THE EFFECT OF GROUP SIZE ON THE SURVIVAL AND FEEDING ECONOMY OF PSEUDOWORKERS OF BUILDING DAMAGING CRYPTOTERMES SPP. (ISOPTERA, KALOTERMITIDAE)

R.M.C. WILLIAMS* and J.V. PEREZ MORALES**

** Centre for Overseas Pest Research*
College House, Wrights Lane, London W8 5SJ

***Instituto Nacional de Investigaciones sobre Recursos Bióticos –*
Laboratorio de Ciencia y Tecnología de la Madera,
Apdo. Postal 63, Xalapa, Ver., México

SUMMARY

5 replicates of groups of 1, 2, 4, 8, 16 and 32 pseudoworkers of *Cryptotermes brevis, C. dudleyi* and *C. havilandi* were kept on beech (*Fagus sylvatica*) veneer for 60 days. There were no significant species differences in survival. Single individuals survived much less well than groups of 2, and groups of 2 less well than groups of 4 or 8. Production of neotenic reproductives and the establishment of a male-female pair was slower in *havilandi* than in the other two species, but was no less successful. Many groups of 8 or more became potentially successful colonies, and some groups of 4 in *brevis* and *dudleyi*. More neotenics were produced by *brevis* than by the other two species, and differences in survival, neotenic production and establishment of a pair suggested a strain difference between *brevis* from West Africa and from Brasil. Progressive attack on supernumerary neotenics was observed in all three species. Wood consumption was +' vely correlated with group size in *brevis* and *havilandi*. There was no correlation between wood assimilation efficiency and group size in any species.

RESUMEN

Efecto del tamaño del grupo sobre la supervivencia y la economia de los seudobreros de Cryptotermes **spp. (Isoptera, Kalotermitidae).**

5 repeticiones de grupos de 1, 2, 4, 8, 16 y 32 seudobreros de *Cryptotermes brevis, C. dudleyi* y *C. havilandi* fueron mantenidos en chapa de haya (*Fagus sylvatica*) durante 60 días. No se manifestaron diferencias importantes de las especies en la supervivencia. Los individuos aislados sobrevivieron con mucha mayor dificultad que los grupos de 2, mientras que los grupos de 2 lo hicieron con más dificultad que los de 4 o los de 8. La producción de reproductores neoténicos y el establecimiento de parejas macho-hembra demostró ser más lenta en la *havilandi* de lo que lo fué en las otras dos especies, pero no por ello menos lograda. Muchos grupos de 8 o de más individuos se transformaron en colonias potencialmente logradas, y algunos grupos de 4 en *brevis* y en *dudleyi*. Un porcentaje mayor de neoténicos fué producido por *brevis* en comparación con los producidos por las otras dos especies. Las diferencias detectadas en la supervivencia, la producción neoténica y el establecimiento de una pareja sugirieron una diferencia de razas entre *brevis* procedente de Africa Occidental y del Brasil. Se observó un ataque progresivo en los neoténicos supernumerarios de las tres especies. La cantidad consumida de madera fué correlacionada de modo positivo con el tamaño de los grupos en la *brevis* y la *havilandi*. No se observó correlación alguna entre la eficacia de absorción de madera y el tamaño de los grupos en ninguna de las especies.

INTRODUCTION

Williams (1977) has shown that colonies of the building pest dry-wood termites *Cryptotermes brevis* and *C. dudleyi* tend to retreat from timber more than about 30 % damaged, and that their numbers decline when the average amount of damage exceeds that figure. One may surmise that at about this point parts of the outer skin of wood remaining are beginning to allow too much gaseous exchange, and may crack, so that the colony finds it increasingly difficult to maintain its water balance and to defend itself against predators. Isolated groups will be increasingly cut off from the main colony as the more vulnerable galleries are abandoned, and in *Cryptotermes* spp., as in other Kalotermitidae, such groups should produce neotenic reproductives readily. It would clearly be advantageous if such groups in building timbers could form small colonies competently, so that the wood was exploited to the full and the maximum number of imagos produced for further colonisation.

The least possible size for such a group would of course be two, a male and a female, but the true least size might be much larger, as it would depend on the ability of the group to maintain itself as a functional colony behaviourally and physiologically. The work of Grassé and his associates (reviewed by Grassé, 1958, and by Harris and Sands, 1965) has shown the importance of the group effect, the mutual sensory stimulation between individuals and, in the lower termites, the trophallactic exchange of food by proctodeal feeding. The purpose of the present work was to determine how small a group might form a functional colony in the three major building pest *Cryptotermes* species found in the western hemisphere.

This study was part of the Centre for Overseas Pest Research (COPR) research programme on building pest dry-wood termites. It was carried out in 1978 by the second author at the COPR termite group laboratory in the British Museum (Natural History), London, as part of a MSc course at London University, his visit to the U.K. being financed by the Consejo Nacional de Ciencia y Tecnologia, Mexico, and the British Council.

MATERIAL AND METHODS

The live material was provided by *Cryptotermes* colonies taken from building timbers or furniture and maintained mainly on beech (*Fagus sylvatica*). The 3 species, with their years of acquisition, were *Cryptotermes brevis* (Walker) from Brasil (1967), Ghana and The Gambia (1973), *C. dudleyi* Banks from Kenya (1976), and *C. havilandi* (Sjöstedt) from Ghana (1973).

Pseudoworkers (wood-feeding instars functioning collectively as a worker caste) were taken from these colonies and randomly made up into groups of 1, 2, 4, 8, 16 and 32 individuals, after the unfit had been removed as described by Williams (1965). Pseudoworkers of at least the 4th instar were used, but brachypterous individuals were excluded as far as possible, and always from groups of fewer than 8, to avoid moults to the pre-imago instar which soon ceases to behave as a pseudoworker. In the event no pre-imagos appeared.

The group sizes were replicated 5 times for each species. The groups within each replicate were matched by being from a single large colony, or else from an amalgamation of 2 or more smaller ones. Colonies of Kalotermitidae can readily be amalgamated, and there was no suggestion in the data subsequently obtained that this practice had any deleterious effect.

Each group was placed on a 40 x 20 x 0.7 mm piece of beech veneer in a 50 x 19 mm glass tube (Fig. 1). The cap of the tube was pierced with a 0,5 mm hole, large enough for gaseous exchange but small enough to prevent internal draughts when handled. The tubes were kept in a container at 28 ± 1° and c. 93 % relative humidity for 60 days.

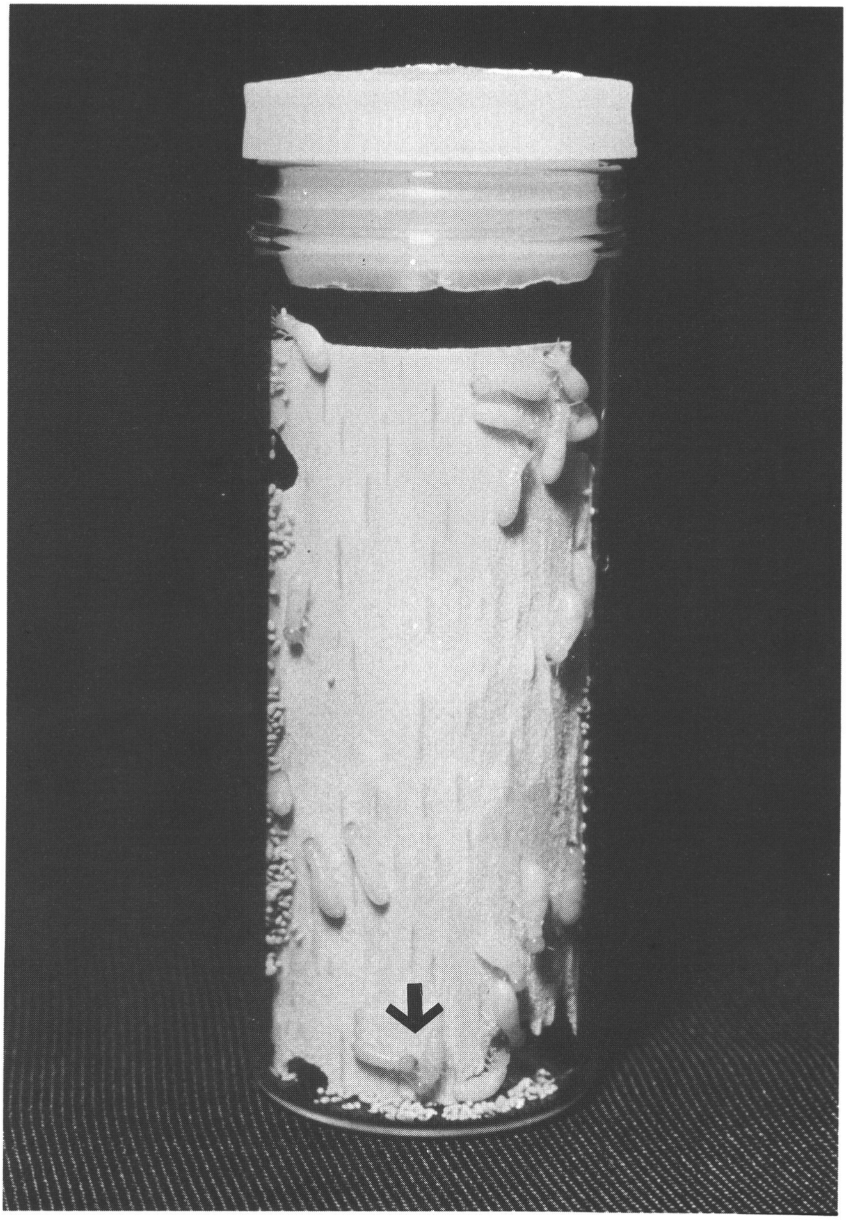

Fig. 1 – A tube set up with 32 pseudoworkers of *Cryptotermes dudleyi*, after 18 days. The two arrowed individuals are a pair of neotenic reproductives.

Fig. 1 – Probeta preparada con 32 seudobreros de *Cryptotermes dudleyi*, después de haber transcurrido 18 días. Los dos individuos marcados con una flecha son una pareja de reproductores neoténicos.

The success of each group was measured firstly by survival, expressed as the mean life length of the individuals in the group. This was obtained from daily counts of survivors, the count being assigned to the mid-point between readings to give the best estimate of true life length ; this applied when counts were missed at week ends and on public holidays. Individuals becoming unfit during the first 3 days were presumed to be handling casualties, and were replaced (3 instances, 1 in each species). At the end of the experiment the surviving individuals were taken to have died on the 61st day for the purpose of analysis.

Besides dead and dying individuals, those which appeared unfit by shortening of the abdomen were also discounted (unless they later recovered), because they had presumably ceased to feed and contribute to the social life of the group. Such individuals often lived for many days before death in the smaller groups, but rarely did so in the larger groups. Their greater vulnerability to cannibalism in the larger groups is suggested by the fact that this mean life length, the social life length, is shorter than that measured by death or a dying condition by only about a day or less in groups initially of 4 to 32 individuals, but by about 3 days in groups of 2 and 12 days in single individuals.

Cannibalism could not be prevented, and so dead and dying individuals were left in the tubes until seen to be infected with mould. They were then removed as it was presumed that no further cannibalism would take place. The work of Dhanarajan (1978) on *Reticulitermes santonensis* suggests that the products of autolytic decomposition would probably make the cadavers repellent before mould appeared.

The second measure of group success was the production of neotenic reproductives, particularly the establishment of a definite male-female pair, after which no further neotenics would be produced, or those which were would live only a short period. This raised the group to the level of a potentially successful colony. Any slight yellowing of the integument or increase in eye pigmentation was noted as the first indication that a pseudoworker had become a neotenic, provided that this was confirmed by further changes. It was found that a female neotenic could sometimes be confirmed to be such by the pink colour of eggs visible through the abdominal wall at a time when other changes were hardly discernable.

The presence of neotenic reproductives stimulates the production of soldiers in *Kalotermes flavicollis* (Springhetti, 1970), a male-female pair having the greatest influence. One 16 group and two 32 groups of *Cryptotermes dudleyi*, and one 32 group of *C. havilandi* each produced a pre-soldier after a pair had been present for 1 to 5 weeks, though in one instance it was not the pair finally established.

Normality of behaviour and physiology in each group was assessed by measurement of the rate at which the wood was consumed and by the efficiency with which the eaten wood was assimilated. The wood consumption of each group was determined as mg oven-dry wood eaten / g termite live weight / day, from the mean number of termites present during the experiment, or the group's survival period if shorter, the mean initial weight of the pseudoworkers of the group, and the oven-dry weight loss of the wood slip. The assimilation efficiency was found as the percentage of eaten wood assimilated by the group, from the oven-dry weight loss of the wood slip and the oven-dry weight of the faecal pellets and other faecal material produced.

No initial oven-dry weight of the wood slips was taken in case the drying affected their food value or moisture holding capacity. Instead, their initial weight was taken after conditioning for 3 days at 45 % relative humidity, fairly close to that of the room in which they were weighed. They were then reconditioned at 93 % RH for at least a day before use. During the experiment any slip as much as 1/3 to 1/2 destroyed was replaced with a second slip, so that many of the 32 groups and some 16 groups had two. At the end the damaged slips were weighed first after reconditionig at 45 % RH, and then after oven-drying to constant weight at 105°. The moisture content of the slip at 45 % RH was then used to calculate an initial oven-dry weight. This should have been sufficiently accurate if there was little variation in moisture content over the slip, or little selection of wood for its moisture content by the termites. The slips were usually attacked in a fairly uniform way by cutting through at various points where the edge of the slip was close to the glass, and by a more general erosion over the surface of the side nearest the glass, the side preferred by the termites for thigmotactics reasons (see Fig. 1). The erosive attack in particular might have allowed selection of the wood, but the slips were chosen for uniformity of appearance and absence of knots, grain irregularities, blue-stain patches and other blemishes, so that any selection should have had a very limited effect.

A problem arose because it was evident, from bizarre values for wood consumption and assimilation efficiency lying far beyond the general level of experimental error, that for reasons unknown some weights of slips and faecal pellets must have been very inaccurate. A small number of grossly outlying values were discarded on the basis of a test for rogue observations (Pearson and Hartley, 1970).

RESULTS AND DISCUSSION

Survival

Table I gives the means of the mean life length values for the 5 pseudo-worker groups of each initial group size. The three species show a broadly similar pattern. Analysis of variance of the whole data indicated no significant species differences, a significant variance ratio for replicates ($F = 2.74$, $P < 0.01$), clearly due to differences within *Cryptotermes brevis* (see below – *Cryptotermes brevis* strains), and a highly significant variance ratio for group sizes ($F = 11.40$, $P < 0.001$). The group size variances are homogeneous by Bartlett's test. The mean life length for single individuals is significantly lower than in groups of 2 ($P < 0.001$), and lower in groups of 2 than in groups of 4 or 8 ($P < 0.05$), by Duncan's multiple range test.

Table I – Mean life length (days), ± S.D., of 5 pseudoworker groups of the initial size indicated in 3 *Cryptotermes* spp. The analysis of overall group means by Duncan's multiple range test is given below. Means sharing the same letter are not significantly different.

Tabla I – Duración media de vida (en días), ± desviación típica, de 5 grupos de seudobreros del tamaño inicial indicados en 3 *Cryptotermes* spp. A continuación se incluye un análisis de los promedios de grupos totales mediante la prueba de alcance múltiple de Duncan. Los promedios que comparten la misma letra no se diferencian de modo importante.

Group initial size	*C. brevis*	*C. dudleyi*	*C. havilandi*	Overall group mean
1	17.9 ± 5.1	28.7 ± 15.9	12.9 ± 4.9	19.8
2	36.6 ± 22.8	45.1 ± 22.1	31.8 ± 22.0	37.8
4	50.3 ± 17.0	48.8 ± 13.0	51.5 ± 10.0	50.2
8	49.2 ± 15.0	54.2 ± 10.6	40.2 ± 6.2	47.9
16	33.8 ± 14.2	53.4 ± 4.0	40.7 ± 7.7	42.6
32	44.9 ± 10.1	51.0 ± 5.8	34.6 ± 13.7	43.5

Group size	1	2	16	32	8	4
Group mean	19.8	37.8	42.6	43.5	47.9	50.2
$P < 0.05$	a	b	bc	bc	c	c
$P < 0.001$	a	b	b	b	b	b

None of the single individuals survived the experiment in a fit condition, only 2 unfit *C. dudleyi* remaining alive. All of the groups of 2 which survived had both individuals living, except in one instance where the first died on the 52nd day. Otherwise no second individual lived long after the first had died. Nevertheless 5 of the 15 groups of 2 survived the test with both fit, so the presence of a second individual considerably enhanced survival. Group of 4 showed the best survival overall, 7 groups surviving with 4 fit individuals, 2 with 3 individuals and 2 with 2 individuals. The results were compressed by the necessity for terminating each replicate at 60 days, the time for the study being limited. But for this the mainly very healthy but sometimes very reduced 16 and 32 groups would certainly have differed significantly from the groups of 2.

It was expected that survival would improve with group size, as Grassé and Chauvin (1942) found in groups of 1 to 10 *Reticulitermes lucifugus* workers. A probable reason for the poorer survival of the 16 and 32 groups, by comparison with the 4 and 8 groups is that any individuals which were rendered slightly unfit by transfer to the experimental conditions, but which

Table II – The mean number of days elapsing before the appearance of the first neotenic reproductive, and before the establishment of a definite male-female pair (number of pseudoworker groups in brackets). The means, ranges and analyses beneath each table are of the 8, 16 and 32 groups only.

Tabla II – El número medio de días transcurridos antes de la aparición del primer reproductor neoténico, y antes del establecimiento de una pareja macho-hembra determinada (el número de grupos de seudobreros se indica entre paréntesis). Las medias, los alcances y análisis incluidos debajo de cada tabla son los de los grupos de 8, 16 y 32 solamente.

First appearance

Group initial size	*C. brevis*	*C. dudleyi*	*C. havilandi*
1	9.5 (2)	8.0 (1)	13.0 (1)
2	16.8 (5)	21.0 (3)	19.7 (3)
4	10.0 (4)	26.3 (3)	11.0 (3)
8	13.0 (5)	7.2 (4)	17.2 (4)
16	6.8 (5)	7.2 (5)	15.4 (5)
32	6.4 (5)	5.8 (5)	16.4 (5)
Mean	8.7	6.7	16.3
Range	4 - 29	4 - 10	6 - 29

Kruskal-Wallis H = 14.68, $P < 0.001$

Mann-Whitney U tests : *brevis - havilandi* $P < 0.01$
dudleyi - havilandi $P < 0.002$

Establishment of pair

2	–	–	–
4	20.7 (3)	49.0 (2)	–
8	20.3 (3)	15.7 (3)	16.3 (3)
16	12.5 (2)	17.4 (5)	29.8 (5)
32	16.0 (4)	11.0 (4)	27.2 (4)
Mean	16.7	14.8	25.6
Range	8 - 32	6 - 31	14 - 40

Kruskal-Wallis H = 9.29, $P < 0.01$

Mann-Whitney U tests : *brevis - havilandi* $P < 0.05$
dudleyi - havilandi $P < 0.01$

could recover, were more likely to be cannibalised the larger the group and the greater the frequency of contact with other termites. The percentages of individuals with shortened abdomens, but seen to recover, amongst the pseudoworkers of the groups of 1 to 32 individuals were, in order of group size, 13, 7, 3, 4, 2 and 0.2 %.

Production of neotenic reproductives

Survival is only the first, though most fundamental, requirement for colony success. No isolated group can become a successful colony unless it produces a male-female pair of neotenic reproductives. Table II gives the mean number of days elapsing before the first neotenic was observed in those groups which produced them, and before the establishment of a definite male-female pair.

Sometimes the first 2 or more neotenics to appear were of the same sex, and in some instances one or both members of a pair might be replaced before a definite pair was established. Observation supported the view of Grassé and Noirot (1946) and other workers that supernumerary neotenics are often attacked by other individuals. In the larger groups the process of cannibalism was so rapid that it was not possible to determine whether the neotenic was attacked or was cannibalised after it had become unfit for other reasons. In the 4 and 8 groups of all three species the process sometimes took 2 days or more, and it was possible to observe that some neotenics received severe injuries to legs and antennae while still active, and were more fully cannibalised as they became unfit and immobile.

Williams (1973) found that neotenics of *C. havilandi* could feed themselves, and that a pair isolated by the deaths of the pseudoworkers in the colony could survive on its own for a long period. However an isolated group of 2 pseudoworkers may rarely be able to become a successful pair. Apart from the probability of both sexes present being only 50 %, survival is further prejudiced by the reduced readines of neotenics to donate proctodeal food, at least in *C. brevis* (McMahan, 1969). Thus the second neotenic of a pair would be less likely to refaunate after its prior moult than when pseudoworkers are present. Here all 5 groups of 2 which survived the experiment had one neotenic and one pseudoworker, but the appearance of two neotenics in 3 of the *brevis* groups was followed by the death of the pair soon after.

The analyses of the data of Table II were carried out only on the 8, 16 and 32 groups because of the disparate numbers of smaller groups producing neotenics, and because brachypterous pseudoworkers, which might be better able to become neotenics than apterous individuals (Wilkinson, 1962), were excluded from groups of up to 4 (see Materials and Methods). The distributions tend to be skewed, as can be seen from the means and ranges, so the Kruskal-Wallis test has been used to compare species (there being no suggestion of significant group size differences). The test indicates significant differences both for the first appearance of neotenics and for the establishment of a definite pair. The Mann-Whitney U tests between species indicate that *C. havilandi* was significantly slower than the other two species in both instances. This is not associated with relative lack of success and may be a characteristic of the species, the reason for which may become apparent when more is known of the long-term development of colonies of all three species, and the natural ecology of *C. brevis* and *C. dudleyi*, whose natural distributions remain unknown.

Colony success

All groups of 4 to 32 individuals producing an established male-female pair (Table II) were healthy at the end of the experiment, except for one *brevis* 4 group which had later died out, and a *havilandi* 32 group the male of which died shortly before the end of the experiment. All the rest, 11 groups each of *C. brevis* and *C. havilandi* and 14 of *C. dudleyi*, out of a possible total of 20 in each species, could be regarded as potentially successful colonies. Thus as few as 4 isolated pseudoworkers might form a successful colony, certainly in *brevis* and *dudleyi* and probably also in *havilandi*, as Wilkinson (1962) noted that a pair might be established by as few as 5 individuals.

4 colonies of *C. brevis*, 5 of *C. dudleyi* and 6 of *C. havilandi* produced eggs, but the open conditions in the tubes precluded the normal handling of eggs by the termites. The greatest number seen was 4, 7 and 3 in the three species respectively, but egg mortality might have been high in some instances. No eggs were observed in the 4 group colonies, but one was seen in a fit but unsuccessful *havilandi* 4 group with a ♀ neotenic.

Cryptotermes brevis **strains**

3 replicates of *C. brevis* were set up with material from Brasil, 1 replicate with material from Ghana and 1 with material from The Gambia, all being adequately comparable as regards the instars represented and the numbers of stock colonies drawn upon. However, examination of the figures for the numbers of neotenic reproductives produced, for survival and for the establishment of groups as potentially successful colonies suggests that the West African and Brasilian *brevis* material may represent two strains with genetically determined differences.

In earlier work (Williams, 1977) it was found that *C. dudleyi* and *C. havilandi* tended to produce a neotenic pair competently, with few supernumerary neotenics, while groups of *C. brevis* produced numerous supernumerary neotenics with a correspondingly high mortality, in the seemingly incompetent pattern found by Nagin (1970) in *Neotermes jouteli*. All the *brevis* material for that study came from The Gambia, and was maintained on balsa in plates of the pattern described by Williams (1973). The mean percentage of individuals observed to become neotenics in the present study in shown in Table III, and the same pattern is shown as before. Regarding species differences, Friedman's $\chi^2 = 9.08$ ($P < 0.01$), clearly due mainly to the consistently much higher percentages in *C. brevis.*

Table III – The mean percentage of individuals observed to become neotenic reproductives in each group size. The numbers of pseudoworker groups are as in Table II. Bracketed figures give percentages for *Cryptotermes brevis* from West Africa (WA) and from Brasil (B).

Tabla III – El porcentaje medio de individuos observados que se transformaron en reproductores neoténicos en cada tamaño de grupo. Los números de los grupos de seudobreros son como los de la tabla II. Las cifras entre paréntesis indican porcentajes para la especie *Cryptotermes brevis* procedente de Africa Occidental (WA) y del Brasil (B).

Group initial size	*C. brevis*	(WA	B)	*C. dudleyi*	*C. havilandi*
1	40	(0	67)	20	20
2	80	(100	67)	20	30
4	40	(25	50)	25	25
8	32	(38	29)	20	27
16	29	(44	19)	16	21
32	18	(22	15)	11	9

The figures for *C. brevis* in Table III are further broken down into means for the 2 W. African groups and for the 3 Brasilian groups of each initial group size. There was a consistently higher proportion of neotenics in the larger W. African groups, and this overproduction of neotenics is associated with very poor survival. Mean life length ± S.D. was 26.9 ± 8.3 days in the 2 W. African replicates, and 46.7 ± 1.6 days in the 3 Brasilian replicates, a significant difference ($t = 3.31$, $P < 0.05$).

The magnitude of the difference suggests that many W. African individuals may have died, or been killed, before their differentiation into neotenics was observable. This has been found in *C. brevis* from N. America by Lenz, McMahan and Williams (in press), though mortality was about as in Australian groups, in which a greater number of clearly differentiating neotenics was observed. However in these strains, and likewise in Hawaii (McMahan, 1963), a pair is usually established, whereas in most W. African groups of 4 or more individuals all the neotenics produced died or were killed, or all but one, or a succession was produced and died without the establishment of a definite pair. Amongst the 20 groups of 4 or more, 9 out of 12 Brasilian groups formed potentially successful colonies, but only 2 out of the 8 W. African groups.

It has been found in experiments of a longer duration than this, that if a *brevis* group successfully establishes a neotenic pair its brood production commonly exceeds that of *dudleyi* or *havilandi* pairs, perhaps because overproduction and cannibalism of neotenics circulates extra protein through the colony (R.C. Steward, personal communication). Thus the W. African strain, if strain it is, may differ from the others mentioned in being poorly adapted to make use of neotenic overproduction.

Feeding economy

Figures for the rate of wood consumption and the efficiency with which the eaten wood was assimilated (Table IV) exclude several gross outliers (see Material and Methods) and two instances where data was accidentally lost. Assimilation efficiency figures could only be obtained where there were enough faecal pellets to weigh with acceptable accuracy, over 0.5 mg, and so were few amongst single individuals and groups of 2.

The amounts of wood eaten by single individuals were so small that their consumption figures were appreciably affected by the experimental error. Hence the -'ve value for *C. havilandi*, the smallest species (mean initial pseudoworker weights : *C. brevis* 4.1 mg, *C. dudleyi* 4,5 mg and *C. havilandi* 2.7 mg), and also the shortest lived (Table I). However the collective figures for the three species, the one assimilation efficiency figure for *dudleyi*, and the fact that all the single individuals produced a number of pellets, albeit usually undersized, indicates that they fed to a slight extent, and perhaps to a level comparable with those in larger groups in some *brevis* and *dudleyi*.

Single individuals of more complex societies suffer a breakdown of normal behaviour and die within a few days, as Grassé and Chauvin (1942) found with *Reticulitermes lucifugus* and the present first author (unpub.) with *Cubitermes testaceus*. However isolated pseudoworkers of *Kalotermes*

Table IV – Mean wood consumption, mg oven-dry wood / g termite live weight / day, and mean assimilation efficiency, % wood assimilated (number of pseudoworker groups in brackets). The species means and standard deviations exclude the figures for single individuals.

Tabla IV – Consumo medio de madera, mg. madera secada al horno / g. peso de termita en vivo / día, y la media de eficacia de absorción, % de madera absorbida (la cifra de grupos de seudobreros entre paréntesis). Las media de las especies y las desviaciones típicas no incluyen las cifras para individuos aislados.

Wood consumption

Group initial size	*C. brevis*	*C. dudleyi*	*C. havilandi*
1	19.3 (2)	12.1 (4)	- 7.1 (3)
2	19.7 (5)	14.5 (4)	13.9 (4)
4	25.1 (4)	15.7 (5)	19.2 (5)
8	23.1 (5)	16.0 (5)	17.6 (5)
16	23.8 (5)	16.2 (5)	24.6 (5)
32	33.5 (5)	18.5 (5)	25.2 (5)
Species mean	25.0	16.2	20.3
S.D.	8.2	10.6	9.01
Assimilation efficiency			
1	–	78.6 (1)	–
2	64.6 (2)	52.4 (3)	79.8 (2)
4	71.1 (4)	59.8 (3)	65.8 (5)
8	70.0 (5)	67.9 (4)	59.3 (5)
16	67.8 (4)	64.5 (4)	63.7 (5)
32	62.5 (5)	65.3 (5)	63.7 (5)
Species mean	67.3	62.8	64.6
S.D.	8.1	10.8	10.4

flavicollis can survive for over a year if artificially refaunated after each moult, the group effect of trophallaxis and stimulation by other forms of contact being manifested by a greater frequency of moulting and caste differentiation (Grassé and Noirot, 1960). Our isolated *Cryptotermes* were able to remain active for several weeks, but feeding was usually reduced and unfitness and death were preceded by a moult in only 4 of the 15 individuals. No part of a shed integument was seen in the tubes of the other 11. So in these species isolation was slowly deleterious, though not catastrophic as in *R. lucifugus* and *C. testaceus.*

The figures for groups of 2 (Table IV) are rather more reliable than those for single individuals. They and the larger groups give mean consumption and assimilation efficiencies broadly similar to values for various Kalotermitidae summarised by Wood (1978).

Groups of 2 to 32 individuals showed a +'ve correlation between wood consumption and the mean size of each group during the experiment, or during its survival period if shorter, in *C. brevis* and *C. havilandi* ($r = 0.62$ and 0.50, $P < 0.002$ and 0.02 respectively). *C. dudleyi* showed the same trend, but not to a significant level. This correlation accords with the expectation that increasing group size and frequency of mutual stimulation would lead to increased activity. However, because of it the figures are not a satisfactory indication of consumption in large colonies kept under similar conditions, which might be appreciably greater than that of the groups of 32 here.

This group effect can be largely removed in an analysis of variance by removing the effect of initial group size differences, the correlation between consumption and initial group size being close to that above. When this is done, the considerable consumption differences between species shown in Table IV are found to be non-significant, as are those for assimilation efficiency.

The expected +'ve correlation between mean group size and assimilation efficiency was not shown by *C. brevis*, and was shown only weakly and non-significantly by *C. dudleyi* and *C. havilandi*, suggesting that the reduced opportunities for trophallaxis in the smaller groups were compensated for by increased pellet eating.

CONCLUSIONS

The most important fact emerging from this work is that very small groups of isolated individuals, as few as 4 pseudoworkers in *Cryptotermes brevis* and *C. dudleyi*, can form a potentially successful colony with an established male-female neotenic pair. Thus it can never be safe to re-use susceptible timber from an infested building if it has had even the lightest penetration by a colony in adjacent wood.

Both survival and the proportion of groups establishing a neotenic pair to become potentially successful colonies was much the same in the three species. However, there were considerable differences in these respects within *C. brevis*, suggesting that the Brasilian and West African material used may represent two distinct strains with genetically determined differences.

Observation confirmed that in all three species some supernumerary neotenic reproductives were attacked while still active and progressively cannibalised, though others may have become unfit for other reasons.

The isolation of single *Cryptotermes* pseudoworkers appeared to have a slow deleterious effect, in contrast to *Kalotermes flavicollis*. Feeding was usually reduced, though it may have been close to normal in a few individuals until they became unfit. Death always occurred within a few weeks, but followed moulting and loss of hind-gut protozoa in only a minority of instances.

Wood consumption in groups of 2 was of the same order as that in larger groups, though their survival was shorter than in groups of 4. Wood consumption rose with group size in *C. brevis* and *C. havilandi*, though not significantly in *C. dudleyi*.

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