FACTORS INFLUENCING THE BIOLOGY AND DEVELOPMENT OF COLONIES OF *POROTERMES ADAMSONI* (FROGGATT) (ISOPTERA:HODOTERMITIDAE:POROTERMITINAE)

by

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CONTENTS

SUMMARY

The biology and development of Porotermes adamsoni was studied with particular emphasis on the early development of cultures of isolated larvae. The factors that influenced the maturation and survival of supplementary reproductives have been examined and the processes which appear to cause the stabilisation of young colonies have been reported. The environment and the mature ovipositing female both appear to exert an effect on neoteny. In young colonies developed by primary reproductives the fecundity of queens seems to increase as the number of larvae reaching the third instar increases. Such colonies develop slowly and may take more than a year before soldiers or other dependent forms appear within them.

DECLARATION

The work presented in this thesis is my own, unless otherwise acknowledged in the appropriate place; it has not previously been published or submitted to this or any other university for the award of any degree.

(A. Mensa-Bonsu)

1.0 INTRODUCTION

Porotermes adamsoni (Froggatt) is the only species of the sub-family Porotermitinae (family Hodotermitidae) recorded in Australia. Although it has been known to cause damage to timber and forest trees (Hill, 1942; Greaves, 1959), little is known of its biology and habits and the information available comes mainly from general field observations. Even so there is more information on this species than on Porotermes quadricollis from Chile or on Porotermes planiceps which occurs in South Africa.

Greaves (1957-62a, 1962b, 1963) observed that field colonies and laboratory incipient cultures developed slowly. Most field colonies have been found to contain several supplementary reproductives (Hill, 1942; Gay and Calaby, 1970). Evidence from my studies indicates that supplementary reproductives play a prominent role in the fecundity of this species and in the survival and development of colonies. Also, the behavioural and physiological mechanisms involved in the determination of castes in P. adamsoni may not be as precise or as well developed as in some other termites.

The aims of this study were to investigate the factors associated with the biology and development of colonies of P. adamsoni and, in particular, the relative importance of primary and supplementary reproductives. The factors considered included the size and structure of field colonies, the effect of some environmental factors on the development of colonies and on the differentiation of castes. The study has emphasised the role of the colony as the biological unit

rather than the individual components of it.

1.1 Literature Review

Termites are social insects living in highly organised communities called nests or colonies. The nest may be constructed in wood or in soil, below the ground, on the surface of the ground or in trunks or branches of trees. The nest serves as a storeroom for food in species which construct them away from their food supply (Harris, 1960; Noirot, 1970).

In other species the nest may house the reproductives, eggs, soldiers and young nymphs as well as the itinerants which enter it to feed the dependent forms.

The castes in a termite community are the reproductives, soldiers and workers and there are two types of functional reproductives in the colonies of most species. Primary reproductives are the founders of new colonies and derive from alates or sexually matured males and females which fly from the parent colony, shed their wings and pair within a suitable nesting site (Light, 1934; Grassé, 1949; Harris, 1958; 1961 and Nutting, 1969). Supplementary reproductives form when the colony loses either of its primary reproductives or when the colony increases in size sufficiently to support more than one centre of reproduction. There are different types of supplementary reproductives:- those which are sexually matured alates which do not fly away from the parent colony and those which are neotenics or matured larvae and nymphs. The former occur only in the Termitidae.

A distinction in the neotenics of other termites is that those developed from larvae have no wing buds while those with wing buds are developed from nymphs (Miller, 1969; Noirot, 1969). The production of brood by supplementary reproductives is higher, at least initially, than that of the primary reproductives. This comparison has been made from isolated pairs of primary reproductives and from supplementary reproductives which are being cared for by various numbers of "workers" (Light, 1934; McMahon, 1962). Trophallaxis might quite expectedly influence the higher rate of brood production by the supplementary reproductives in such comparisons and their validity is therefore questionable (Weesner, 1969).

A true worker caste is found in the Termitidae and possibly in the Rhinotermitidae and some Hodotermitidae. They have rudimentary genital organs and no wing buds. They have moulting glands and in some cases they may transform into other castes. However, their main function is to forage and care for the dependent forms such as eggs, larvae, reproductives and soldiers. In "lower" termites, which do not have true workers, their function is performed by the "pseudergates" and nymphs (Light, 1934; Miller, 1969; Noirot, 1969). Pseudergate, meaning "false worker", was proposed by Grassé and Noirot (1947) to refer to individuals which have either regressed from nymphal forms by moulting to eliminate or reduce their wing buds or which are larvae undergoing "stationary" non-differentiating moults.

The soldier is a sterile caste found in all known genera except Anoplotermes and Speculitermes (Harris and Sands, 1965). Its sole

function is to protect the colony against predators and it cannot develop into another caste.

1.11 Differentiation of castes in lower termites

While there is no information on the differentiation of castes in species of Porotermes, a great deal of research has been reported on such differentiation in species of other genera. The caste which has been most studied is the supplementary reproductive. Research on caste differentiation in termites has been reviewed by Weesner (1960), Weaver (1966), Miller (1969), Noirot (1969) and Wilson (1970). The differentiation of castes in Isoptera has been considered in terms of two theories: (a) that concerned with "Intrinsic Factors" (Imms, 1919) which postulates that there is genetic control over the development of the individual and (b) that concerned with "Extrinsic Factors" (Grassi and Sandias, 1893, 1894) which assigns the initial stimulus in caste development to such things as nutrition and other environmental factors. Thompson (1919, 1922) showed that there were apparent anatomical differences between larvae that developed to different castes but Heath (1927, 1928) in repeated experiments did not confirm her results. Most convincing data supports the view that individual termites have no predetermined caste and that the structure and needs of the colony are met by development of certain castes as required from any individual not functionally an end-line caste such as a reproductive or soldier. Directly related to this is the elimination of individuals that are no longer required so that an appropriate balance between "providers" and

"dependents" is maintained.

Transformation of larvae and nymphs to the various castes is to some extent dependent upon certain environmental factors, particularly temperature and nutrition (Lüscher, 1961b; Buchli, 1956a, b; 1958).

The production of alates is particularly affected by ambient temperature and the maturity and nutritional status of the colony, the latter being related to its size (Lüscher, 1960; Buchli, 1958).

Termites exert a measure of control over the temperature of the nest but not to the same degree as do honeybees. Greaves (1967) showed that the temperature variations in the nests of Coptotermes acinaciformis Froggatt closely followed those of the air surrounding the infested trees. Since temperature has been shown to affect insect activity, optimal ranges of temperature for caste-differentiation would be expected.

Nutrition of the colony, while affected by many factors, is usually related to the availability of suitable wood and the proportion of foragers to dependents within the colony. It is difficult, and perhaps not profitable, to attempt to separate nutrition of the colony and its size. There is strong evidence that these factors combined may influence both the number of any caste that develops and the time taken for it to differentiate from an immature form. In this regard, the transformation of workers of Reticulitermes lucifugus to supplementary reproductives appeared to be quicker in larger groups than in smaller groups (Grassé et al., 1950). If colonies of R. lucifugus and its subspecies santonensis had a satisfactory food supply, formation of

supplementary reproductives, soldiers and nymphs was always possible, irrespective of the proportion of these castes present. On the other hand if the food supply became critical, some soldiers and supplementary reproductives were killed, nymphs often regressed to pseudergates and further development of supplementary reproductives and soldiers was inhibited. Disturbance also promoted the development of supplementary reproductives. When field colonies were disturbed by say artificially opening and closing them or when individuals in a laboratory colony were measured, large numbers of supplementary reproductives developed in 5 to 6 days but later disappeared from colonies under observation (Buchli, 1956a).

Being a dynamic entity, the termite colony must, and does, respond to changes in environmental factors critical to its survival. Thus it is commonly found that under certain stresses a colony may redistribute available resources through cannibalism or the maturation and release of alates. In the honeybee, drones are driven from the hive, a behaviour analogous to alate release (see Butler, 1954).

There is little precise data on the effect of environmental factors on caste differentiation. This has given the erroneous impression that Buchli's results support a theory opposed to the theory of inhibition by pheromones. But the results may rather seem to indicate that R. lucifugus and its subspecies may be more influenced by environmental factors such as nutrition than by pheromones under certain conditions.

The differentiation of castes in a colony may be regarded as a

logical response to changes in the environment of that colony, a fundamental requirement being that reproduction is concentrated in few individuals and that the number of reproductive units is maintained in a certain proportion to non-fecund forms. The mechanism responsible for maintenance of this critical proportion, is thought to be initiated by a substance of endocrine origin and much effort has gone into the demonstration of a pheromone, produced by gravid queen termites and spread among the individuals of the colony through the behaviour called grooming. While results have not always been conclusive, it is now regarded as having been demonstrated that such a chemical mechanism exists in several termites of three families.

When colonies of Zootermopsis angusticollis (Hagen), Kalotermes flavicollis, (Fabricius), Neotermes jouteli (Banks) and Prorhinotermes simplex (Hagen) were isolated from functional reproductives (primary or supplementary), supplementary reproductives developed from undifferentiated individuals. However, the presence of a pair of functional reproductives, inhibited the development of supplementary reproductives (Castle, 1934; Miller, 1942; Grassé and Noirot, 1946; Light and Weesner, 1951; Lüscher, 1952a and Nagin 1972). This inhibition was associated with the sex of the individual, in that transformation of undifferentiated females was strongly inhibited by existing female reproductives but male reproductives did not have an equally strong inhibitory influence on undifferentiated males (Light and Weesner, 1951; Grasse and Noirot, 1960*; Lüscher, 1964 and Nagin, 1972).

The functional reproductives are believed to produce an

inhibitory pheromone which suppresses the development of supplementary reproductives. Castle (1934) fed alcohol and ether extracts of functional supplementary female reproductives of Z. angusticollis to undifferentiated larvae. The formation of supplementary female reproductives was delayed compared with the controls. Light (1944a, b) repeated Castle's experiment on a larger scale. He used various methods for his extraction but did not obtain complete inhibitions in all tests as occurred in natural colonies headed by primary reproductives. Light, however, considered the results indicated the presence of an inhibitory substance (Light,1944a,b Light and Weesner, 1951). It seems possible that with such methods of chemical extraction, some activity may be destroyed or modified by the process or by existing impurities and therefore variable results in large experiments using different processes of extraction may not be unexpected.

Lüscher (1955) fastened functional primary female reproductives between two colonies so that the head and thorax were in one colony and the abdomen in the other. There was inhibition in the colony exposed to the abdominal region of the gravid queen but not in the other, indicating that the inhibitory substance was produced in the abdominal region. In another experiment (Lüscher, 1956b) pseudergates were fastened between two colonies so that their heads were in one colony with functional reproductives and their abdomen in another colony without reproductives. There was inhibition in the colony without reproductives. Luscher claimed that the pseudergates could transmit the inhibitory substances from the reproductives to the individuals in

the culture that had no reproductives. Nagin (1972) repeated Luscher's experiment but failed to confirm his results.

Colonies whose functional reproductives were removed, produced supplementary reproductives from fourth instars or older larvae and nymphs. The individuals which were going to transform into supplementary reproductives were observed to empty their alimentary tracts, become pale in colour and moult into supplementary reproductives in about 5 days. This period was shorter than that for moults to larvae or nymphs. Transformation into reproductives also involved reduction in headwidth, reduction or loss of wing buds and atrophy of the prothoracic glands (Grassé and Noirot, 1946; Luscher, 1952 a, b, c; Buchli, 1956a). The larvae and nymphs which were able to transform into supplementary reproductives more readily were those which had undergone an ordinary larval or nymphal moult within 10 days (Lüscher, 1953a, 1960).

When functional reproductives were removed from colonies a number of supplementary reproductives were formed with females more numerous than males. However, only a pair survived and became functional. The surplus supplementary reproductives were eaten by larvae and nymphs (Grassé and Noirot 1960 Luscher 1952b, Nagin 1972)..

The little information available on the differentiation of soldiers seems to indicate that a similar inhibitory mechanism as that associated with supplementary reproductives is involved. For instance, in incipient colonies whose first and successive soldiers were removed, the number of soldiers that developed in the first year was more than usual for first year colonies (Castle, 1934; Light, 1942-43; Light

and Weesner, 1955). Also, isolated groups of individuals without soldiers developed more soldiers than control groups with soldiers (Miller, 1942, Nagin, 1972). The number of soldiers a colony can support is related to the size of the colony and the ability of the individuals in the colony to support dependent castes. If soldiers present in the colony exceed the number it can support, the surplus are killed by the larvae and nymphs (Lüscher, 1961; Nagin 1972). Colonies, disturbed regularly over a period will develop more soldiers than undisturbed controls. The proportion of soldiers in the disturbed colonies decreases soon after the disturbance ceases (Morgan, 1959).

1.12 Discussion

The differentiation of castes in termites may, therefore, result from the interaction of environmental and pheromonal factors, the former dominating in the development of end-line forms and the latter controlling the proportion of a particular caste that forms in relation to the other components of the colony. When imbalance in the proportion of dependents to providers occurs, cannibalism and killing of surplus dependents may recycle available resources and re-establish a norm appropriate to the operative conditions for the colony. The trigger that initiates cannibalism is unknown but seems in Porotermes adamsoni to be related to "excessive grooming" which in turn may indicate that the providers are unable to work at a rate necessary to maintain adequate nutritional levels within the colony without using more readily available energy sources. Thus cannibalism may be innate to individuals and initiated

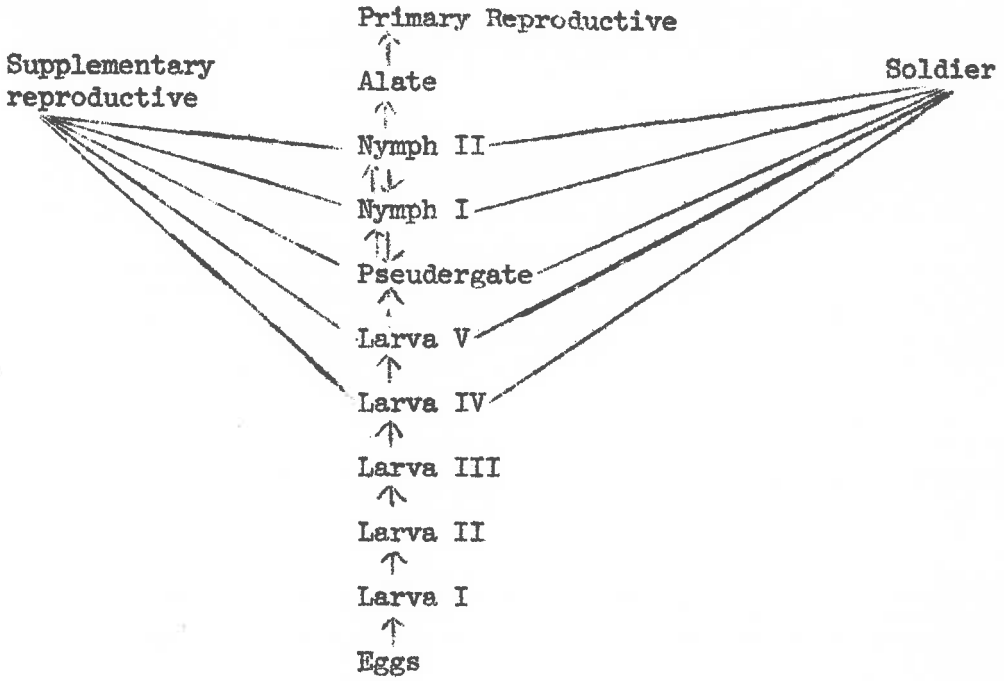
in them by phenomena such as hyperactivity and hunger.

1.13 Development pathways in the "Lower" termites

In social Hymenoptera, males are haploid and workers are imperfect females that may not mature sexually. In the Honeybee, the absence of a functional Queen, may result in ovarial development in some workers. Since these may not mate or are unable to mate their progeny will be males and haploid. In the Isoptera, any individual may develop into a diploid sexually mature form as indicated above but this line of development may be interrupted in certain instars when final-form, sterile, diploids develop.

The differentiation of castes in "lower" termites is better explained by the "extrinsic theory". The development of an individual from egg to alate involves about nine instars, development during the first four instars being similar but from the fourth instar onwards sexual maturity and maturity to sterile castes is possible. While supplementary reproductives and soldiers may develop from individuals of the fourth larval to second nymphal instar, alates only develop from second stage nymphs. The possible developmental pathways of an individual in the "lower" termites with special reference to Kalotermes flavicollis are shown in Figure 1. The diagram indicates not only development but also where "regression" may occur. The pseudergate may continue to moult without development to a "higher" instar.

FIGURE I.



1.2 Distribution and attack patterns of Porotermes adamsoni (Froggatt)

Porotermes adamsoni is confined to areas of south of Queensland, the coastal belt of New South Wales, the Australian Capital Territory, southern and eastern Victoria, South Australia and Tasmania. In South Australia and Tasmania it occurs from sea level to about 2000 ft elevation but in Eastern Australia it is most common in forests at higher altitudes (Ratcliffe et al., 1952).

It may cause the most serious damage to alpine forests in New South Wales, Tasmania and Victoria. When the termite attacks a tree, usually the entire centre of the tree is eaten and replaced by faecal material. (Greaves, 1959; Greaves et al., 1965; Hill, 1942; Gay and Calaby, 1970). It may attack green and dead wood of living trees, decaying logs and timber (Ratcliffe et al., 1952; Gay and

Calaby, 1970).

Alates appear in field colonies from late December to early February. They fly during the early evening. Supplementary reproductives are found in field colonies especially those with extensive and diffuse gallery systems (Gay and Calaby 1970).

Greaves (1962a) felled about 18 infested trees in two different forest reserves but only 2 contained large colonies. He therefore suggested that the colonies either grow slowly or are reduced by predators such as ants.

During the first two years of the development of laboratory colonies only 42 pairs out of 100 survived at 78°F (25.5°C) and only one pair produced brood. At 60°F (15.5°C) on the other hand 73 pairs out of 101 survived and 52 of these produced brood. After one year, 2 pairs had produced brood in 78°F (25.5°C) and 8 pairs in 60°F (15.5°C). Colonies of P. adamsoni were therefore considered to grow slowly (Greaves, 1962b, 1963).

2.0 MATERIALS AND METHODS

2.1 General:

Separation of individuals from the nest or substrate is a first vital step in the development of culturing techniques suitable for the studies designed. The method of Gay et al. (1955), which is simpler and more successful than other methods, involves breaking up the nest covering the exposed termites and debris with paper to which they cling and from which they can be dislodged easily into a clean container.

The undamaged and active individuals can then be selected and brushed into smaller containers containing the food supply upon which they are to be cultured.

Laboratory cultures have been kept in small containers so that fungal growth could be controlled by the termites (Becker, 1969). To allow easy observation with minimum disturbance to the termites, one either cultures them between glass plates or in petri dishes (Adamson, 1941; Luscher, 1949; Sampaio, 1963; Watson et al., 1972). The Jucci-Grassé tube is also used. This consists of either a test-tube or boiling-tube with a hole in the bottom (Hickin, 1963).

The cultures are fed on wood which has been attacked by fungus, especially brown-rot Basiodiomycetes such as species of Lenzites and Polyporus. The fungi apparently increase the nutritional value of the wood by providing essential nutrients like vitamins (Esenther et al., 1961; Lund, 1959; Becker, 1969). Agar-sawdust mixture has also been used successfully to maintain cultures (Light and Weesner, 1947).

Almost all termites require high microclimatic humidities. Laboratory cultures are therefore well-watered although excessive moisture is avoided. The cultures are also maintained in a humidity control room or container (Hickin, 1963, Becker, 1969).

2.2 Collection and Storage of Colonies

All the termites used for these studies came from Second Valley Forest Reserve in South Australia. The forest is approximately 8,000 acres (4,000 hectares) of Pinus radiata planted in an area originally

covered by several species of Eucalyptus including E. baxteri. At the time of study, the area contained variously aged pine plantations, eucalypt stands native scrubland and pasture. It is within 3 km of the sea and is on hilly country ranging in altitude from about 100 to 500 m.

Logs containing colonies of P. adamsoni were brought into the laboratory, sawn into pieces and stored in 44 gallon drums with open tops. Mixing of colonies was avoided by ensuring that each drum contained only pieces from the same log. Dishes of water in the drums maintained desirable humidities. The drums were not tightly closed to allow ventilation.

2.21 Collection of Termites from logs

When insects were required for experiments the log was split and the termites were shaken into a plastic tray. Separation of the termites from debris in the tray was based on methods of Gay et al. (1955).

The termites were then divided into a series of samples in 14 cm petri dishes. When these dishes were inverted and placed above another 14 cm petri dish, undamaged, active termites would move hurriedly into the lower dish and all slow-moving termites could then be removed by hand. This process was repeated with all samples so that only the most active and therefore, presumably, healthy termites were used in experiments. The number required for each experimental group was selected by random sampling from bulk cultures, those assigned to treatments and controls being chosen randomly from the groups of sub-cultures set up in 9 cm petri dishes. These, in turn, were placed in

whichever of the culture vessels was appropriate to my purpose.

2.3 Culturing Techniques

A number of culturing methods were tried initially including glass plate (Adamson, 1941; Lüscher, 1949), glass vials (Light and Weesner, 1947) and petri dishes. Various substrates such as saw-dust-agar mixture filter paper and wood were used either alone or in combination. Once successful handling of P. adamsoni was obtained, rearing was possible by a number of techniques. However Jucci-Grasse' tubes and petri dish culturing using wood taken from natural infestations proved most useful. One feature of the Jucci-Grassé tube was that the diameter of the hole made at the bottom was critical and had to be varied with the size of the tube used (Table 1).

TABLE 1. The different size of tubes (used to culture termites) with their corresponding weights of cotton wool and sand placed at the bottom of each tube.

Tube	Size		Wt of cotton wool	Wt of sand
Length	Diameter	Volume		
15.3cm	1.3cm	25cc	0.43 g	3 g
15.3cm	2.6cm	65cc	1.2 g	8 g
20.4cc	2.6cm	85cc	1.5 g	10 g

Initially the bottom of the tube was filled with a plug of absorbent cotton wool with sterilised washed sand above it. The hole at the bottom of the tube was placed in a beaker of distilled water

until cotton plug was just moist. The sand was then gradually moistened by water from the damp cotton wool. Then sterilised slices of wood, from the log which contained the termites' being used in the experiment, and measuring 4 mm thick but varying in length and breadth according to the size of tube, were pushed into the sand so that only about 10% of the piece was buried. Termites were put into the tube and a damp pad of absorbent cotton wool pushed into the top half of each of the different sized tubes. Each damp pad was in contact with the wood but did not block the tube. The tube was then plugged with dry cotton wool ensuring that it did not touch the damp cotton wool below.

When the culture was drying out, which could be detected by examination of the damp plugs, the bottom of the tube was held in a beaker of distilled water for a few seconds until the lower plug was just moist. A few drops of water were also added to the upper pad.

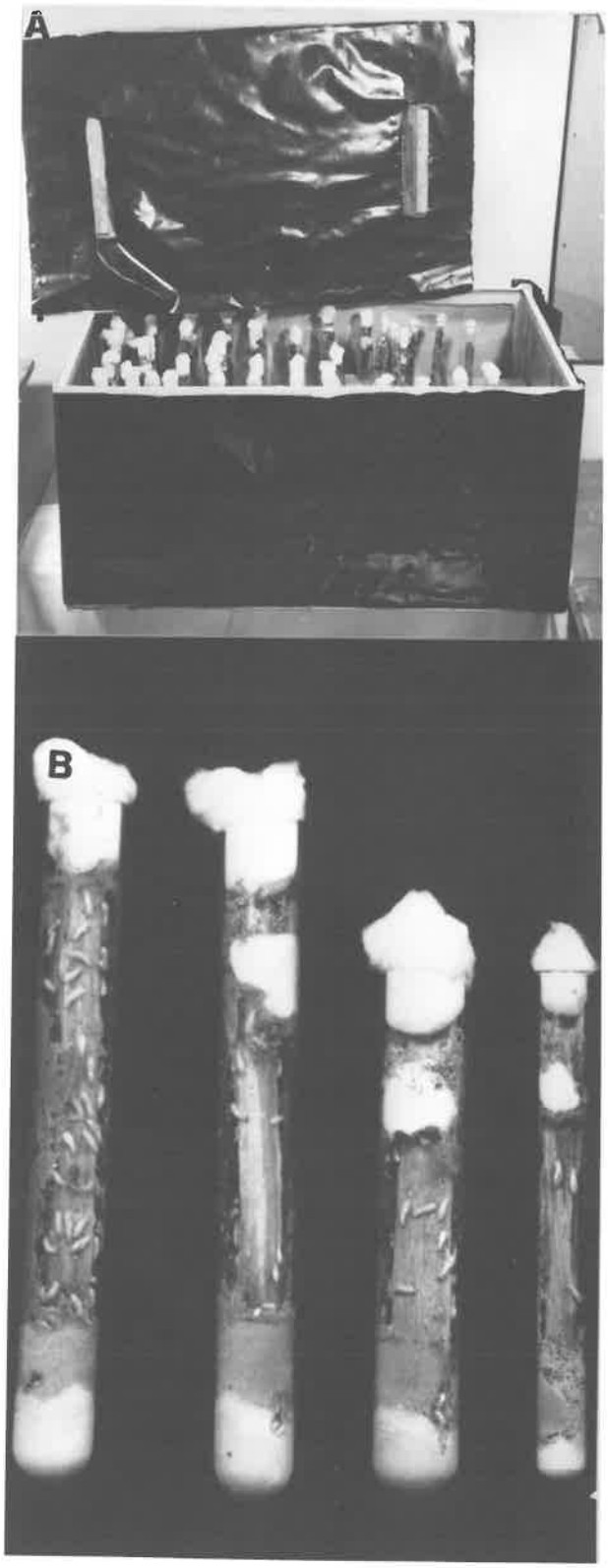
Cultures were kept on shelves in glass aquaria, 76.3 x 48.4 x 32.8 cm in dimension which each contained 12 litres of tap water below the shelf. A glass lid covered the container. The whole system was covered on the outside with black polythene sheeting. The culture tubes were supported in an asbestos board holder (Figure II).

Some cultures were also kept in 9 cm petri dishes. The bottom of the dish was covered with filter paper discs. A block of wood from the appropriate infested log and measuring 8 cm x 4 cm x 4 mm was placed on the filter paper and drops of water added to the top of the wood. This technique was used in the experiments with primary reproductives and those concerned with the development of supplementary reproductives

Figure II(i). Techniques for culturing *Porotermes adamsoni*.

A. Glass aquarium for holding cultures.

B. Various sizes of Jucci-Grassé tubes.


A
B

where supplementary reproductives were marked with nail polish as they differentiated. Different colours of nail polish were used and the cultures were observed daily. This made it possible for individual supplementary reproductives to be observed as required. The wood in the cultures of primary reproductives had a 2.5 cm x 1.5 cm hole made in its centre to serve as a nuptial chamber. After the alates had been introduced, the artificial nuptial chamber was covered with a microscope slide which inturn was covered with a block of wood. A pad of moist absorbent cotton wool was maintained at the side of the wood.

These cultures were also held in glass aquaria as previously described. All experimental cultures were maintained at 25°C unless otherwise stated.

3.0 THE BIOLOGY OF POROTERMES ADAMSONI

Flight and subsequent colony foundation were studied in the laboratory to obtain some evidence on the development of primary colonies in this species. The habitat and the structure of the populations of colonies in the field were also studied in an attempt to correlate field and laboratory colony development. In addition, general rearing in the laboratory provided information on the incubation period, the number of immature stages and on the proportional development of the castes.

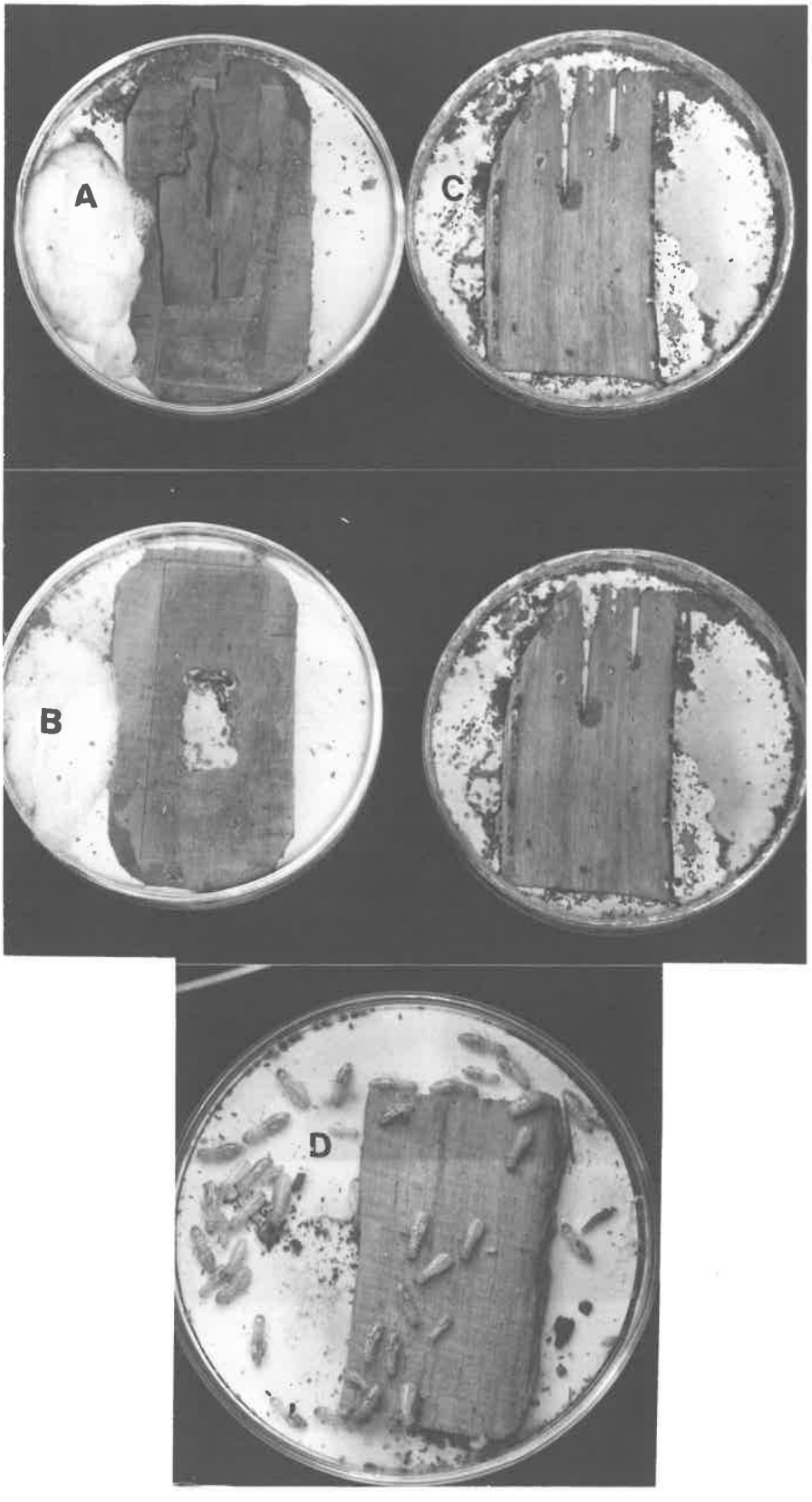
In most hodotermitids the alates fly from colonies in the evening or night and following the shedding of the wings typical tandem pairs may form. These pairs crawl into cavities in decaying wood particularly at the point of contact with the ground. A nuptial chamber is formed

Figure II(ii). **A. Primary reproductive culture with the nuptial chamber covered.**

B. Primary reproductive culture with the nuptial chamber expose.

C. Supplementary reproductive culture with individuals sealed underneath the block of wood.

D. Supplementary reproductive culture with individuals exposed.


A
C
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D

and, after several weeks or months, the first eggs are laid.

3.1 Flight and Colony Establishment by Porotermes adamsoni

Mature colonies containing well developed nymphs were collected in the field. The nymphs developed into alates in the laboratory and were used for studies on flight and post-flight behaviour. Observations in the field were associated with laboratory experiments in an attempt to correlate the two lines of evidence.

Alates were flown in groups of 20 in a cardboard chamber 52.2 x 33.2 x 35.7 cm in dimension and provided with a glass cover. When alates with shed wings formed tandem pairs they were collected in 7.7 x 1.3 cm tubes. Sex was determined by immobilising them at 0°C for 3 minutes. The majority of pairs consisted of a male and a female so they were set up in the petri dish cultures described in 2.3 above. The few pairs that were unisexual were separated and allowed to pair with members of the opposite sex and then placed in the prepared petri dishes. About half of the cultures were kept at 25°C and about a half at 20°C in constant temperature rooms. All cultures were observed daily for the first six months of their development then five cultures at 25°C were observed daily and the rest were observed weekly.

Five field colonies in an open area and five in a shaded area of the forest were observed regularly over three years to follow the development of alates. Two colonies in decaying Eucalyptus stumps in the open area produced alates; one of these produced alates each year for three years. Light traps were set up on 16/1/73 near a stump

with alates in an attempt to catch them during their mating flight.

Nymphs in an advanced stage of development towards the alate caste appeared in the field colonies in early September and the alates appeared in early January. Mature alates were caught in one trap on 19.1.73. The colony which had included alates was examined on 21.1.73 and as no alates were found, presumably all had left the colony in one flight.

Only two out of 10 colonies observed regularly for the development of alates, developed alates and only 5 field colonies out of 40 examined, were headed by primary reproductives. Most had several pairs of supplementary reproductives. A pair of dealates were also collected from the bottom of a log within a nuptial chamber. They had no brood. The small number of colonies which developed alates or were headed by primary reproductives seemed to indicate that the supplementary reproductives might be of greater relative importance in this than in other species. New colonies are initiated by primary reproductives only following the flight period. Supplementary reproductives may establish new colonies at any time of the year and this may explain the high proportion of colonies headed by supplementary reproductives in the area of study. Scarcity of alates in colonies has been reported in Reticulitermes flavipes and R. lucifugus (Harris 1956). Buchli (1958). has suggested that new colonies may not usually be started by alates in R. lucifugus. Nevertheless it would appear that in such termites as P. adamsoni the alate role is to disperse the species while the supplementary reproductive increases the size of and maintains the

colony.

The alates of P. adamsoni form clusters in surface galleries and when removed aggregate under pieces of wood. When introduced into the flight chamber singly or in small groups they started to fly. After short flights sometimes interspersed with landing and crawling most landed and shed their wings. This was done, in the main, quickly by catching the wing on the wall or floor of the chamber and turning sharply. Some did not shed all wings and a few kept one or two of their wings for several hours after completing flight.

3.2 Colony Development

After establishment within prepared nuptial chambers, the pair started feeding. There was mild cannibalism towards partners in some cases, antennal segments of partners being damaged and eggs eaten. Mating was not observed. Both partners took part in caring for the first brood which was usually small in number. The reproductives groomed the larva as it hatched and appeared to assist in the release of the larval mouth parts and legs which were still adhering to the body. The development of five colonies with a total of 10 eggs were followed in a constant temperature of 25°C. The stadium considered to be the time from the appearance of one instar to its next ecdysis was measured for the first three larval instars. Their respective head-widths are given in Table 2. The first two larval instars were fed by the reproductives but the third instar appeared also to feed itself as well as accepting food from its parents. The fourth instar was

TABLE 2. The duration of the early stadia and size of each instar* in Porotermes adamsoni determined from individual rearings of eggs and larvae at a constant temperature of 25°C.

Stadium	Duration (Days)		Size (mm)	
	Mean	Range	Mean	Range
Egg	36.4	25-45	1.36 x 0.56	1.48 x 0.62 - 1.32 x 0.49
I	10.8	8-13	.64	.60 - 0.68
II	13.1	7-23	.86	0.83 - 0.93
III	47.5	36-61	1.03	0.96 - 1.17

* Relative size = Diameter and length of egg or width of headcapsule of larva respectively.

active, completely fed itself and took part in the construction of the nest.

No soldiers developed in any of the cultures in the first year of development. This has also been reported for R. lucifugus and R. hesperus (Light and Weesner 1955) Stolotermes ruficeps (Morgan, 1959) and Cryptotermes brevis (McMahan, 1962).

Attempts were made to determine the number of instars for P. adamsoni by measurement of headwidth of a range of immature and mature forms. A combination of headwidth measurement and antennal segment and a combination of headwidth measurement and molar plate ridges on the right mandible were also tried as characters useful for this purpose. Whilst none of these proved completely satisfactory, there was a strong correlation between headwidth and the number of molar plate ridges (Fig. III). All nymphs measured had 16 or more molar ridges and larger larvae also overlapped into this range.

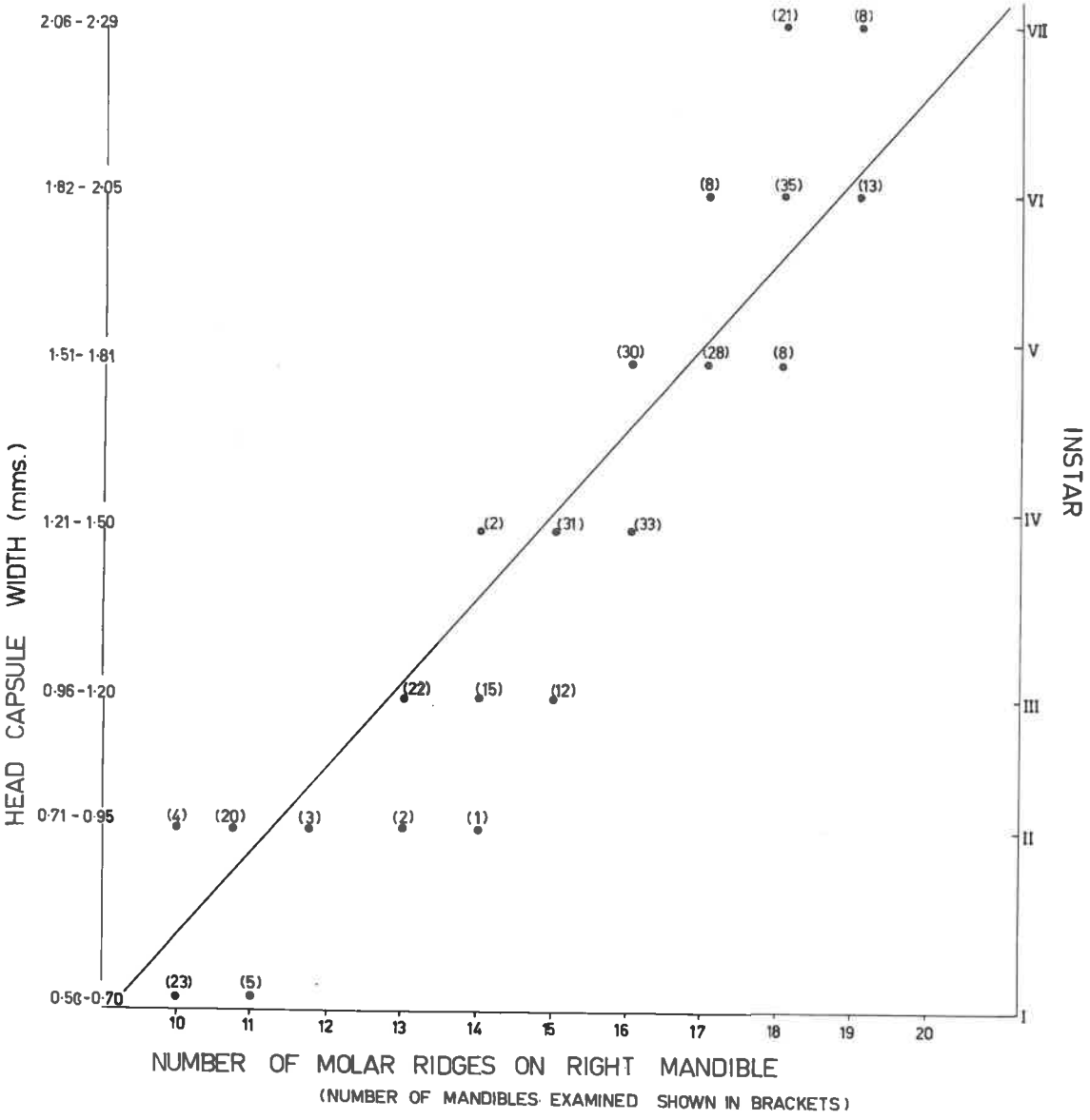
Although overlap occurs between the number of molar ridges in the instars (Fig.III) the values indicate a straight line relationship. This is probably more related to the size of the individual jaw than to the instar per se. That is, in the jaws of instar I, most individuals will have 10 molar ridges though some of the larger sized termites may have 11 ridges. Instar II, on this basis, is more variable in size than the others and though most have 11 ridges the range is 10-14. The data does indicate that in P. adamsoni the basic number of larval instars is seven such as has been found in Zootermopsis (Castle, 1934) and Stolotermes (Morgan, 1959). However, the pseudergate (which may moult several times without further biological development), the regression of larvae and nymphs from more advanced stages and end-line development of supplementary reproductives and soldiers, all introduce instar-complexity relative to the moults completed. On the basis of my data and observations the following may represent usual relationships:

TABLE 3. Individual stages and their probable instar in colonies of P. adamsoni.

Form	Instars Likely
Nymphs	VI - IX
Larvae	I - VII
Soldiers	V - VII
Supplementary Reproductives	V - IX
Pseudergates	V
Alates	VIII - X

Figure III. The relationship between the head-capsule width of instars of *P. adamsoni* and the number of molar ridges on their right mandibles.

(Instars I-III) values were from actual measurements on reared specimens - Instars IV-VIII obtained from application of Dyars Low modified to the values obtained for the first three instars.


HEAD CAPSULE WIDTH (mms.)
2·06 - 2·29
1·82 - 2·05
1·51 - 1·81
1·21 - 1·50
0·96 - 1·20
0·71 - 0·95
0·56 - 0·70
INSTAR
VII
VI
V
IV
III
II
I
10
11
12
13
14
15
16
17
18
19
20
(21)
(8)
(8)
(35)
(13)
(30)
(28)
(8)
(2)
(31)
(33)
(22)
(15)
(12)
(4)
(20)
(3)
(2)
(1)
(23)
(5)
NUMBER OF MOLAR RIDGES ON RIGHT MANDIBLE
(NUMBER OF MANDIBLES EXAMINED SHOWN IN BRACKETS)

3.3 Habitat, Structure and size of mature colonies in the field

3.31 Habitat

Porotermes adamsoni was found in damp decaying logs and stumps on the forest floor Fig. IV. The species does not construct a nest as do the higher termites but rather excavates a series of tunnels in the wood. The inhabited tunnels were not localised but rather would ramify through the whole infested log. Termites were found at times to be in contact with the ground, in litter on the ground directly below logs or in wood in contact with or buried in the ground. In some cases they occurred in fairly deep roots of dead trees or stumps and some appeared in galleries in soil from which they emerged to attack wood in contact with the ground.

Hill (1942) and Greaves (1959) have reported that this species causes damage to living trees but no evidence of this was found in these studies. Although there were fallen and rotten logs and stumps of both P. radiata and Eucalyptus spp. in the study area, P. adamsoni was mostly to be found in old decayed logs and stumps of Eucalyptus, more rarely in pine logs and none were found in pine stumps. Other termites associated in the study area were Coptotermes acinaciformis (Froggatt), Microcerotermes serratus (Froggatt) and Nasutitermes exitiosus (Hill).

3.32 Structure and Size of Mature Colonies

A large number of Porotermes colonies were examined in the field during the study and most contained several supplementary reproductives

Figure IV. The floor of matured *Pinus radiata* forest.

a) Upper photograph: an infested decaying *Eucalyptus* stump.

b) Lower photograph: infested decaying *Eucalyptus* logs.

and a majority of larger larvae and nymphs. Sometimes supplementary reproductive females were less than 15 cm apart and within what appeared to be open connected galleries. Few obvious centres of reproduction containing eggs and young larvae were recorded which suggested that the reproductives either left these to wander in the galleries or produced brood at intervals.

Three colonies in isolated logs were collected from the field on 9/12/72 and a fourth was collected on 20/1/73. The wood in which each was located was chopped up and all individuals extracted and counted.

All four colonies were small (Table 4) relative to the colonies of higher termites. Colonies of Nasutitermes exitiosus (Hill), for example, may each have more than 2.5 million termites (Gay and Wetherby, 1970). However the counts for P. adamsoni are comparable with those reported for other lower termites such as Cryptotermes havilandi 3,000 (Wilkinson 1962); Pterotermes occidentis 2,911; Paraneotermes simplicicornis 1,394; Zootermopsis laticepts 2,367 (Nutting 1969).

Over 90% of the population in P. adamsoni colonies consisted of larvae and nymphs and the soldier to non-soldier ratio was 1:22 (range 1.10 - 1:41). The ratio of larvae and nymphs to reproductives was more variable than for soldiers (498:1; 373:1; 2518:1 and 51:1). None of the colonies had primary reproductives and only one supplementary reproductive was collected from colony 3. It is possible it was headed by a pair of supplementary reproductives, one being lost in extracting the members of it. Since there was variation in condition of wood it would appear that the development of the dependent castes (soldiers

TABLE 4. The size and caste-structure of field colonies of Porotermes adamsoni at Second Valley Forest Reserve South Australia. (conditions of logs given below)*

Colony No.	Larvae and Nymphs	Soldiers	Reproductive ♀	Reproductive ♂	Total
1	3,487	209	6	1	3,703
2	1,121	117	2	1	1,241
3	2,518	112	1	0	2,631
4	2,052	51	23	17	2,143

* Conditions of logs infested.

Colony I. Log was damp and in advanced stage of decay. Small pieces would crumble on squeezing between fingers.

Colony 2. Decayed log but would not crumble on squeezing between fingers. It was slightly damp.

Colony 3. Log was similar to that of Colony I but was very damp.

Colony 4. Log was in a very advanced stage of decay but was very dry.

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and reproductives) may be influenced by environmental conditions. Data here is insufficient to form valid conclusions on this. Although the colonies were collected during the summer months, about the time alates appear in field colonies, none contained alates. In estimates of this kind, where the assumption made is that isolated groups including

reproductives, represent the entire colony, may not be valid. Such isolated groups may well represent parts of a colony, the main breeding centre of which, could be in another log or stump adjacent to or even some distance from the site examined.

As groups that contained alates during January were all in stumps, one is forced, without much more intensive effort, to conclude that the whole colony of P. adamsoni may not be located in one piece of wood. The observations made and data given in Table 4 could well be in error if established old colonies of P. adamsoni release alates each year. Again, my observations tend to indicate that they do not, but, because of the complexities of the field situation, no definite stand on this is currently possible. Likewise, the absence of primary reproductives and the presence of supplementaries in most logs examined may mean only that I was examining sub-colonies and that these may well form an active component of the whole colony and contribute nymphs to the total alatae released by that colony.

3.4 Moulting Time

I noted in early studies that the time taken from cessation of feeding to completion of ecdysis appeared to vary. By marking individuals and noting the time taken from evacuation of the alimentary tract to completion of the subsequent moult, I was able to show that not only the mean time but also the range about the mean varied, depending on whether the larva moulted to another larva or nymph or whether it developed into a reproductive. The results (Table 5) show that a larva to larva or larva to nymph moulting time is much longer than a larva to supplementary reproductive moulting time.

TABLE 5. Time taken to moult in P. adamsoni.

Form Moulting	Form Developed	Time in Days	
		Mean	Range
Larva	Larva/Nymph	7.0	1 - 11
Larva	Supplementary Reproductive	4.2	3 - 10

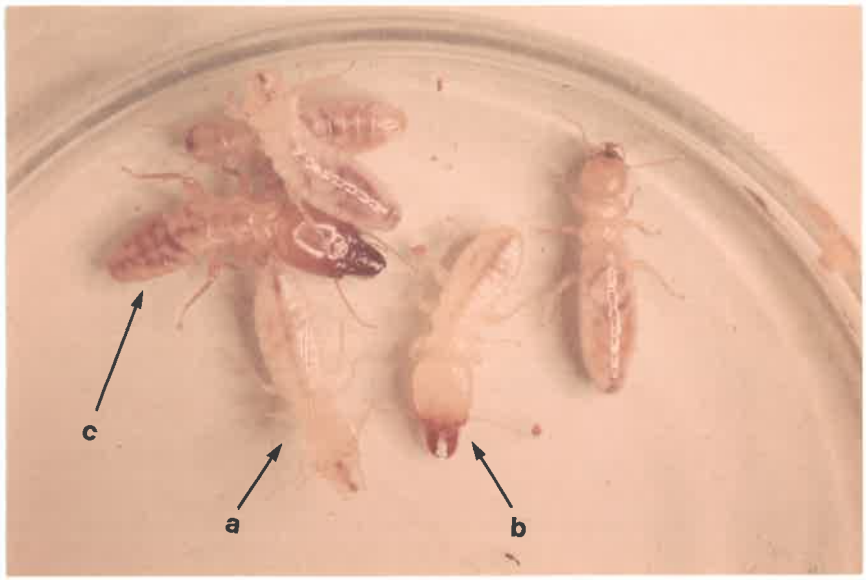
In soldier-development, two successive moults from the larva are involved. The first produces the so-called, white soldier, its head being smaller than but similar in shape, and in the formation of the jaws, to that of mature forms. The second moult results in the typical-sized head and colour. Darkening begins with the mandibles and proceeds backwards to the occiput region of the head capsule. (Fig. V)

Figure V. The various stages in the development of a soldier (see text).

a) First stage (white) soldier.

b) Second stage soldier with darkened mandibles.

c) Fully matured soldier.


c
a
b

4.0 EFFECTS OF TEMPERATURE AND TIME ON DEVELOPMENT OF COLONIES

The development of termite colonies from paired reproductives or dealates is influenced by a number of factors, particularly nutrition and temperature. Greaves (1963) found that more primary reproductives of P. adamsoni survived and produced more brood at 15.5°C than at 25.5°C. It therefore seemed appropriate to define, in a more precise way, the effect of temperature on the development of colonies of the species.

The temperature of galleries in a log held in a constant temperature of 25°C, was measured. Under these conditions, temperature in the galleries varied slightly about a mean of 24°C and the termites appeared to be behaving in a normal way.

It was also noted that cultures behaved in a similar way at 15°C to that at 25°C. Therefore, to test Greaves' results and to define an optimum range for P. adamsoni I chose the range 15°C to 28°C because it was available and also because it covered the known temperatures at which the species had been reared with some success.

4.1 Materials and Methods

Groups of 100 larvae and nymphs were cultured in 83 cc Jucci-Grassé tubes. Seven randomly selected replicates (cultures were maintained at each of the following temperatures: 15°C, 20°C, 25°C and 28°C. Preliminary study had shown that this would result in about four replicates in each group surviving the period of the experiment. The cultures were observed daily and as each supplementary reproductive appeared the date was recorded. Numbers of brood produced were recorded

on the 50th and 75th days.

4.2 Results and Discussion

Results of experiments on the effects of temperature on the formation of supplementary reproductives are presented in Table 6 and indicate a strong influence of temperature on the time taken for such reproductives to differentiate.

TABLE 6. The effect of temperature on the time of formation of first supplementary reproductives. (Mean days for 7 replicates).

Temperature °C	Mean days for first reproductive to form	Range of days for first reproductive to form
15	33.6	14 - 39
20	24.1	22 - 27
25	19.9	17 - 24
28	15.9	13 - 19

A regression equation was calculated for the appropriate values and a regression line fitted by the method of least squares (Fig. VI). The F value for the regression was highly significant ($P < .001$).

No soldiers were added to the original cultures and at the end of the experimental period, one culture each in 20°C and 25°C and two cultures in 28°C rooms had produced soldiers. None of the cultures in the 15°C room produced soldiers. Thus it appeared that in the time of this experiment complete colonies (larvae, reproductives, eggs and soldiers present) formed at all temperatures except 15°C.

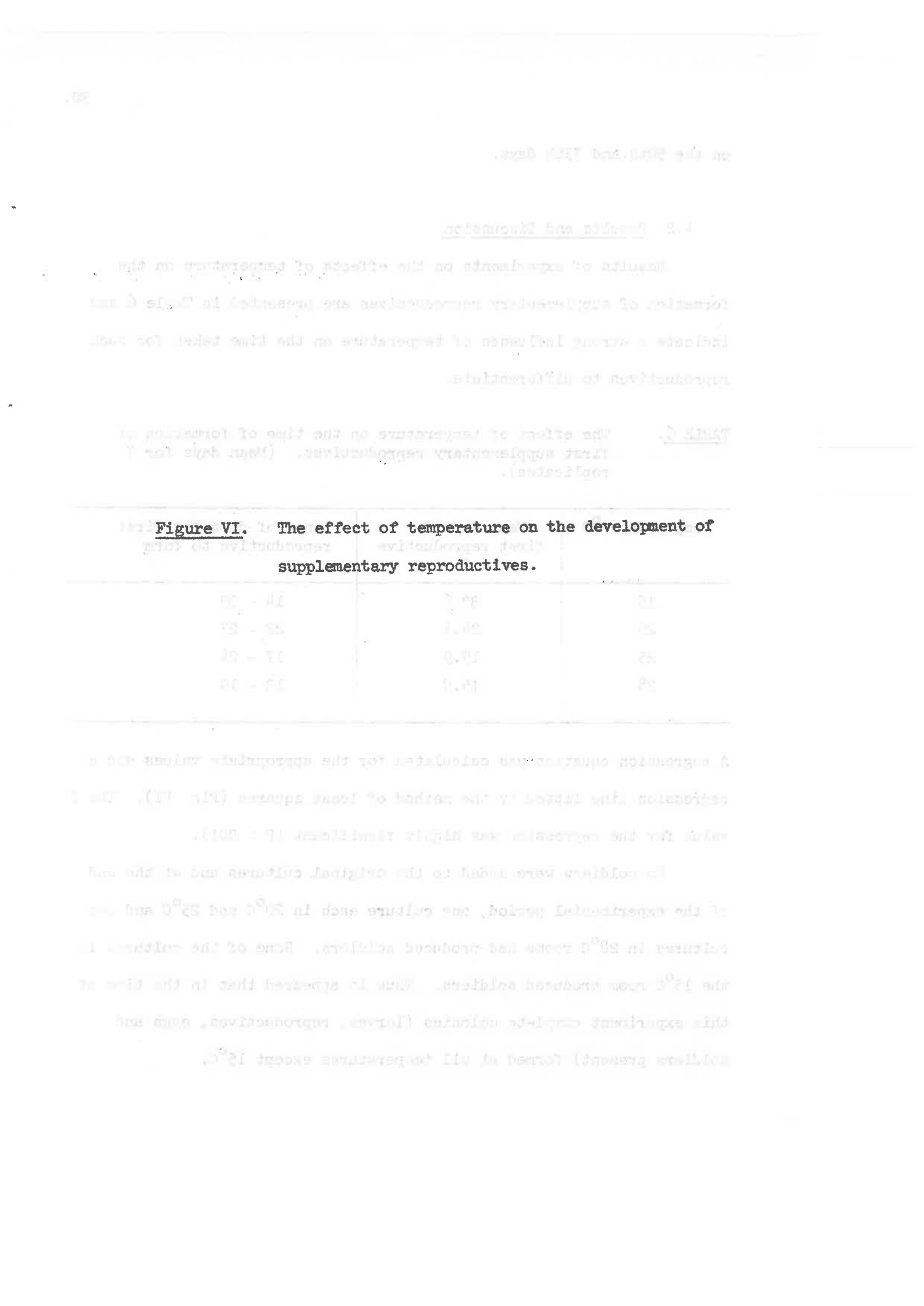
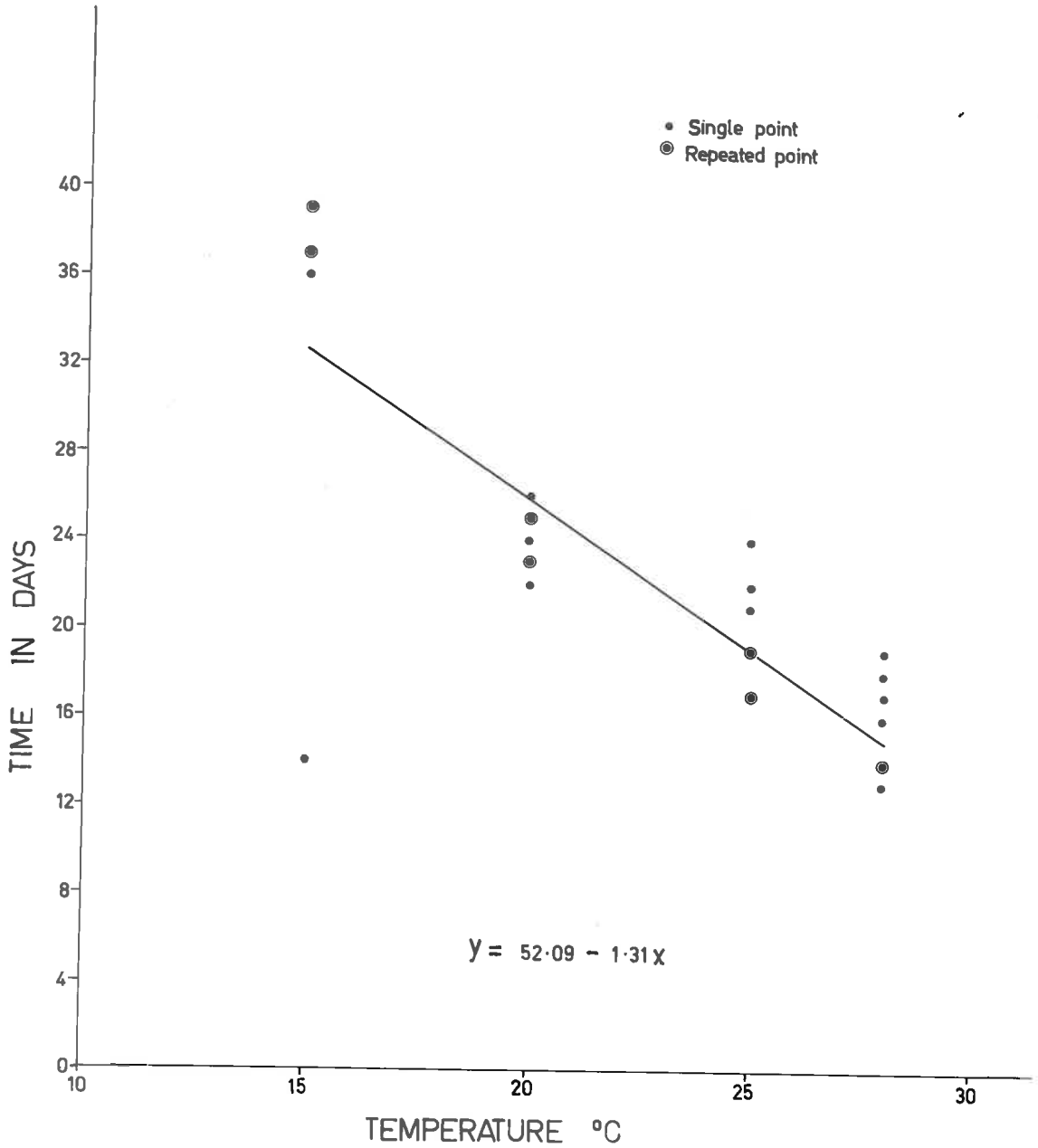


Figure VI. The effect of temperature on the development of supplementary reproductives.


Single point
Repeated point
TIME IN DAYS
0
4
8
12
16
20
24
28
32
36
40
10
15
20
25
30
TEMPERATURE °C
y = 52·09 - 1·31 x

The effect of temperature on the production of brood by supplementary reproductives is shown in Table 7.

TABLE 7. The number of progeny produced by supplementary reproductives that developed in random cultures of 100 larvae and nymphs, showing the effect of temperature on production of brood. (Period of experiment = 75 days)

Temperature °C	No. of surviving cultures	Mean number of brood/culture (Range in brackets)
15	5	3.6 (0 - 6)
20	4	4.0 (2 - 6)
25	4	6.8 (4 - 13)
28	4	0

None of the cultures had produced brood by the 50th day. At this time, one culture was dead in each of the 15°C and 25°C groups but none of those in the 20°C and the 28°C groups had died.

By the 75th day cultures held at 25°C had produced most brood but none of the 28°C cultures had produced any brood. Four out of five cultures held at 15°C produced brood and all cultures at 20°C and 25°C produced brood. After the cultures had been opened, examined and re-established on the 50th day, some died, probably due to the effects of the disturbance. Nevertheless, the numbers of cultures that survived were about what was expected and were sufficient for my purpose.

The results of these experiments showed that development of supplementary reproductives occurred at all temperatures tested but that the time taken for the first supplementary reproductive to develop

decreased with increasing temperature. On the other hand, brood production was inhibited at 28°C and was apparently optimum at 25°C. This temperature was therefore considered most suitable for future experiments.

The survival of cultures was similar for all temperatures and indicates, very strongly, the need to allow for about a 33% loss of young colonies when designing experiments of this kind.

5.0 THE NUMBER OF EGGS PRODUCED BY YOUNG PRIMARY REPRODUCTIVES AND NEWLY-MATURED SUPPLEMENTARY REPRODUCTIVES

A number of experiments of this kind have indicated that pairs of dealates lay fewer eggs than supplementary reproductives of about similar maturity. This comparison, however, is not realistic since the latter are cared for by varying numbers of larvae and nymphs whereas the primary reproductives feed themselves, build the nest and care for their progeny. Nevertheless, I designed a series of experiments to see what the differences were in young colonies of both kinds, and to determine how long primary colonies took to reach the same levels of fecundity recorded for supplementary colonies.

Using previously determined parameters and cultures obtained from laboratory-induced flights of alates and random selection of nymphs, I placed about half of each group at each of the temperatures 20°C and 25°C and examined them at appropriate times when oviposition should have occurred.

5.1 Materials and Methods

Twenty-six pairs of dealates in prepared nuptial chambers in wood within petri dishes were cultured at a constant temperature of 25°C and twenty similar cultures were placed in a room held at 20°C. Due to shortage of older larvae and nymphs only ten cultures of fifty individuals with supplementary reproductives could be established at each of the temperatures selected. The only difference in the method of the establishment of these cultures was that no nuptial chamber was constructed in the wood supplied.

All cultures were assessed for brood produced at the end of three months. Then the surviving primary colonies were allowed to continue development for a further nine months to determine their variation in fecundity with time. They were assessed at intervals of three months. Unfortunately all of the supplementary colonies with supplementaries were lost after 3 months so that continuous comparisons could not be made.

5.2 Results and Discussion

The data derived at the first assessment of both primaries and supplementaries (Table 8) supports that reported by others (Light, 1934; McMahan, 1962) and shows that w :le 15% to 25% of primary colonies produced brood, 50% or more of the supplementaries produced more brood in the same time. The results also indicated that 25°C was more satisfactory for development of colonies than 20°C, thus supporting my earlier data. The difference between the brood produced by two types of

TABLE 8. Comparison of broods produced at two constant temperatures by primary reproductives and supplementary reproductives.

Age of Culture (months)	Primary reproductives initially without larvae and nymphs				Supplementary reproductive cultures, each culture initially with 50 larvae and nymphs			
	No. of cultures with brood		Mean No. of Brood/culture		No. of cultures with brood		Mean No. of Brood/culture	
	20°C	25°C	20°C	25°C	20°C	25°C	20°C	25°C
3	4	5	1.25	1.60	5	5	1.00	11.00

cultures is probably the result of better nutrition of the supplementaries combined with the fact that they are not required to construct the nest or care for the young, as are primaries.

The production of brood by the surviving primary cultures for six, nine and twelve months is shown in Table 9.

TABLE 9. The effect of temperature and time on brood production by primary reproductives.

	20°C		25°C	
Age of Culture (months)	No. of cultures with brood	Mean Brood/culture	No. of cultures with brood	Mean Brood/culture
6	4	1.25	5	1.60
9	13	9.00	5	1.60
12	14	8.40	5	1.60

While there was no change in the cultures at 25°C, distinct increases both in number of cultures with brood and in the average number of brood per culture were recorded at 20°C up to nine months but the trend did not continue to twelve months. There is little doubt that pairs of dealates develop colonies slowly and that even after a year only about half the pairs established will have produced progeny. In this time it is also unlikely that any soldiers or other developmental end-lines will be present in those with brood. Of interest is the indication that 20°C is more satisfactory to continued development of colonies of P. adamsoni than is 25°C.

Great difficulty was experienced in establishing isolated pairs

of supplementary reproductives, probably due to their induced dependency on foragers. Therefore a valid comparison between the two forms of reproductive in young cultures may be achieved by placing new dealates with older larvae and nymphs from the same colony. Unfortunately availability of dealates and time did not permit me to attempt this approach.

It would seem that both temperature and nutrition are extremely important to the commencement and continuation of colony-development, as one might expect, but the evidence from the small laboratory experiments I have described provides only a basis for more intensive studies.

6.0 EFFECT OF COLONY-SIZE ON THE DEVELOPMENT OF THE COLONY

The rate of development of colonies depends primarily upon the availability of food, satisfactory temperature and adequate protection from enemies. The nutritional level of the colony is related both to the quality and the quantity of food available to it. While the quality of food depends on the type of food material available to the species, the quantity of food would depend mainly on the number of individuals available to forage and the number that must be fed. In species that readily develop sub-colonies by supplementary reproductives, the number of reproducing sub-units that can be maintained is a factor of importance to the development-rate of the whole colony. In this regard the rapidity of maturation and the number of supplementaries produced may be a useful measure of the effects of certain factors on the rate of development of colonies. Grassé et al., (1950) have suggested that supplementary

reproductives probably form more quickly in larger than in smaller colonies but Luscher (1952b) claims that most individuals in smaller colonies transform into reproductives. This difference in view indicated wide variations in the Isoptera and I, therefore, set up experiments to determine the factors involved in the rate of differentiation and survival of supplementary reproductives in P. adamsoni. In these experiments the amount of food was varied according to the number of individuals initially placed in each culture-group. The experiments were designed to provide evidence on the time taken to develop mature supplementary reproductives and the number that could be supported by cultures of various sizes. I also wished to determine the optimum size of cultures for subsequent experiments.

6.1 Materials and Methods

6.11 Experiment I:

Randomly selected cultures with six replicates each of 20, 50, 100 and 200 large larvae and nymphs were set up in 25 cc, 65 cc and (for the larger numbers) 85 cc Jucci-Grassé tubes respectively. Each replicate consisted of termites from the same colony. The cultures were maintained at 25°C and examined daily and the day the first supplementary reproductives appeared was recorded. The number of supplementary reproductives surviving as well as the number of brood in each culture were recorded at the end of 4.5 months.

The results were analysed by regression and by the Kolmogorov-Smirnov test, whichever was appropriate.

6.12 Experiment II:

The above experiment was repeated with three replicates each of 50, 200 and 1600 large larvae and nymphs to test the effect of a thirty-two fold range in size of cultures on the development and survival of supplementary reproductives. Each replicate consisted of termites from the same colony and to provide similar spatial conditions, I placed the larger groups in 600 cc Jucci-Grassé tubes. The results of the experiment were assessed at the end of two months by recording the number of supplementary reproductives present.

6.2 Results and Discussion

6.21 Experiment I:

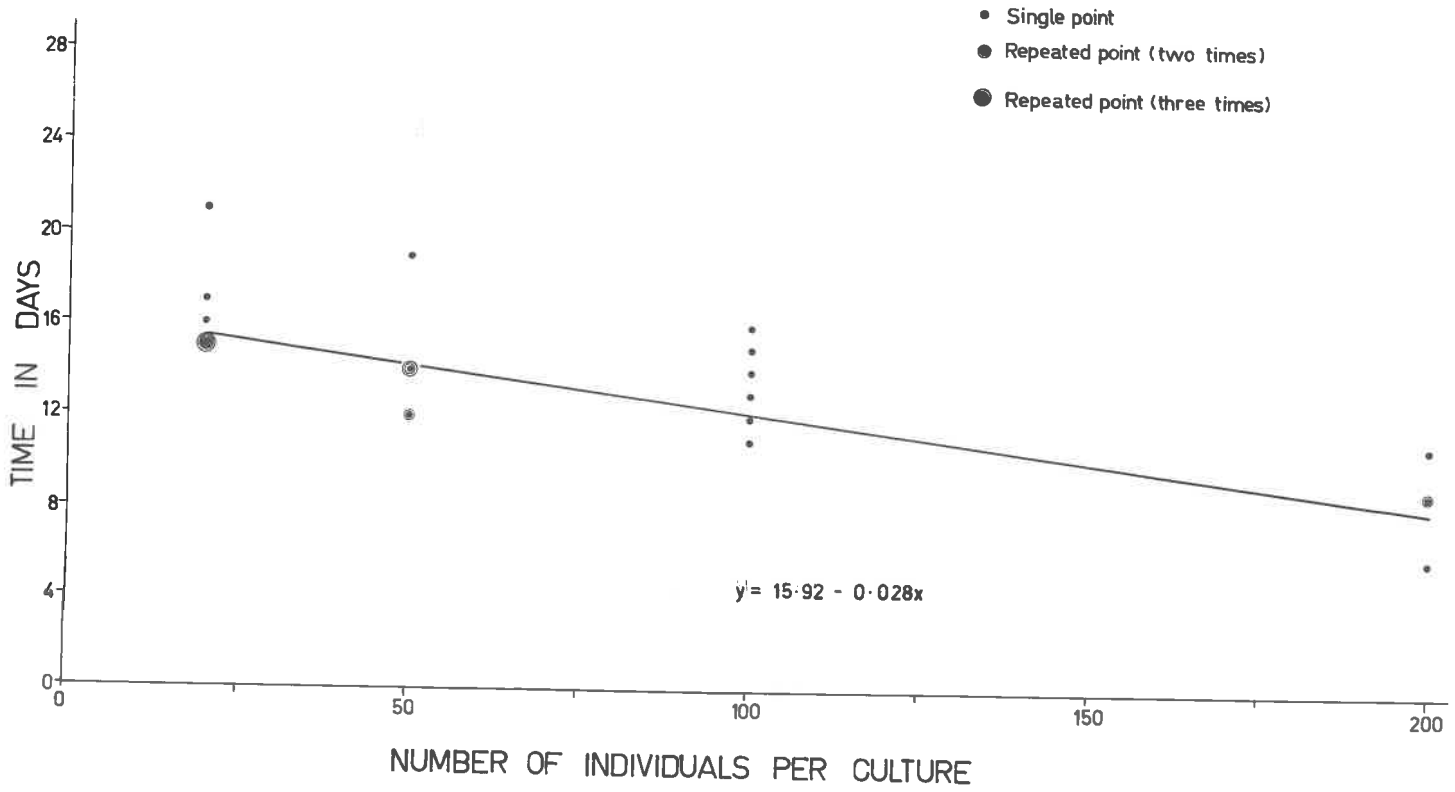
The results are shown in Figure VII and Tables 10 and 11.

TABLE 10. The effect of number of individuals per culture on the time taken for first supplementary reproductives to develop.

Number of termites per culture	Mean time for first supplementary reproductive to form. (in days)	Range for first reproductive to form. (in days)
20	15.5	13 - 21
50	14.2	12 - 19
100	13.5	11 - 16
200	10.3	6 - 13

The regression analysis (Figure VII) of the scatter diagram of the time supplementary reproductives took to develop in each culture-group

Figure VII. **The effect of the initial number of individuals per culture on the time taken for first supplementary reproductives to form.**


Single point
Repeated point (two times)
Repeated point (three times)
TIME IN DAYS
28
24
20
16
12
8
4
0
0
50
100
150
200
y = 15·92 - 0·028x
NUMBER OF INDIVIDUALS PER CULTURE

provided the line of best fit and the difference in time of development proved significant. The F value was highly significant ($P < .01$).

It can be concluded, therefore that the larger the culture the quicker the development of supplementary reproductives.

There was, however, no significant effect of the size of initial culture on numbers of supplementary reproductives produced under the conditions of this experiment. This would be expected as there must be a limitation on numbers of reproductives any colony can sustain and cultures of up to 200 individuals are probably able to maintain only a single pair of reproductives.

No soldiers were added to the original cultures and some cultures had produced soldiers at the end of the experiment. One culture in the groups containing twenty had produced one soldier; three in the groups of fifty had produced an average of 1.3; four cultures in each of the groups of one hundred and two hundred had produced an average of 3.3 soldiers.

It is clear that the larger the culture, the greater the number of brood produced (Table 11). These data show a higher survival rate of cultures than expected from previous studies and indicate that better comparisons might be obtained by having at least fifty individuals in each culture. There seemed to be no advantage in having more than one hundred individuals in each culture for experiments of this kind and this represents a saving, both in time, and in numbers of individuals required. It means also that one may increase the number of replicates when only one hundred individuals per culture are needed instead of

TABLE 11. Brood produced by culture of various sizes in 4 - 5 months from establishment. (Means for six replicates in each group)

Initial number of individuals per culture	Total number of brood produced	Number of brood produced per culture	Number of brood per initial individual per culture	Number of cultures surviving	Number of cultures that produced brood
20	3	0.6	0.03	5	2
50	70	11.7	0.28	6	5
100	292	58.5	0.58	5	5
200	488	97.6	0.49	5	5

larger numbers. On analysis the difference in brood produced by the culture groups of 100 or 200 was not significant.

It would seem that the rate of reproduction by young supplementary queens may be similar, and that this may be influenced by the number of foragers feeding each. This may continue until her potential is reached. Subsequent increases in brood production would then depend upon her potential increasing with age or upon the establishment of further reproductive units. This concept involves the food/energy relationships of the colony and therefore the balance between the harvest of food and the work-load. It is reasonable to assume that each larger larva can obtain enough food for itself and more than one young larva. This is the basis of the colony and the caste system. Since late larval stadia are usually longer and more numerous than the stadia of young dependent larvae, a surplus of food energy may develop when the reproduction rate falls relative to the growth rate of the larvae. Such a situation may in itself have an impact on the stimulus to initiate another reproducing unit unless dependent forms such as soldiers increase in number to take up the excess of available "energy". If this concept holds, then the larger the number of individuals per culture the greater chance there will be of maintaining more than a single pair of reproductives. At the same time, increasing numbers of other dependent forms such as soldiers and young larvae should be formed. However, the proportions of each of the dependent forms need not alter in the long-term, because other factors influence these and the ratios of any one dependent form to the number of foragers may change in the short-term. These relation-

ships are already reported in many termites.

6.22 Experiment II:

There was no significant difference in the number of supplementary reproductives surviving in the different-sized cultures of this experiment. Although a far larger range in size of culture was tested, the period of the experiment, however, was much shorter. The results of the two experiments are therefore difficult to compare. The numbers of supplementary reproductives in the cultures are shown in Table 12 and the brood produced in the second experiment set out in Table 13.

Disregarding the lack of significance between the values for reproductives in Table 11, one sees that the number of supplementary reproductives found in cultures after 2 and 4.5 months respectively

TABLE 12. Number of supplementary reproductives produced in cultures of different initial sizes.

Experiment	Initial Number of individuals per culture	Period of experiment (months)	Mean number of supple mentary reproductives
I	20	4.5	2.0
	50	4.5	2.0
	100	4.5	2.2
	200	4.5	3.3
II	50	2.0	2.0
	200	2.0	2.3
	1600	2.0	2.7

TABLE 13. Brood produced by cultures of different sizes in two months from establishment. (Means of three replicates in each group)

Initial number of individuals per culture	Total number of brood produced	Number produced per culture	Number produced per initial individual per culture	Number of cultures surviving	Number of cultures that produced brood
50	30	10	0.20	3	3
200	254	84.7	0.42	3	3
1600	386	128.7	0.08	3	3

indicate that fifty or less individuals tend to sustain a single pair but more than one pair may be found in larger cultures. The inference is that the continuous development of these forms and their subsequent elimination tends toward the maintenance of a single reproductive pair with the likelihood that more than one reproductive unit might be sustained at numbers above some undefined number of individuals per culture. In Table 12, the data suggests that this threshold may be somewhere above two hundred larvae per culture.

The size of the culture therefore appears to affect the time taken for supplementaries to develop, the number differentiated with time and possibly the number sustained per culture.

7.0 EFFECT OF THE MEAN WEIGHT OF INDIVIDUALS IN A CULTURE ON THE NUMBER OF SUPPLEMENTARY REPRODUCTIVES PRODUCED BY THE CULTURE

Colonies of Zootermopsis nevadensis and Neotermes jouteli vary in their ability to produce supplementary reproductives (Light, 1942 - 43; Light and Illg, 1945; Nagin, 1972). Nagin observed that the increased production of supplementary reproductives in Neotermes jouteli was correlated with the age of the colony. He used the size of pseudergates as an index of the ages of colonies examined. Nagin's techniques were interesting and, because my studies on P. adamsoni indicated that they might be equally applicable to this species, I tested them in the following way.

7.1 Materials and Methods

Termites were collected from nine field colonies on the same day. Four cultures, each of fifty large larvae and nymphs from each of these were weighed, the average weight of an individual being obtained by dividing total weight by fifty.

Two soldiers were added to each of the cultures in an attempt to prevent the transformation of undifferentiated larvae and nymphs into soldiers. The numbers of soldiers used were determined by the soldier to non-soldier ratio observed in the field colonies. The cultures were set up in 9 cm petri dishes and observed daily for twenty-five days. The supplementary reproductives were removed as soon as they were recognised and their antennal segments and molar plate ridges were counted.

7.2 Results and Discussion

The data (Table 14) shows no consistent trends relative to the increasing average weight of the larvae in the respective culture groups. Indeed the heaviest cultures produced fewer reproductives than some of the lighter ones. The variability in all groups was high. The medium group generally produced few reproductives and was more consistent than the other two.

All reproductives developed from the larger members of each culture and this is also indicated by the large number of molar ridges and antennal segments recorded for them. The results of the experiment differ from Nagin's findings for Neotermes jouteli but as other factors

TABLE 14. The influence of larval weight on the number of supplementary reproductives formed in cultures of P. adamsoni. (Data from twelve replicates in each category)

Weight category	Weight of larva (mg.)		Number of supplementary reproductives per culture	Mean number of molar ridges (Rt. mandible)	Mean number of antennal segments
	Average	Range			
Light	14.3	12.4-16.0	5.5	18.8	15.7
Medium	16.7	15.8-18.2	2.4	18.9	16.0
Heavy	18.2	17.0-20.0	6.9	19.4	17.4

may be involved, such as daily handling of cultures, clear-cut conclusions at this stage are not possible. My results do suggest, however, that weight of larvae is not necessarily a good index of the likelihood of a culture forming reproductives and that other things such as isolation from reproductives and the nutrition/energy relationships in the colony are more likely to be important.

8.0 THE INFLUENCE OF FUNCTIONAL SUPPLEMENTARY REPRODUCTIVES ON THE DEVELOPMENT OF FURTHER SUPPLEMENTARY REPRODUCTIVES IN INCIPIENT COLONIES

Cultures without functional supplementary reproductives appear to begin developing supplementary reproductives almost immediately after their establishment and the first mature forms may be recognised in two to three weeks. The presence of functional supplementary reproductives tends to inhibit the development of further supplementary reproductives in those species in which these processes have been studied.

The situation in Porotermes was unknown and was therefore examined in the following ways:-

8.1 Materials and Methods

Groups of one hundred larvae and nymphs were cultured in Jucci-Grassé tubes and replicated four times. A pair of functional supplementary reproductives and four soldiers were added to each culture. All individuals used in the experiment came from the same field colony. The reproductives were not marked because the dark brown colour of their

cuticle distinguished them from those that subsequently developed in the cultures- Four replicates of cultures without supplementary reproductives were established as a control. The experiment was assessed for surviving supplementary reproductives at the end of four months.

8.11 Results and Discussion

Supplementary reproductives appeared in all cultures of the control by the thirteenth day. When the cultures were examined after four months, three of the control cultures contained a single reproductive pair and one had two females and a male.

Three of the cultures which were started with supplementary reproductives still contained the original supplementary reproductives and no new ones. One culture, however, lost its female supplementary reproductive and contained the original male and a new female.

The results clearly showed that cultures sustained a single reproductive pair. Those that originally had a pair tended to retain it and those originally without a pair quickly developed one and sustained it. Such a result confirms the experience of many who have done such experiments on other termite species.

8.2 Materials and Methods

Cultures of fifty larvae and nymphs were cultured in 9 cm petri dishes. A pair of reproductives was taken from bulk cultures, each was marked and then smeared with gut contents from larvae of the culture to which it was added (Castle, personal communication).

The treatment was replicated seven times with the control group having no reproductives present.

Two soldiers were also added to each treatment and control and all were examined daily. Each supplementary reproductive was removed from treatments and controls, as soon as it was recognised. The counts obtained for the experiment were analysed by the Mann-Whitney "U" test.

8.21 Results and Discussion

More supplementary reproductives were formed in control cultures started without functional reproductives. Initially reproductives developed rather rapidly, the first being distinguished in five days. The rate of formation increased for about a further ten days then declined. A total of fifty-two supplementary reproductives were formed in the cultures and compared with seven that formed in cultures started with functional reproductives. The difference between the numbers of supplementary reproductives produced in the two groups of cultures was highly significant ($P < .001$).

Three of the cultures started with functional reproductives did not produce any new reproductives and none of the reproductives originally added was lost during the experiment.

These results confirmed those obtained in Section 9.11.

8.3 Materials and Methods

In earlier experiments I had noticed that "stability" of the colony structure occurred about the 30th day after establishment of the cultures.

"Stability" in this case is denoted by the fact that number of reproductives produced was about equal to the number eliminated.

The following experiment was designed to test the effect of removing reproductive unit.

Eleven groups of fifty large larvae and nymphs plus two soldiers were cultured in 9 cm petri dishes. The cultures were observed daily and new supplementary reproductives produced were chilled at 0°C and marked with different colours of nail polish as soon as they were recognised. After cultures had been observed for fifty-five days, the supplementary reproductives surviving in six cultures were taken out whilst those in five cultures were retained. New supplementaries in both cultures were recorded and marked as before.

3.31 Results and Discussion

New supplementary reproductives began to appear about ten days after the reproductives were removed from the six cultures and increasing numbers appeared over the next fifteen days. No new reproductives appeared in the controls.

It appearsthen that in stable colonies of small numbers of termites, existing reproductives either inhibit the maturation of other supplementary reproductives or stimulate their elimination soon after they appear. If the "controlling pair" is removed a number of individuals begin to mature and a period of maturation and elimination begins. Stability in this species occurs after some thirty days.

This experiment therefore shows that removal of the reproductive

unit results in the same developmental processes as occur in isolated groups of larvae and nymphs. It provides an understanding of the processes which might occur in natural colonies when either or both of the reproductives are lost or where groups of larvae and nymphs become isolated from the influence of the reproductive unit in the colony.

8.4 Effect of continuous removal of supplementary reproductives that mature in cultures on the rate of development of reproductives

In isolated cultures without a functional reproductive pair, a proportion of larvae and nymphs transform into supplementary reproductives in a given period (Light and Weesner, 1951; Lüscher, 1952a, b, c; Nagin, 1972). Castle (1934) and Grassé and Noirot 1946 have found that all newly emerged larva have the potential to differentiate into any caste. With time therefore all larvae and nymphs in isolated cultures without a pair of functional reproductives should transform into supplementary reproductives and this was tested for P. adamsoni in the following way.

8.41 Materials and Methods

A pair of marked supplementary reproductives and two soldiers were introduced into each of ten cultures of forty large larvae and nymphs in the way previously described (Section 9.2). After one month, five surviving cultures which had not produced any new supplementary reproductives were each divided into two groups of twenty larvae and

nymphs. One group was continued with the reproductives and each group kept one of the soldiers. The cultures were observed daily for one hundred and ten days and new supplementary reproductives formed were taken out as soon as they were recognised.

8.42 Results and Discussion

Results are shown in Table 15. Two cultures without supplementary reproductives and one culture with supplementary reproductives were lost. At the end of the experimental period, most larvae and nymphs had matured in those cultures from which continuous removal of reproductives occurred. This confirms the results of Castle and Noirot for other species and emphasises that all larvae in these "lower" termites retain the ability to mature sexually for the greater part of their lives. The results also support earlier data that indicate that functional reproductives in small colonies exert some control over maturation of larvae.

8.5 Effect of the sexes of functional supplementary reproductives on differentiation of further supplementary reproductives of the same sex

When a pair of functional supplementary reproductives was introduced into cultures of larvae and nymphs further development of supplementary reproductive was usually prevented. It is not known, however how the individual sexes affect this inhibition of sexual maturation. It has usually been found that males inhibit the maturation of other males and

TABLE 15. The effect of removing reproductives that developed cultures on the maturation of larvae that remained, compared with larvae maturation in stable colonies. (Period of experiment one hundred and ten days).

Group	Number of larvae at start/culture	Number of larvae at end/culture	Number of reproductives formed during experiment/culture
With reproductives removed	20	1.7	13.7
With reproductives retained (stable colonies)	20	14.5	0.5

females inhibit maturation of females. To provide evidence on this inhibition in P. adamsoni I designed the following experiment:

8.51 Materials and Methods

Cultures of fifty larvae and nymphs were established in 9 cm petri dishes. A supplementary reproductive was added in the way described in Section 9.2.

The following combinations of functional reproductives were added to the cultures:-
one male, two males, one male and one female, one female, and two females. The control cultures had no reproductives.

There were six replicates of each treatment. The supplementary reproductives that developed were taken out of the cultures as soon as they were recognised and their sex was determined. Due to increasing mortality in some cultures, the period of the experiment varied from twenty-one to thirty-three days.

The numbers of supplementary reproductives formed in the cultures of the control were compared with the following treatments:-
a single female, two females, and a male and female, using the Friedman two-way analysis of variance. Because some of the cultures with a single male and some with two males died, the surviving ones were compared separately with the control and with each other using the Mann-Whitney "U" test.

8.52 Results and Discussion

As found in earlier experiments, more larvae and nymphs transformed into supplementary reproductives in the controls (having no reproductive unit) than in any of the treatments. There was a significant difference between the number of reproductives formed in the controls and those recorded for treatments having (i) a single female, (ii) two females and (iii) a pair of reproductives. ($P < .01$ in each case).

The least number of transformations occurred in those treatments having one male and one female (a reproductive unit).

The differences in the number of reproductives formed in the controls and in the treatments having a single male or two males per culture was significant ($P < .05$). There was no difference between the number of reproductives formed in treatments beginning with a single male or with two males per culture, respectively. The only result that proved significant when sex ratio was considered was the number of reproductives formed in treatments having initially a single female or two females.

It is clear that functional reproductives inhibit the production of further reproductives to a certain extent although this inhibition does not appear to be initially complete. The inhibitory effect of functional females on the sexual maturation of other females appears to be stronger than the corresponding effect of functional males on other males (Table 16).

TABLE 16. The effect of functional reproductives of one sex on the sexual maturation of larvae of the same sex.

Initial mature reproductives present		Number of cultures that survived	Number of reproductives matured per culture		Total reproductives matured	
Male	Female		Male	Female	Male	Female
1	1	6	0.33	0.33	2	2
1	0	5	1.60	1.60	5	8
0	1	6	2.33	0.17	12	1
2	0	4	1.25	1.50	5	6
0	2	6	1.67	1.0	10	6
Control 0	0	6	3.33	1.67	20	10

8.6 The time required for larvae and nymphs to respond to the absence of a pair of functional supplementary reproductives

Supplementary reproductives are produced in cultures soon after they have been isolated from the "influence" of their original reproductives.

It seems likely that there is a critical time after larvae and nymphs are so isolated before the introduction of a pair of functional supplementary reproductives will inhibit further sexual maturation of larvae. This experiment was designed to determine whether such a critical time exists in P. adamsoni, for this inhibition to become effective.

Earlier experiments indicated that the addition of a "reproductive unit" to a larval culture significantly reduced the number of reproductives that transformed relative to controls having initially no reproductive unit. A test of the time taken for the inhibitory effect to become operative might be to find out how long it takes from establishment of a culture to addition of a reproductive unit before there is a difference between the number of reproductives formed by treatments and controls.

8.61 Materials and Methods

Thirty groups of fifty larvae and nymphs and two soldiers were cultured in 9 cm petri dishes using described techniques. A pair of supplementary reproductives was added to each of five cultures on day zero (i.e. the day the experiment was started) another pair was added to each of five cultures on day one, two, four and eight. There was a

control of five cultures without reproductives. The cultures were observed daily and reproductives removed as soon as they were recognised.

8.62 Results and Discussion

Results are presented in Table 17.

TABLE 17. The time taken for the inhibitory effect of the reproductive unit to become ineffective in cultures of *P. adamsoni*. Based on the similarity - numbers of supplementary reproductives formed by treatments and controls.

Time before reproductive unit added (days)	Number of new reproductives that developed per culture
0	1.4
1	2.6
2	4.0
4	6.2
8	10.2
Control	7.2

The data indicates that the inhibitory activity of functional reproductives is ephemeral. Because of the similarity of reproductive formation in treatments and controls, inhibition appears to be entirely lost in about four days and probably in as little as two or three days. Of the treatments which received a pair of functional supplementary reproductives each on day one, two out of five did not develop new reproductives but this could have been expected from the results of

earlier experiments. While no attempt was made to identify the inhibitory factor, I believe that two aspects, "inhibitory substance" "unused feeding activity" or foraging energy which must be intense on the loss of reproductives which in small colonies are the main dependents. These effects may be involved either independently or together in the stimulation of sexual maturity in some of the remaining larvae or nymphs. Because, in the early stages any stimulus in the food regurgitated or excreted by foragers may be spread over a number of individuals in a more or less random manner, the maturation of more than one pair, and even differing numbers of each sex, might occur. This is the situation found experimentally in P. adamsoni and my observations reinforce the idea that attempts by larvae to feed each other might well precede the maturation of some and the secretion of the inhibitory substance by resultant sexually mature forms which then inhibit, with increasing effect, the sexual maturity of further larvae. Whatever the true situation is, there can be little doubt that this thesis satisfies the experimental and observed data in most respects.

8.7 The relationship between differentiation and elimination of supplementary reproductives

Field colonies of P. adamsoni had been found to contain different numbers of supplementary reproductives and laboratory cultures also developed varying numbers of supplementary reproductives with time. The laboratory experiments described earlier in this section showed that there were more reproductives transformed than were sustained in true

colonies of the same numerical size, or indeed were present in each culture at the end of the particular experiment. Such reduction in the number of supplementary reproductives produced in cultures has also been reported in laboratory cultures of K. flavicollis, N. jouteli and R. lucifugus (Grassé and Noirot, 1960, Lüscher, 1952b, Nagin, 1972 and Buchli, 1956a, 1958). These authors attribute cannibalism of extra reproductives to a defined behaviour pattern called "elimination". This seems to be related to the relationship between the number of food-producing individuals and "dependent" individuals in any culture. It must also be influenced by the presence of "functional" reproductives and by the relative strength of their inhibitory activity. The trend towards the production of a certain number of supplementary reproductives in cultures of a standard size was examined to determine the method of elimination of the surplus individuals for Porotermes.

8.71 The relationship between time and differentiation and elimination of supplementary reproductives

A certain proportion of larvae and nymphs in isolated cultures are transformed into supplementary reproductives in a given time and such cultures tend to "stabilise" about the thirtieth day. The following experiment was designed to examine the influence of time of differentiation of supplementary reproductives and elimination of those reproductives if indeed they are eliminated.

8.72 Materials and Methods

Groups of fifty large larvae and nymphs plus two soldiers all from the same colony were cultured in 9 cm petri dishes. The cultures were examined daily and the number of supplementary reproductives present on each day was counted. As the new supplementary reproductives were recognised, they were chilled at 0°C, sexed and marked on the head and thorax. Different coloured nail polishes were used to separate newly matured insects from older ones.

Cultures were photographed at seven day intervals using positive films and the termites were counted on the film. This technique reduced the chances of injury to the termites.

8.73 Results and Discussion

Most cultures had developed their first supplementary reproductives by the seventeenth day while others varied up to twenty-nine days from establishment. Males outnumbered females as the first supplementary reproductives formed by seven to three. Within twenty-four hours of a termite moulting into a supplementary reproductive its cuticle had hardened and had turned yellowish-brown. As the reproductive aged its cuticle darkened further and many sclerites became dark brown. This was the colour of most mature supplementary reproductives collected in the field (Figure VIII). Supplementary reproductives which developed from early alates or alate intercastes were frequently encountered in the cultures (Figure IX).

Differences in structure of the different sexes of supplementary

Figure VIII. A. The differences in colour of the main individuals in a colony of *Porotermes adamsoni*.

a) Larva

b) Supplementary reproductive

c) Primary reproductive

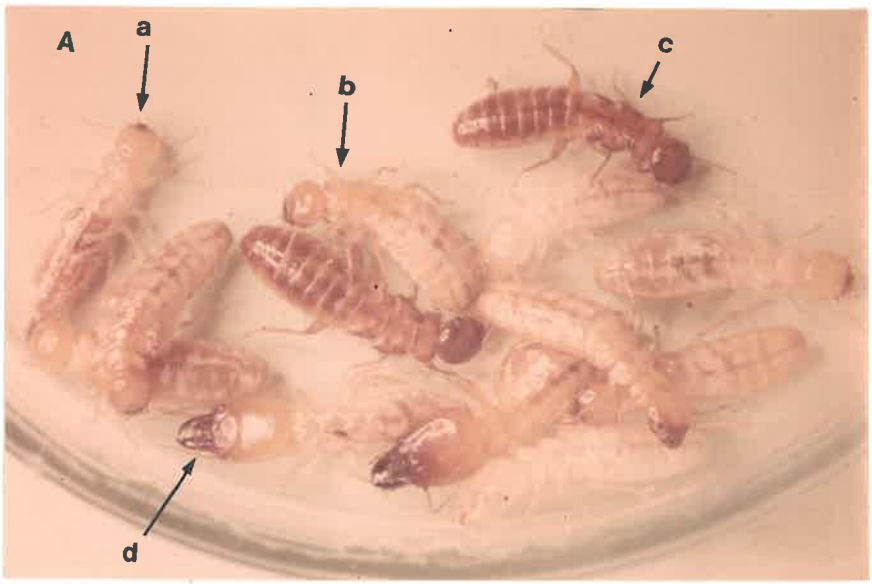
d) Soldier

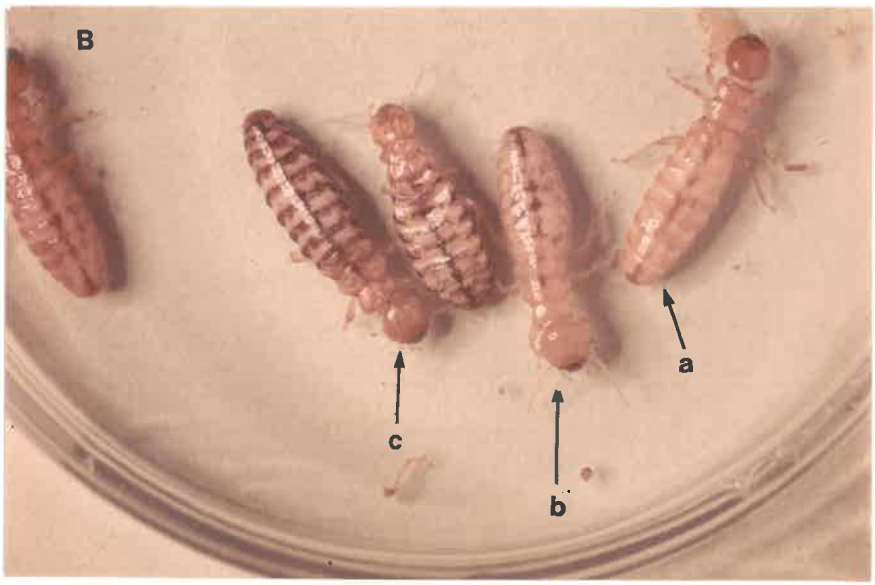
B. The different colour stages of supplementary reproductives.

a) One month old supplementary reproductive developed in the laboratory: With yellowish brown cuticle.

b) Five month old supplementary reproductive developed in the laboratory: with some sclerites becoming dark brown.

c) Supplementary reproductive collected from the field with dark brown sclerites.


A
a
b
c
d


B
a
c
b

reproductives were also noted. Usually the female had the styles reduced in size or absent although they were present in female larvae and nymphs. The seventh sternite of female reproductives is larger than in larvae and covers the U-shaped eighth sternite and most of the ninth sternite. The eighth sternite is entire in the male reproductive and the seventh is not enlarged. Males also retain the styles.

Most supplementary reproductives appeared in cultures between the tenth and thirtieth days during which time further reproductives, additional to the first pair, developed. On the thirtieth day eggs were usually present in the cultures and it was about this time that further development of reproductives markedly decreased until usually a reproductive pair was left in each (Figure X). Eighty per cent of the cultures produced more than a pair of supplementary reproductives and 9% of all larvae and nymphs cultured actually transformed into reproductives. More than 56% of the reproductives formed were males but the male/female ratio approached one with increasing time.

In most cultures observed, reproductives of the same sex, additional to the first formed, were either eaten by the larvae and nymphs or were starved as indicated by the shrunken abdomen. In the latter case reduced activity was followed by death. Elimination of male reproductives usually proceeded much more quickly then did elimination of females. In a few cultures only one reproductive pair was developed and so there was no elimination recorded in these. In four of the cultures in which reproductives continued to develop, sometimes all were eliminated and when the experiment was completed there was still only a single

Figure IX. A. Alates: With and without wing.

B. Supplementary reproductive - alate inter castes.


A


B

reproductive in each of these cultures. The population of three of these cultures had decreased to less than half of their original number indicating that conditions were unsatisfactory. This could have been the cause of the excessive elimination noted in these cultures which died out ten days later. A culture which developed a single female and three male reproductives eliminated the female leaving the three males, whilst another produced four females and one male, but none were eliminated. One culture produced only male supplementary reproductives.

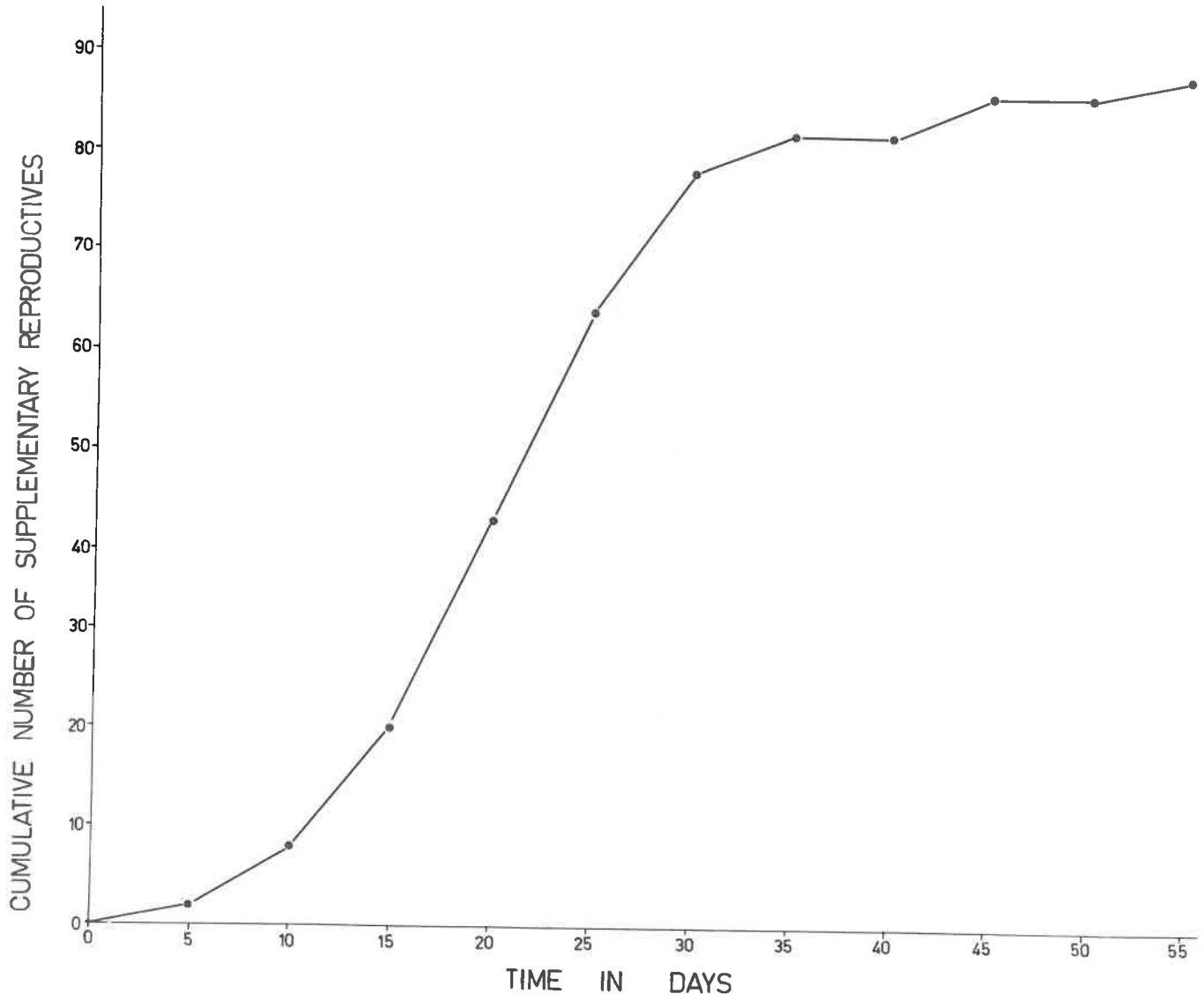
The time of formation of a supplementary reproductive did appear to influence its chances of elimination (Table 18); the first ones that developed had higher survival rate than those that developed later.

TABLE 18. The relationship between the survival of initial and subsequent supplementary reproductives in cultures of larvae and nymphs maintained for fifty-five days. (Data for twenty cultures).

% Initial supplementary reproductives that survived			% subsequent supplementary reproductives that survived		
♀	♂	Total	♀	♂	Total
33	29	62	18	20	38

The formation of supplementary reproductives in most isolated cultures of larvae and nymphs of Porotermes adamsoni is initially continuous with elimination by cannibalism or starvation usually of the later ones matured.

Figure X. The development of supplementary reproductives in cultures of Porotermes adamsoni with time, showing that the rate of their development levels off at about 30th day of continuous culture. (Data for 20 cultures).


CUMULATIVE NUMBER OF SUPPLEMENTARY REPRODUCTIVES
0
10
20
30
40
50
60
70
80
90
0
5
10
15
20
25
30
35
40
45
50
55
TIME IN DAYS

There is, in these results therefore, some evidence for both inhibition and elimination of reproductives in P. adamsoni. In some cases these phenomena do not appear to be as strongly developed as has been reported for other species and there is little doubt that the variation reported for Porotermes may sometimes be due to the conditions existing within particular cultures. At least some of the problems in cultures appear to be due to the disturbance necessary for experiments of the kind I have designed.

9.0 EFFECT OF DISTURBANCE OF CULTURES ON THE SURVIVAL OF THEIR REPRODUCTIVES

In some of the cultures in previous experiments in which all reproductives were at times eliminated, and some decreased in number of individuals relative to their initial numbers. Daily handling appeared to place some cultures under stress and an experiment to test this possibility was carried out.

9.1 Materials and Methods

Thirty-eight cultures each containing sixty larvae and nymphs and two soldiers from the same colony were cultured in 9 cm petri dishes. The cultures were randomly assigned to four groups which were subjected to the following treatments: Group I: ten cultures were handled daily; Group II: ten cultures were left undisturbed until eggs had appeared in all cultures of Group I (on the forty-seventh day). Then they were disturbed daily; Group III: eight cultures were treated the same way as

Group II but were disturbed at weekly intervals after the forty-seventh day; Group IV: ten cultures were left undisturbed for the full three months of the experiment.

The number of supplementary reproductives and undifferentiated termites in each of the surviving cultures in all the treatments and controls were then assessed.

9.11 Results and Discussion

Though all colonies decreased in number of individuals during the experiment, clearly the highest survival rates were in those which were handled least. (Tables 19, 20 and 21). There did not appear to be a similar significant effect of handling either on the number of reproductives found per culture or on the numbers of cultures that developed reproductives. However, only in the group not handled at all, did all cultures survive the three months of the experiment.

TABLE 19. The effect of handling on survival of cultures of *P. adamsoni*. (Mean number of individuals/culture assessed twelve weeks from establishment). (Each culture originally of sixty-two individuals).

Control (not handled)	Handled daily	Handled daily after forty-seventh day of establishment	Handled weekly after forty-seventh day of establishment
55	24	32	48

TABLE 20. Analysis of variance for the effect of handling on survival of cultures.

Variation due to	d.f.	S.S	M.S.	V.R.	P.
Handling	3	6316.68	2105.56	6.1	< .01
Error	34	11735.87	345.17		
Total	37	18052.55			

TABLE 21. The effect of handling on the survival of supplementary reproductives that developed in cultures of sixty larvae and nymphs. (Data from thirty-two cultures assessed at twelve weeks from establishment).

Group of cultures	Status of cultures at assessment - Number of cultures with:-		
	Less than one pair of reproductives	One pair of reproductives	More than one pair of reproductives
Control (not handled)	0	7	3
Handled daily	0	4	3
Handled daily after forty-seven days	1	7	0
Handled weekly after forty-seven days	0	5	2

Records on formation and elimination of reproductives (Table 21) strongly supported previous data, as did indications of suppression of reproductive development at about the time eggs appeared in cultures. There were no unusual effects on the sex ratio of reproductives that developed.

9.2 The influence of sex ratio on the development and elimination of supplementary reproductives

Most of the cultures in previous experiments had produced more than a single pair of supplementary reproductives and usually males outnumbered females, at least initially. In the most vigorous cultures, the number of supplementary reproductives fluctuated with a tendency toward the survival of a pair. In one case a culture produced only male supplementary reproductive. As this culture included both sexes of larvae and nymphs, the ratio of the sexes initially present may have influenced the result. An experiment was therefore designed to test the influence of sex ratio on the formation and survival of reproductives.

9.21 Materials and Methods

Using the 9 cm petri dish culturing technique, I established cultures of suitable larvae and nymphs from the same colony. These were all sexes and assigned to cultures each of fifty individuals according to the following male to female sex ratios:- four to one; one to four; one to one; fifty to nil; nil to fifty. Each culture was replicated four times. Two soldiers were added to each culture and the number of

supplementary reproductives formed assessed from daily observations.

9.22 Results and Discussion

Results are presented in Table 22.

TABLE 22. The influence of the sex ratio of larvae in initial cultures on the formation of supplementary reproductives in them. (Culturing time = fifty days).

Initial sex ratio of larvae/ culture		Number of cultures that survived/ group	Number of reproductives produced per culture		Number of individuals that survived per culture
Female	Male		Female	Male	(Sex ratio in brackets) (female to male)
50	0	4	4	0	42.00 (42:0)
0	50	4	0	2.5	36.25 (0:36)
40	10	4	3.25	1	34.25 (4:1)
10	40	4	1	3.25	39.0 (2:9)
25	25	3	2.3	1.3	35.0 (1:1)

There was a distinct trend toward the development of four reproductives in each culture except those of males only. In those cultures with both sexes present, the numerically dominating sexual form developed most reproductives.

Where the sexes were initially equal, females tended to out-number males among the reproductives matured.

Observations during this experiment indicate that the rate of development of new supplementaries tended to be offset by the rate of their elimination. Inhibition may also have been involved. The interesting point was that the development of this stabilisation in cultures again occurred about the 30th day of culture.

10.0 GENERAL DISCUSSION

The biology and behaviour of Porotermes adamsoni are basically similar to those of other termopsids such as Zootermopsis and Stolotermes. After initial problems of rearing, I developed and used a number of techniques similar to those used by most other Isopterists. Under such culturing systems, P. adamsoni proved to be a good laboratory animal, not too drastically affected by careful handling.

It seems basically to have seven larval instars, though this may rarely occur due to both pseudergate and nymphal-regressive development involving ecdysis without an "advance" toward sexual maturity or other "biological end-lines". Flight of alates takes place in the evenings during late summer and early autumn.

Perhaps the main role of the alates is dispersal of the species for there can be little doubt that those dealates that successfully establish develop colonies slowly at least in the initial period. It is during this time that much of their energy is used in constructing the nest, foraging and caring for their progeny through the first two stadia. At the same temperature, their eggs incubate over a similar period (25 - 45 days) to those of supplementaries. My data, though anything but conclusive, indicate that supplementaries are more fecund than primaries (see also, Light, 1934; McMahon, 1962). The differences are probably due to the care and feeding, absent in the young primary colony, that the supplementaries receive from other members of their sub-colony. Such is a natural factor of sub-colony formation and development. The lack of such care and feeding of primaries is likewise

a natural circumstance of the establishment and development of primary colonies.

Proper comparisons of the fecundity of the two sexual froms may only be made after primary colonies and supplementary colonies have established to the stage where both reproductive units are supported by similar numbers of foragers and feeders which also take over the care of the eggs and young larvae. The data I obtained from young primary colonies about nine months old show clearly that the fecundity of the young queens now supported by foraging larvae approaches that for supplementary queens about three months old, even though the numerical strength of the supporting larvae was still a small fraction of that supporting the supplementaries. Though these data infer that such comparisons of fecundity may not be useful in the longer-term view, there can be no doubt that supplementaries are extremely common in natural infestations and are important in the survival of the species.

In attempting a better understanding of the factors involved in the development of colonies of Porotermes therefore, I have placed much emphasis on the role of the supplementary reproductive caste.

As well as attempting to define its biological parameters (such as initial developmental period and fecundity) I have examined environmental and social factors (such as inhibition and elimination) that may influence both its rate of development and survival. Though these factors, especially social factors, have been reasonably investigated, no attempt to identify precursors for any of the behavioural responses noted has been made here. However, observations and quantitative

data in certain of my experiments have indicated that such factors and the behaviour they stimulate are operating in the colonies of this species.

The rate of transformation of larvae and nymphs into supplementary reproductives is similar to that reported for Zootermopsis but the influence of the number of individuals in a culture on the number of supplementary reproductives maintained by it appears to differ (see Light and Illg, 1945). This could be due to differences in the elimination-potential of the two species. The ability of larvae and nymphs to transform into supplementary reproductives appears to be influenced by their respective intermoult periods. This assumed, the potential of colonies to develop supplementary reproductives would then depend on the availability of recently moulted larvae and nymphs. This would be an adequate explanation for the observed differences in the number of supplementary reproductives formed in different colonies of P. adamsoni. It may also explain why this varied with time for the same colony as has also been reported for other species by Lüscher (1952b) and Light and Illg (1945). My results for P. adamsoni differ greatly from those of Rupli (1969) for K. flavicollis, but this could be expected not only on ecological grounds but also on the fact that the two species are not closely related. The variability in the number of supplementary reproductives developed by different colonies of N. jouteli (Nagin, 1972) may not be due to the differences he reported in the weight of individuals of those colonies. He used only one replication and, if my results with P. adamsoni are any indication of the variability that might occur in experiments of this kind, Nagin's

results should be considered tentative until confirmed. The same may be said about his reference to the effect of age of individual on the formation of supplementaries by cultures of N. jouteli. The inhibitory influence of supplementary reproductives which appeared in cultures of P. adamsoni initially with functional reproductives, appeared to increase with time. This has also been reported for K. flavicollis (Grassé and Noirot, 1960; Rupli, 1969).

There appears to be a relationship between two major factors in the process of colony development and stabilisation (in the sense I have used it in this text) in Porotermes. These factors are:

(i) The relationship between feeders and dependents involving an imbalance towards "feeding energy" in the colony when the reproductives are lost.

(ii) When "feeding energy" is dominated by dependency, because of the number of reproductives that are stimulated to mature, starvation and cannibalism provide the main ways of eliminating the extra dependents. The development and elimination of reproductives stabilises at about the onset of oviposition by the young queen. This strongly suggests that the inhibitory substance (whatever it may be) is produced and distributed from about the time of ovarian maturity. If this is correct, it stresses the importance of using functional reproductives in all experiments on inhibition.

> The inhibitory substance in P. adamsoni is sex-specific, but female reproductives are apparently more effective in inhibiting female maturation than males are in inhibiting the maturation of other males. This suggests that there may be a quantitative difference either in the responses of the sexes or in the potency of the inhibitory substance produced by each sex. The inhibition of the development of reproductives was more effective when both male and female reproductives were present which may indicate a synergistic effect of the substances produced by one sex on those produced by the other. This has also appeared to be the case in other termites (see Light and Weesner, 1951; Grassé and Noirot, 1960; Lüscher, 1964 and Nagin, 1972).

My results with unisexual cultures of P. adamsoni where stabilisation occurred with time, cast some doubt on Lüscher's (1962) hypothesis that the distribution of the "inhibitory pheromone" is sex specific and that male pseudergates "collect and distribute" female pheromone and vice-versa. Other research on K. flavicollis (Grassé and Noirot, 1960) is supported by my results and unless Lüscher's theory is subsequently confirmed with quantitative data, it would seem that the type of pseudergate transmission of the inhibitory substance postulated by him must be considered doubtful.

In Porotermes as in other termites, the influence of the inhibitory substance is lost with the loss of the reproductive unit. This loss of influence occurs more quickly in cultures of P. adamsoni from which supplementary reproductives are removed than in those of Z. angusticollis from which primaries are removed (Light and Weesner, 1951). But it was quickest for cultures of K. flavicollis from which primaries were removed (Lüscher, 1952a, b). However, these temporal differences could be due to innate characteristics of these species, or differences in reproductives involved (Light, 1942-43).

The disturbance of colonies of P. adamsoni affected the survival of the nymphs and larvae but did not influence the stabilisation of the colony or the survival of the reproductive unit. Furthermore the development and elimination of supplementaries appeared to proceed similarly in disturbed and undisturbed cultures. In other words the end results in various cultures of fairly short duration were similar whether disturbed regularly or not. The pattern of elimination of the extra reproductives in cultures of Porotermes compared well with that reported for Kalotermes and Neotermes but differed from that of its closer relative, Zootermopsis (see Castle, 1934; Lüscher, 1952a, b, c; Grassé and Noirot, 1946 and Stuart, 1970; Nagin, 1972).

My emphasis on the supplementary reproductive in these studies derives from common occurrence of these forms in the galleries of field colonies or sub-colonies. However, the field situation is extremely complex and difficult to unravel. There were instances where supplementary reproductives were present with older larvae, nymphs and soldiers but

eggs and young larvae were absent, giving the impression that brood production by such reproductives is spasmodic or seasonal. Another explanation for this common situation is that the supplementaries wander about the galleries with older larvae and soldiers and that eggs laid are carried to nurseries and cared for by the larvae or pseudergates. This may involve common nurseries for several reproductive units or separate nurseries for each sub-colony. Certainly nurseries with resident reproductives are found and, at the same time as other reproductives attended only by older larvae, nymphs and soldiers. Sometimes both of these situations are present in the same log.

Porotermes may therefore exist either as separate primary and secondary colonies or as complex colonies, the sub-units of which might be located in different logs and stumps or in different parts of the same log or stump. Occassionally underground galleries, in use by larvae and soldiers and linking adjacent infested logs, have been discovered during this study. This behaviour is similar to that of higher termites of subterranean groups. It should be remembered, however, that Hodotermes, in the same family as Porotermes, is a subterranean termite. Perhaps dispersal by what Harris (1956) has called "colony-budding" occurs in Porotermes. The colony-supplementary colony (sub-colony) relationship in Porotermes adamsoni remains uncertain but factors that may infer the common nursery and linked sub-colonies are:-

(i) Supplementaries (attended by older larvae and nymphs) removed with their "sub-colony" to the laboratory were found to be ovipositing regularly on arrival.

(ii) Mature alates in large numbers have been found only in stumps in the field, yet nymphs collected from logs matured in the laboratory within sections of those logs.

(iii) Groups containing nymphs found in logs and examined from time to time did not appear to develop mature alates within those logs. Intensive searching of logs in the flight season rarely resulted in the discovery of advanced nymphs. Commonly, reproductives, larvae and soldiers were found in logs throughout this period.

Alternative explanations may well apply to each of these observations, but taken together they strongly support the existance of a colony, sub-colony relationship in Porotermes.

In final analysis then, Porotermes adamsoni is comparatively large, easily located in the field and amenable to reasonable handling. There is therefore no reason why it would not be used to attempt to solve some of the basic questions on the control over castes apparent in the termite society. The concept of pheromonal production and control of castes may not be a good one as the developmental processes involved appear similar to those influenced by ecdysone and juvenile hormone in other insects. Whatever the process is, there seems to be an initial effect involving loss of the reproductive, followed by a surplus of "feeding energy" which is expended in trying to feed other individuals. This seems to trigger the sexual maturation of recently moulted larvae.

As ovarian maturity is attained in one female, and perhaps following mating, the processes of maturation and elimination come to an equilibrium and the colony subsequently retains one reproductive pair.

In P. adamsoni, the number of individuals in the new "supplementary colony" influences the degree of control exerted by the reproductive unit so that, in larger groups, further reproductives may mature. Depending on the number of individuals, other reproductive units may be sustained and further small numbers of other dependents, such as soldiers, develop and survive. The resultant colony relationships are obscure but the existence of common nurseries and sites for maturing alates, on present evidence, seem possible as components of complex colonies.

Whilst I have presented evidence for the above hypothesis, I recognize the need to examine certain of the components of it more thoroughly than has been possible in such a short period of about two years. I have, however, developed the techniques to make such research possible.

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