workers from 27 nests.*

Small Soldiers Unit=0.04 mm.	4	3	2	1	0	4	3	0	1	2	0	3	27
221-224	—	—	1	—	—	—	—	—	—	—	—	—	1
225-228	2	—	—	—	—	—	—	—	—	—	—	—	2
229-232	1	2	1	—	—	—	—	—	—	—	—	—	4
232-236	1	0	2	—	—	—	—	—	—	—	—	—	3
237-240	—	—	1	1	—	—	—	—	—	—	—	—	2
241-244	—	—	2	0	1	1	1	—	—	—	—	—	5
245-248	—	—	—	—	1	2	—	—	—	—	—	—	3
249-252	—	—	—	—	—	—	—	—	—	—	—	—	0
253-256	—	—	—	—	—	1	1	—	—	—	—	—	2
257-260	—	—	—	—	—	—	—	—	—	—	—	—	0
261-264	—	—	—	—	—	—	—	—	1	—	—	—	1
265-268	—	—	—	—	—	—	—	—	—	1	—	—	1
269-272	—	—	—	—	—	—	—	—	—	1	—	—	1
273-276	—	—	—	—	—	—	—	—	—	—	—	—	0
277-280	—	—	—	—	—	—	—	—	—	—	—	2	2
Large Workers Unit=0.04 mm.	224-227	228-231	232-235	236-239	240-243	244-247	248-251	252-255	256-259	260-263	264-267	268-271	

(9) *Standard Deviation of the Means.*

The standard deviation of the means of the large soldiers for random samples taken from 20 nests is 16.90, for small soldiers from 27 nests 15.29, and for large workers from 27 nests, 13.04. It is thus seen that the means of different nests vary very considerably, and reference to Table I. will show that this variation is not entirely or even mainly due to the fact that the material was not all collected at the same time of the year. We have here to do with the effect of inheritance, or with that of the slightly different environment of each nest. It will be noticed that the standard deviations of the means for the three castes are all of the same order of magnitude, although that for the large workers is the lowest.

(10) *Correlation of the Coefficients of Variation.*

The variability of the members of a nest varies in different nests; thus the standard deviation of the coefficients of variation of random samples of small soldiers taken from 27 nests is 4.42 units, and of large workers 3.40 units. The coefficient of correlation between the coefficients of variation of small soldiers and large workers in 27 nests is .453; but the probable error is $\pm .103$, which is so great that it is scarcely safe to conclude that we have this correlation very closely.

* The smallest number of individuals from a nest was 32.

TABLE VII.

Termes Natalensis Haviland.

Correlation of the Coefficients of Variation of Small Soldiers and Large Workers
from 27 nests.

Small Soldiers Unit=0-15	3	3	4	4	1	3	0	4	1	3	1	0	0	1	27
244-258	—	—	1	—	—	—	—	1	—	—	—	—	—	—	2
259-273	2	1	1	1	0	0	0	3	1	—	—	—	—	—	9
274-288	—	1	1	1	0	1	—	—	—	—	—	—	—	—	4
289-303	—	—	1	1	0	2	0	0	0	1	—	—	—	—	5
304-318	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
319-333	1	1	—	—	—	—	—	—	—	—	—	—	—	—	2
334-348	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
349-363	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
364-378	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
379-393	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
394-408	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
409-423	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
.....
564-578	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
Large Workers Unit=0-15	173-187	188-202	203-217	218-232	233-247	248-262	263-277	278-292	293-307	308-322	323-337	338-352	353-367	368-382	

A correlation table of the coefficients of variation of large soldiers and small soldiers was prepared; but without actual calculation it was obvious that there was practically no correlation present.

From this we gather that in any given nest when one caste happens, say, to be particularly variable, it does not follow that every other caste is correspondingly variable. From *a priori* reasons one would have expected that the variability of the different castes in a nest would have been closely related, if the variability is to be regarded as an inherited character. If, on the other hand, the variability is to be mainly referred to nurture or to the general environmental conditions, the above results are intelligible.

(11) *Comparison of various Species.*

In Table VIII. are given the means, standard deviations and the coefficients of variation of the different castes for all the more commonly occurring Natal termites.

TABLE VIII. Constants of a Series

Name of Species	No. of Nest	Locality and Date	LARGE SOLDIERS				SMALL SOLDIERS			
			No.	Mean	Standard Deviation	Coefficient of Variation	No.	Mean	Standard Deviation	Coefficient of Variation
<i>Hodotermes havilandi</i> , Sharpe	635	Natal, Altitude 8000 ft. June 26, 1898	51	421.4	24.46	5.80	None found			
	636	Natal, Altitude 8000 ft. June 27, 1898	—	—	—	—				
	—	Hlabisa, Zululand, June 25, 1903	—	—	—	—				
<i>Calotermes durbanensis</i> , Haviland	601 & 602 608	Durban, Feb. 15, 1898 Durban, Feb. 15, 1898	80 —	178.3 —	4.45 —	2.49 —	None occur			
<i>Termes natalensis</i> , Haviland	653	Natal, Altitude 3500 ft. July 1898	213	456.6	13.81	3.38	1100	267.7	9.50	3.55
<i>Termes badius</i> , Haviland	626	Natal, 1894 ...	124	288.73	10.26	3.55	—	—	—	—
	625	Natal, 1894 ...	—	—	—	—	7	229.0	—	—
<i>Termes latericius</i> , Haviland	647	Slievrye, Estcourt, Natal, June 25, 1898	500	187.4	3.86	2.81	None occur			
<i>Termes vulgaris</i> , Haviland	624	Natal, Altitude 4000 ft. May 28, 1898	500	156.2	3.97	2.55	None occur			
	628	Natal, Altitude 4000 ft. June 1, 1898	—	—	—	—				
<i>Termes incertus</i> , Hagen	629	Natal, Altitude 4000 ft. June 1, 1898	47	76.2	2.25	2.95	None occur			
	Taken from one nest	Natal ...	—	—	—	—				
<i>Termes parvus</i> , Haviland	633	Natal, Altitude 3600 ft. June, 1898	25	83.4	2.62	3.14	None occur			
	Swarm	Slievrye, Estcourt, Natal, March 30, 1899	—	—	—	—				
	644	Natal, Altitude 3800 ft. June 23, 1898	50	82.7	2.12	2.56				
<i>Termes bilobatus</i> , Haviland	621	Natal, Altitude 3500 ft. May 26, 1898	57	148.1	2.81	1.90	None occur			
	623	Natal, Altitude 3500 ft. May 28, 1898	21	151.8	—	—				
	632	Natal, Altitude 3600 ft. June 15, 1898	25	147.5	2.60	1.76				
	Swarm	Natal, Oct. 24, 1898 ...	—	—	—	—				
	639	Natal, Altitude 3500 ft. June 17	20	148.8	—	—				
	640	Natal, Altitude 3500 ft. June 18	27	147.5	2.74	1.86				
	—	Natal, 1894 ...	—	—	—	—				
	615	Natal, Altitude 3500 ft. April 5	—	—	—	—				
<i>Termes trinervius</i> , Rambur	—	Town Bush, Pietermaritzburg, April 20, 1907	64	142.3	6.23	4.38	70	89.8	3.58	3.99
	Taken from one nest	Natal, Oct. 19, 1898 ...	—	—	—	—	—	—	—	—
	—	Park, Maritzburg, Sept. 15, 1908	—	—	—	—	—	—	—	—
<i>Rhinotermes</i> Sp.	603	Durban, Feb. 1898	93	187.5	6.06	3.23	91	92.04	3.23	3.51

of Species. Unit = 0.01 mm.

LARGE WORKERS				SMALL WORKERS				MALES				FEMALES			
No.	Mean	Standard Deviation	Coefficient of Variation	No.	Mean	Standard Deviation	Coefficient of Variation	No.	Mean	Standard Deviation	Coefficient of Variation	No.	Mean	Standard Deviation	Coefficient of Variation
43	860.3	15.45	4.29	50	237.8	14.84	6.05	—	—	—	—	—	—	—	—
50	880.8	18.71	3.60	84	268.9	12.79	4.76	—	—	—	—	—	—	—	—
12	886.2	—	—	16	278.5	—	—	—	—	—	—	—	—	—	—
50	149.8	7.42	4.95	None occur				—	—	—	—	—	—	—	—
1100	262.7	8.41	3.20	1100	168.5	5.35	3.18	Nymphs with wing rudiments				Nymphs with wing rudiments			
50	187.1	8.16	4.36	50	182.2	5.74	4.34	100	300.1	4.71	1.57	100	298.4	4.78	1.60
100	177.9	5.68	3.20	51	112.9	4.88	4.32	—	—	—	—	—	—	—	—
55	156.8	4.40	2.81	100	110.5	2.41	2.19	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	34	261.7	6.16	2.35	33	262.3	6.92	2.64
50	88.2	3.13	3.55	None found				—	—	—	—	—	—	—	—
—	—	—	—					35	184.2	2.71	2.02	32	185.9	2.98	2.15
28	77.2	3.67	4.76	None occur				—	—	—	—	—	—	—	—
—	—	—	—					30	113.0	3.09	2.73	25	119.9	1.94	1.62
—	—	—	—					—	—	—	—	—	—	—	—
20	105.1	—	—	None occur				—	—	—	—	—	—	—	—
—	—	—	—					50	112.9	1.71	1.52	43	120.4	2.40	1.99
—	—	—	—					—	—	—	—	—	—	—	—
29	95.1	2.28	2.40					—	—	—	—	—	—	—	—
36	94.6	2.83	2.99					—	—	—	—	—	—	—	—
160	166.4	11.42	6.86	None occur				—	—	—	—	—	—	—	—
—	—	—	—					26	193.8	4.18	2.16	46	192.4	3.69	1.92
100	165.9	7.73	4.66					—	—	—	—	—	—	—	—
36	144.4	7.79	1.93	Stated to occur, but no specimens				—	—	—	—	—	—	—	—

TABLE IX.
Ratios of Means $\times 100$.

Species	Small Soldiers Large Soldiers	Small Workers Large Workers	Large Workers Small Soldiers	Small Workers Large Soldiers	Small Workers Small Soldiers	Large Workers Small Soldiers	Workers Male Imago
<i>Hodotermes havilandi</i> ...	—	65.8	85.5	56.3	—	—	—
<i>Calotermes durbanensis</i>	—	—	84.0	—	—	—	—
<i>Termes natalensis</i> ...	58.7	64.2	57.6	37.0	63.0	98.1	—
<i>Termes badius</i> ...	70.3	70.7	64.8	45.8	73.6	81.7	—
<i>Termes interiorius</i> ...	—	63.5	129.5	82.2	—	—	—
<i>Termes vulgaris</i> ...	—	70.5	100.4	70.7	—	—	60.0
<i>Termes incertus</i> ...	—	—	115.7	—	—	—	65.7
<i>Termes parvus</i> ...	—	—	92.6	—	—	—	68.3
<i>Termes bilobatus</i> ...	—	—	64.0	—	—	—	84.0
<i>Termes trinervius</i> ...	63.1	—	116.0	—	—	185.3	85.9
<i>Rhinotermes</i> ...	49.1	—	77.0	—	—	156.9	—
Means ...	62.5	66.9	89.8	58.4	68.3	130.5	72.8

Relative Sizes of the various Castes.—Ratios.

Soldiers of two sizes occur in *Termes natalensis*, *Termes badius*, *Termes trinervius* and *Rhinotermes* sp., and the ratios are given in the 2nd column of Table IX. There is considerable variation in the ratios, and the mean is 62.5.

Two sizes of workers occur in five species. It should be noticed that it does not follow that there are two sizes of soldiers when there are two castes of workers and *vice versa*. The ratios are given in the 3rd column of Table IX. It will be seen that they are fairly constant, the mean (66.9) is somewhat similar to that for the soldiers (62.5).

The ratios of large workers to large soldiers are given in the 4th column of the table and they are exceedingly variable, ranging from 57.6 in *Termes natalensis* to 129.5 in *Termes latericius*.

Various other ratios are given in the remaining columns of the table, and there is no marked tendency for constancy in any of them; although the ratio of workers to winged imagos is less variable than the others.

Means of the Coefficients of Variation.

The arithmetic mean of the coefficients for large soldiers for the 11 species (see Table VIII.) is 3.26; for small soldiers (3 species) 3.68; for large workers (11 species) 3.74; for small workers (5 species) 3.89; for male imagos (6 species) 2.06; and for female imagos 1.98.

It is evident from these results that the male and female imagos are considerably less variable than any of the asexual castes. The special manipulation, whether of the nature of specialised food or of any other influence, necessary for the production of these castes, appears to increase the variability.

With regard to the variability of the asexual castes, it will be noticed that the mean results for the series of species are not in accord with those for the species *Termes natalensis*. In this species the soldiers were more variable than the workers, but in the mean values for all the species the reverse is the case.

(12) *Comparison of the termite measurements with those of Wasps.*

Miss Alexandra Wright, Dr Alice Lee and Professor Karl Pearson have recently completed an investigation on the variability of various parts of the wings of worker, drone and queen wasps (*Biometrika*, Vol. v. Part IV. p. 407, 1907). The material employed comprised the individuals from *one* large nest, and it will be of interest to compare as far as possible the results obtained with those from the termites.

In the absolute dimensions the queens, drones and workers of the wasps are in descending order of magnitude with respect to the wing-measurements.

In the case of the termites, the means of the head-breadths of the five species (*T. vulgaris*, *T. incertus*, *T. parvus*, *T. bilobatus* and *T. trinervius*) were for male imagos, 163.15 units; workers, 117.3 and soldiers, 121.3. Thus, although the

dimensions measured are of a different nature, the wasps and termites agree in the sexual forms being the larger.

The absolute variation in the wasps is greater for the workers than for the drones and queens. In the case of the five species of termites, the workers have a mean absolute variation of 4.67 units against 3.51 for the soldiers and 3.57 for the male imagos; that is, a mean of 4.09 for the asexual castes against 3.57 for the sexual form. The general tendency is consequently for the termites and wasps to resemble each other in this matter.

In the relative variabilities (coefficients of variation) the sexual forms (drones and queens) of the wasps are considerably less variable than the workers, the means being: workers, 3.55; drones, 2.60; queens, 1.57.

In the termites the means are, as we have already seen, for: large soldiers, 3.26; small soldiers, 3.68; large workers, 3.74; small workers, 3.89; male imagos, 2.06; female imagos, 1.99.

There is thus a very striking similarity in these results: the mean of the coefficients for drone and queen wasps is 2.08, and for male and female imagos of the termites 2.02.

The asexual wasp caste of workers with a coefficient of 3.55 also compares very closely with the mean of the coefficients of the asexual termite castes, 3.64.

The material at the disposal of the authors of the wasp paper did not permit of the examination of the correlation of the different castes in a number of nests, and consequently a comparison on this point with the termites cannot be instituted*.

(13) *Summary of some of the Results.*

(1) Although the young appear to hatch all alike and in certain species (*T. natalensis*, for example) all are the offspring of one queen and king, yet the various asexual and sexual castes of a nest exhibit marked differences in their variabilities. The differences in the variability cannot therefore be regarded as due to inheritance, but must be supposed to arise mainly through post-embryonic environmental influences.

(2) The sexual caste is much less variable than the asexual castes.

(3) The relative variability (measured by the coefficient of variation) of the population compared with that of a family (the individuals of a nest) appears to be considerably greater than can be accounted for from the ordinary effects of inheritance†, and the cause is almost certainly to be found in the moulding influence of a varying environment on an exceedingly plastic organism.

[* The relative variability of the species and of the members of a nest is now being investigated and the results will shortly be published. Ed.]

[† The reduction in variability for the case of *assortative mating* of a large amount has not yet been worked out. For the termites we have in each generation a brother-sister marriage, or an *assortative mating*, say of .5. There is thus only one pair of ancestors in each generation, and the reduction of variability for such a system may quite conceivably be as great as that indicated by the termite measurements, i.e. nest variability 7.87 and general population variability 17.08. Ed.]

(4) The correlation of the means of any two castes in a nest of a population of colonies is of very considerable magnitude, being about .9. In other words when, for example, the mean of one caste is above the average, then the mean of any other caste in the nest is correspondingly high. Leaving out the effect of inheritance, this correlation could be accounted for by the fact that similar environmental influences would act on all the members of a nest.

(5) The standard deviations of the means of different castes in a population of colonies are considerable; and there is little doubt that the varying environment of each colony is largely responsible for the great fluctuations in the means.

(6) The correlation of the coefficients of variation of any two castes in a population of nests is either moderate or nil, in other words the variability of one caste is in some instances not appreciably correlated with the variability of any other caste in the nest. Owing to the fact that all the castes spring from the same parentage, we might have anticipated that a fairly high correlation would exist. We have therefore evidence that a similar environment can have a varying influence on the variabilities of the different castes.

A comparison of these results with those obtained from other social insects would be of much interest, and would throw additional light on the significance, or otherwise, of some of the observations made in this paper.