The Ecology and External Morphology of _Stolotermes ruficeps_ Brauer (Isoptera: Hodotermitidae)

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**Introduction**

Though much has been written about the termites, most of the literature available at the time this study was undertaken was concerned with identification of the various species from the external characters of the soldier and winged reproductive Entomologists in the United States, and more recently in Australia, have compiled detailed accounts of the ecology, habits, and life cycles of the three ecological groups (viz., "Drywood", "Dampwood", and "Subterranean") within the order Isoptera. _Stolotermes ruficeps_ has been briefly dealt with from time to time, but no details of the life cycle and, little information on the biology and ecology of the species, has been published. This study is an attempt to fill some of the gaps in the present knowledge of New Zealand's endemic termites.

**Historical Review**

In 1858 Hagen gave the name _Stolotermes_ to a subgenus of the large varied genus _Hodotermes_, using specimens of _Stolotermes brunneicorins_ Hagen as the subgeneric type. Brauer (1865) described _Stolotermes ruficeps_, from the Novara expedition collection, using Hagen's subgenus but giving it generic rank. Hudson (1892) described _S. ruficeps_ and gave the first general account of the biology of the species, and Miller (1925) made brief reference to its economic significance. In 1942 Hill re-described the winged adult and soldier and also referred briefly to the biology and affinities of the species.

**Taxonomy**

As stated above, Hagen (1858) erected the subgenus _Stolotermes_ in the Family Hodotermitidae, and according to Emerson (1942) the morphology of the Stolotermitinae indicates that it rightly belongs to this family. However, on the basis that the Stolotermitinae greatly resemble the _Kalotermitidae_ in appearance and habits the sub-family has been often included in this group (Froggatt, 1913; Hill, 1942). The convenience of the latter viewpoint cannot be denied, but the fact remains that, despite the marked differences between it and other Hodotermitidae, the Stolotermitinae belong here, as originally placed by Hagen.

For the reason that the prejudice against separating them from the _Kalotermitidae_ is strongest in the Australian region and that there are few common grounds for comparing their habits with those of _Hodotermes_, I have linked them with the _Kalotermitidae_ in this study and have drawn comparisons accordingly.

**Materials and Methods**

In all, 450 different colonies were examined in the period of study. Some of them were kept under weekly observation for periods of up to three months. Termites used during the course of the investigation were collected from five localities in the Wellington Province and two localities in the Auckland Province. Approximately 50,000 individual termites have been observed, and measurements were taken of individuals from 10 different colonies representing all instars.
The termites examined for external morphology were:

(i) Killed in Bouin's fluid, cleared in cedarwood oil, and mounted in canada balsam.
(ii) Killed in Schaudinn's and mounted in canada balsam
(iii) Mounted directly in polyvinol alcohol
(iv) Killed in 70 per cent. alcohol and mounted in glycerin.

It was found that method (iii) using polyvinol alcohol was not satisfactory for recording measurements due to the tendency for the termite to stretch and distort under the influence of this mounting agent.

Mounts of the protozoa from the hind gut of nymphs were made using Heidenhain's iron-alum haematoxylin counterstained with aqueous eosin. However, it was found that mounting live protozoa directly in a drop of water or glycerin was generally satisfactory for observing shape, locomotion and movement of flagella.

All material used was identified according to the descriptions given by G F Hill (1942). Identifications were checked by Dr J T Salmon, of Victoria University College.

Due to the fact that dampwood termites have not the economic significance of other groups, little attention has been given to their ecology, the only reasonably detailed account being that by Castle (1934) on the dampwood termites of the Western United States. This reference has been, of necessity, commonly referred to in this work.

**Habits of Stolotermes ruficeps**

Like all members of the O Isoptera, *S. ruficeps* is industrious and hygienic. Being negatively phototropic, the individuals of a colony will rapidly move to regions of low light intensity when exposed. This does not mean that termites cannot live in habitats with high light intensities, for a simple experiment will show that provided suitable food, temperature and humidity requirements are maintained, termites will thrive for relatively long periods under normal night and day light intensity fluctuations. Dampwood termites of the genus *Zootermopsis* have proved to be valuable laboratory insects in the United States of America, where they have been kept indefinitely on a diet of filter paper and under ordinary night/day light intensity fluctuations (Castle, 1934; Light and Ilg, 1945). The perfect insects (Text-fig 3, Fig 9) are positively phototropic for a short time during which swarming takes place.

The colony, within its workings, maintains the galleries in an hygienic state, packing the frass pellets (Text-fig 1, Fig 6) into disused tunnels or pushing them out of the wood by an opening made for the purpose and closed up again afterward. Though fungi are commonly found within termite galleries (Hendee, 1934) fungal activity is normally controlled by the termites. Galleries of no further use, or where fungal activity is not able to be controlled by the nymphs, are sealed off. In *S. ruficeps* these "seals" are constructed by the nymphs from rotten wood, frass pellets, moisture from the galleries and stomodeal and proctodeal fluids. Such plugs or seals are characteristic of other termites (Kofoid et al., 1934).

Apart from keeping their nests or workings clean, termites are noted for their habits of cleaning both parts of themselves and parts of other individuals of the colony. This toilet habit has become universally known as grooming, two types being distinguishable:

(i) **Self Grooming**

This is an occasional cleaning down of the forelegs and antennae using the palps and often the whole of the mouth parts. Individuals will groom themselves several times a day. When ectoparasitic mites are present on their antennae and legs more vigorous efforts, including the rubbing of their bodies against the gallery walls or other termites, may damage certain appendages.
(11) Reciprocal Grooming

This activity within termite colonies often occupies individuals or groups for relatively long periods. Usually the termite being groomed stands flexing its body to facilitate the cleaning of intersegmental areas, particularly on the abdomen, but all parts of the body are cleaned, even the mouth parts. A termite undergoing grooming may turn on its back so that the ventral body surface can be groomed. (Castle, 1934) Individuals of *S. ruficeps* raise the tips of their abdomens so that the groomers can clean the ventral surfaces of the posterior segments. Sometimes where more than one groomer is employed the individual being groomed is lifted and canted, so that the legs on one side of its body are across the dorsal surface of one of the groomers. This appears to allow the cleaning of the sides of the thorax and abdomen as well as the coxae, trochanters, and bases of the femora.

Apparently the secretions present in the depressions of the body are sought after and eaten by other nymphs. Grooming is the most widely publicised habit of termites outside of their wood-boring activities, for until the discovery of modern insecticides it was the basis of most efforts to control termites with toxic chemicals. Briefly, the method used was to blow clouds of finely ground toxic powder into the galleries of the termites. The powder adheres to the bodies of the termites and is later cleaned off during grooming and eaten by members of the colony. In this way the poison is distributed throughout a colony and kills its members. More recently the use of chlorinated hydrocarbons as contact insecticides and fumigants such as methyl bromide has proved more satisfactory.

**Communicatory Behaviour**

In the termite colony much reliance is placed on the senses of hearing, touch, smell and taste, for there has been no indication from observations of termite behaviour that the individuals can see in the darkness of their nests and galleries. Communication within the colony is maintained mainly through the senses of hearing and touch. There are two main types of communication.

(i) Identification. This is going on constantly within the colony. Whenever two termites meet within a gallery they may both stop, play their antennae over each other, or one may commence to bump the other with its head. This bumping ceremony or “nudging” is performed by swinging the body backwards and forwards in the horizontal plane while the tarsi are firmly fixed to the floor of the gallery by the claws. The body is thus held rigid and a piston-like movement is effected with the help of the legs. When a series of short sharp bumps with the head on any part of the other termite have been delivered, both termites will then pass on their respective ways. “Nudging” is very common, and can be observed almost at any time a colony of *S. ruficeps* is examined. Feeling other individuals with the antennae may not always be accompanied by “nudging” and is equally as common within the termite colony as a means of communication between its members.

(ii) Warning: This is a remarkable form of communication in that it can be heard more than three feet from the infested piece of wood and may be demonstrated easily by disturbing the colony. The soldier caste is the main participant though Kofoid (1934) states that the nymphs feebly try to imitate the behaviour of the soldiers. If a piece of wood containing a termite colony is shaken vigorously a distinct repeated tapping sound will be heard. This is the result of a soldier rapidly striking its hard head against both walls of a gallery. This phenomenon has been observed in laboratory-kept *S. ruficeps*. The soldier firmly grips the floor of the gallery with its claws then vibrates the whole body, so that the large head successively hits on either side of the gallery. The sound resembles that of a solid stick being tapped rapidly against a hollow stick and has a marked effect on the activity within the royal cell. Usually the reproductive pair will make their way into a narrow side gallery while the soldiers in the vicinity will guard the openings to the royal cell. The nymphs do not appear to be greatly affected except that their actions may some-
times quicken and smaller nymphs will often quickly return to the galleries adjacent to the royal cell as if either placing themselves between the royal pair and any would-be invader, or returning to the protection of the soldiers.

**Cannibalism**

This habit is one which has been, along with grooming, a basis for termite control. Theoretically, poisoned termites will be eaten by other members of the colony, and successive poisonings and deaths in this way will kill out the colony. Cannibalism can be divided into two relatively distinct categories depending on the original motivating stimulus.

(i) *Unintentional* This usually emanates from a harmless grooming during which an appendage on the insect being groomed is accidentally damaged or broken off. Castle (1934) reports this as occurring in *Zootermopsis sp* but does not distinguish it from other types of cannibalism. The taste of the body fluid which aggregates at the wound probably excites the groomer to attack and eat the accidentally damaged termite. Observations on *S. rufecep* indicate that when a termite is damaged in any way it attempts to move away to an isolated area, and only in a few instances is a slightly damaged termite killed. Often on examining termites from a colony, loss of part of one or both antennae or a part of a leg was observed in otherwise healthy individuals that were evidently maintaining their place in the community.

(ii) *Intentional* This form of cannibalism is often related to the phenomenon known as caste balance. Caste balance arises from the necessity to restrict those castes which cannot feed themselves to numbers that can be cared for by the worker or nymphal caste. At certain times of the year an old termite colony may have a predominance of one caste. For example, from spring to late summer in an old colony of *S. rufecep*, the nymphs as they reach the fifth stage (Text-fig 3, Fig 6) may develop rapidly to perfect insects or alates by successive moults separated by short periods of growth. By early autumn large numbers of alates (Text-fig 3, Fig 9) are present in the colony. To protect the colony at swarming time emergency soldiers (Text-fig 2, Fig 14) develop from nymphs reaching the fifth stage after the alates have matured. After the swarm the colony is left with the reproductive pair and nymphal stages occasionally up to the early seventh instar (Text-fig 3, Fig 8). The latter, which did not have sufficient time to mature for the autumnal swarm, cease further development until the following spring. In addition there are more soldiers than can be fed and cared for conveniently by the remaining nymphs. Instead of a usual complement of soldiers of between 4 per cent and 7 per cent of the colony, the nymphs must now feed between 25 per cent and 40 per cent of the colony. The soldier caste has therefore become imbalanced in its relationship to the colony as a whole. At such times the smaller or emergency soldiers are attacked and partially eaten by the nymphs, or are starved to death, the remains of these soldiers often being finally destroyed by funerary activity. Castle (1934) has observed this phenomenon among colonies of *Zootermopsis sp*.

Intentional cannibalism also includes the eating of weak, diseased and dead termites by the nymphs. Any individual within a colony may be attacked by the other members though nymphs and soldiers are the main castes affected and nymphs are mainly responsible for the attacks. Though not common, one of the primary reproductives in a colony may be killed and eaten by the nymphs and later replaced by a neotenic. In colonies of *S. rufecep* the male primary reproductives was sometimes lost from colonies in their third year.

Termites from separate colonies even of the same species when coming in contact will kill and eat each other (Kofoid et al. 1934). In this study if groups of individuals from the same colony were separated for more than a week then placed together again, cannibalism occurred. In all cases the cannibalism was marked at first followed...
by a gradual decrease in its intensity until the normal rate of cannibalism present in a colony was reached again, and the remaining individuals lived together as one colony.

If a young reproductive pair is removed from a young colony of S. ruficeps after the first batch of nymphs has reached the third instar, the reproductives will die in from 48 to 96 hours. If, however, they are still alive at 48 hours and are returned to the colony from which they were taken the nymphs will attack them.

With S. ruficeps the legs are often attacked first to render the termite immobile, followed by an attack on any intersegmental region from behind the head to between the second and third abdominal segment. Sometimes all the body is eaten except for parts of the head. The anterior three-quarters of the mandibles of a soldier is sometimes the only evidence remaining that cannibalism recently occurred. Often full heads remain, less frequently the head and thorax are left, while at other times only a piece is eaten out of the side of the body. Commonly these remnants are destroyed by fungi, but observations indicate that even long after the first outbreak of cannibalism nymphs will occasionally feed on the remains of termites until they have disappeared.

Defence

Protection against invaders of all kinds is given to the colony by the soldier caste. Though in other termites (e.g., the Termitidae) a type of chemical warfare has been evolved (Kofoid et al., 1934), the soldiers of S. ruficeps rely entirely on their ability to seize and injure invaders with their strong toothed mandibles. Usually as soon as the workings of S. ruficeps are disturbed, a soldier will appear in the opening of the gallery and opening and closing its mandibles in a snapping manner will prepare to guard the colony. Other soldiers then warn the main body of the colony by making the tapping sound previously described and other soldiers guard the entrance to the royal chamber. This sequence of events appears to be normal for S. ruficeps though often there are no organized defence measures when a colony is opened for examination. It appears to depend on whether the colony has been disturbed frequently in the past or not.

In S. ruficeps as in Kalotermes minor (Harvey, 1934) there are, at most times of the year, few soldiers present in the colony. This is probably due to the fact that under normal conditions they are seldom disturbed and their defences are thus seldom taxed. Nymphs take part in the defence of the colony by sealing up breaches made into the runways and eating damaged and dead invaders. No large scale attack by an invader could be repelled by the few soldiers present in a colony of S. ruficeps at most times of the year. The real defence of the termite colony is in the maze of galleries it inhabits and the natural cryptobiotic habit of its individual members (Light, 1934).

Formation of Frass Runways, Plugs and Tunnels

Frass Plugs. (Text-fig. 1, Fig. 1B.)

These are very common in all termite workings, the first frass plug being built by the young reproductives just after their entry into wood. Such plugs are used to seal off disused galleries and any openings made in the gallery walls. They are made from rotten wood and frass pellets stuck together with liquid from the mouth or anus of the termite. Liquid obtained from the galleries or present in the decayed wood used in the construction of the frass plugs is an aid to their manufacture. They protect the colony by segregating it from predators and disease.

Frass Runways. (Text-fig. 1, Figs. 3, 4 and 5.)

Known variously as covered runways or tunnels, covered galleries, and tubes (Kofoid et al., 1934; Fugatt, 1913) these structures are used to protect foraging individuals and are not usually associated with termites other than those of the subterranean group. Covered runways are extremely common in the workings of the Rhinotermitidae and Termitidae as well as in the subterranean members of the
Hodotermitidae. They have been reported occasionally from wood-dwelling termites *Z. angusticollis* will often build runways through earth under laboratory conditions, but this has not been reported from field observations on the species (Castle, 1934).

Colonies of *S. ruficeps*, particularly those inhabiting wood with very high moisture contents and with much free water in their galleries, often form covered runways and tubes from one piece of wood to another under laboratory conditions. These runways are little different in construction from those of the Rhinotermitidae and Termiteidae that I have seen in Australian hardwood importations. Usually much earth or clay is used in the manufacture of covered runways by subterranean termites, but on occasions these termites construct runways from frass pellets, fragments of wood and any soil or dust that may be available.

As far as can be ascertained this is the first time that covered runways have been reported for a termite native to New Zealand, and also the first time it has been reported for the Stolotermitinae.

One runway built by a colony of *S. ruficeps* in the laboratory in August, 1951, was sketched and measured (Text-fig 1, Fig 3). The runway was constructed from one piece of wood ("A") across a splinter of wood to another piece of wood ("B") for a distance of $\frac{3}{4}$ in. It was then continued at right angles to the first section in one direction for a distance of 4 inches along "B". This part of the runway occupied the colony containing 28 nymphs of instars 3 to 7 for 14 days. In the next 10 days a further 3½ inches from the original stem in the opposite direction along "B" was completed. In cross section the runway was in the form of a semicircle slightly flattened on top, the wall of the tunnel being significantly thicker at the base than in the arch. The internal measurements of the tunnel were on the average height 3 0 mm; width, 4 5 mm. The wall was approximately 1 5 mm thick at the base and 0 8 mm thick over the arch. This runway was used constantly, the termites passing from an exit from the wood at one end along the runway to an entrance into the wood at the other.

The commonest type of runway formed in laboratory-kept *S. ruficeps* is better referred to as a shaft or tube (Text-fig 1, Fig 5A). These shafts or tubes are usually built between two pieces of wood, one of which is above and separated from the other. They may be built either from the lower piece of wood to the pieces above or vice versa, and they are constructed of the same materials as runways and plugs. They are spherical in section and seldom reach lengths greater than an inch. Such tubes are also characteristic of other termite groups, notably those of the subterranea³ habit (Pickens, 1934).

**Life Cycle**

Mature alates (Text-fig 3, Fig. 9) swarm in the autumn, dealate, and pairs re-enter a suitable habitation. Matting occurs after the first cell is constructed, and eggs are laid in the following spring. The incubation period varies between 26 and 54 days, depending on the temperature and, following eclosion, the young are fed and cared for by the primary reproductives up until at least the second stage. Thereafter the nymphs take over the task of building the nest and feeding the soldiers and reproductives. In *S. ruficeps* the development of nymphs involves 7 instars, the seventh being the penultimate or the one before the imago is reached. The first batches of nymphs in a colony may represent a temporary worker caste and alates may not be produced until the colony is over 3 years old. All nymphs produced by a reproductive pair, provided that development is not interrupted by death, will ultimately become either soldiers or reproductives. The life cycle occupies various periods of time for the different nymphs of a colony. The first four stages together regularly occupy approximately three months, but the last three vary greatly, depending on ecological conditions, and on the biological necessities of the colony as a whole. In large and therefore old colonies, alates are released each year.
TEXT-FIG 1—Fig 1—The initial cell (royal chamber) of a young pair of reproductives six months after swarming (Natural size) A, the first egg; B, the entrance hole with frass plug; C, the royal chamber proper; D, the egg chamber. Fig 2—The cross section of a decayed log showing the workings of a colony of Stolotermes ruficeps (× 0.08) A, ground surface; B, entrance channel and royal chamber; C, exploratory gallery from site of main infestation to centre of log. Fig 3—Covered runway (A) built by a colony of S ruficeps under laboratory conditions (× 0.33). Fig 4—Cross section of covered runway, Fig 3 (A), (× 1.33). Fig 5—Frass tube built by S ruficeps under laboratory conditions (natural size). Fig 6—Group of frass pellets from colony of S ruficeps showing lateral grooves dotted. Fig 7—Labrum and maxilla of soldier. Fig 8—Labrum and clypeus of soldier. Fig 9—Labrum of nymph. Fig 10—Hypopharynx. Fig 11A—Leg 1, Coxa; 2, Trochanter; 3, Femur; 4, Tibia; 5, Tibial Spur; 6, Tarsus; 7, Claw. Fig 11B—Tarsus.
Transactes

Figure 1—Diagram of Life Cycle, S. ruficeps Blauer.

Reproductive Pair

Fertilised Eggs

Nymphs

Soldier-Nymphs

Soldiers

minimum period possible from egg to alate is from spring to the following autumn (usually about eight months) and these alates will produce eggs the following spring, making a life cycle of one year. In many cases the life cycle will, however, vary up to two years and may extend beyond this length of time under unsuitable conditions and during the first few years of colony development.

Swarming

Three flights, two in April, 1948, and one in May, 1950, were observed during this study. Two of them occurred in the field at Days Bay and the other took place in the laboratory. In all three cases atmospheric conditions were comparable (Table I) based on recordings taken at Kelburn.

Table I—Details of Observed Flights of Alates of S. ruficeps

<table>
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<tr>
<th>Date</th>
<th>Flight No</th>
<th>Altitude, Ft (Above Sea Level)</th>
<th>Aspect</th>
<th>Temperature (Degrees C)</th>
<th>Rainfall (in inches)</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Max</td>
<td>Min</td>
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<tr>
<td>18.4.48</td>
<td>1</td>
<td>400</td>
<td>West Slope, 1 in 14</td>
<td>64.4</td>
<td>52.5</td>
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<td>2</td>
<td>350</td>
<td>West Slope, 1 in 10</td>
<td>60.1</td>
<td>55.3</td>
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<td>19.4.48</td>
<td>3</td>
<td>200</td>
<td>In laboratory</td>
<td>62.8</td>
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In flights 1 and 2 the alates emerged from small oblong holes about 12 mm × 6 mm in dimension. The exits appeared to have been made by nymphs, but these may have been assisted by the first alates that emerged. The swarmings took place about dusk (between 4.30 p.m. and 5 p.m.) and following afternoon rain. The exits were closed up by nymphs after the swarmings. A number of soldiers were observed in and around the exit while the nymphs were at work. In flight 1 some 1,500 to 2,000 alates took part, while only a few hundred were released in flight 2.
In each case the alates struggled and tumbled out from the galleries, many (70 to 80 per cent) shedding their wings immediately and moving quickly to shelter in cracks and holes in the logs from which they had emerged. About 10 to 20 per cent flew up to 20 yards and only a very small proportion (1 to 3 per cent) flew further than 30 yards and attained heights of up to about 30 feet above ground. Flight was clumsy with a slow, strong wing-beat, toward the highest light intensity, and altitude was gained quickly at an angle of about 45 degrees. A certain amount of grouping was observed during flight and numbers of individuals consistently landed in the same vicinity. Up until the landing a strong attraction toward light was exhibited by all individuals, but as soon as the wings were shed the behaviour toward light was negative.

The wings are usually cast soon after the alates complete their first flight. This is in direct contrast to the behaviour of the alates of *Kalotermes brouni* Fragnet, which have been observed to fly and land several times before shedding their wings. In *S. rufeceps* the wings are cast singly. The forewings are in turn thrown forward over the head and tend to bend or break along the basal suture. By turning round and round or rubbing up against objects nearby, the alate brushes off the wing. The same method is used for each wing, and all are discarded within a few seconds.

The dominant activity of the dealates is the immediate return to the cryptobiotic habitat that they so recently left. There appears to be little actual pairing of the sexes before attempts to re-enter suitable wood are made. Certain females were seen to raise the tip of their abdomens and move rapidly among other individuals. In only a few instances were males attracted by such activity. The need to enter wood seems to be so dominant in their behaviour that several individuals cram into each small crack or hole available. The exit holes of cerambycid beetles and the rough broken ends of branches appear particularly suitable to the dealates. Very little boring into wooden surfaces appears to occur in the field as there are always sufficient cracks and holes available to the searching termites. Collections of dealates that entered holes and cracks first showed that females predominated by about 8 to 1. The sex of those that followed was either male or female, with males dominating by 3 to 1. Sometimes more than one male entered with a female, and records of two females per male were made. Single dealates of both sexes were found in some sealed cavities. Where only two dealates were in the initial cell, a reproductive pair was present in seven cases out of every eight. In cases where two females were present no egg laying was recorded. In such cases the boring rate and pattern were similar to those of reproductive pairs.

The behaviour during and following the swarm recorded for *S. rufeceps* has many points of similarity with that reported by Castle (1934) for *Zootermopsis angusticollis*. The time of day, weather conditions, and pattern of flight, however, differ markedly with those reported for *Kalotermes minor* Hagen by Harvey (1934). In this species and in *Zootermopsis* spp. there is also apparently a much stronger pairing behaviour of the sexes before re-entry of wood than has been recorded for *S. rufeceps*.

An examination of both colonies from which flights occurred, indicated that the alates released constituted some 80 to 90 per cent of each colony. Only nymphs to stage 5, soldiers and reproductives remained. It appears that nymphs reaching the fifth stage by the spring or early summer develop to imagines and fly in the autumnal swarm. Those that develop to this stage later in the summer are apparently retained in the colony.

In the flight that took place in the laboratory, individuals were forced to bore into the decayed wood placed in the containers for them. After exhibiting some degree of pairing behaviour, the females searched the surface of the wood with their mouth parts and antennae. When a suitable site was found the female commenced entry. In most cases boring was started in the most sheltered position available. Where two pieces of wood were in close proximity to each other the dealates crawled between
them and "cemented" the pieces together in such a way as to form a cell in which mating and egg-laying took place. Where boring directly into wooden surfaces, the female took from 3 to 27 hours to construct a hole large enough to contain itself. When the hole is constructed other individuals entered it also, and in most cases these were males. The males do not appear to take a very active part in boring the initial entrance, though some did clear away the borings and frass formed by the females. Once wood is entered it seems highly probable that both take part in constructing the royal cell, as both must feed on the wood until the first nymphs are old enough to care for the young colony.

Discussion on Swarming of Alates

From my observations on S. rufecep{s} and records by Castle (1934) on Z. angusticolitis and Light (1934) on Kalotermes sp, it would appear that:

(i) The swarming of alates of S. rufecep{s} and Z. angusticolitis is comparable, though pairing behaviour is more marked in the latter species.

(ii) On release the alates of all three species are strongly attracted to light. Once the wings are shed the behaviour pattern reverses.

(iii) The majority of the alates do not fly at all or fly very short distances. Those of the dampwood group shed their wings after one flight while the alates of Kalotermes spp. may fly and land several times before casting off their wings.

(iv) Altitude during flight is reached rapidly in all species. In S. rufecep{s} no great heights were recorded but in Z. angusticolitis an alate infestation has been recorded on the roof of a seven-storey building (Castle, 1934). Aerial collections of other species have been taken at 3,000 feet. In this instance wind was considered responsible (Light, 1934).

(v) In all three species a majority of the colony is released during swarming.

(vi) Dealates may locate wood suitable for entry by its odour (Castle, 1934). In the case of S. rufecep{s} there is a definite "working" of the wood surface with the mouth parts and antennae before a site is chosen. In most cases dealates crawl into the exit holes made by other insects, cracks in the wood, or crawl between pieces lying in close proximity to each other. Where boring is directly into wooden surfaces it is undertaken only from the shelter of leaves and other debris. Depending on the state of the wood it takes a female dealate 3 to 27 hours to bore the entrance channel. In Kalotermes spp. it takes about 48 hours for dealates to enter sound, dry wood (Light, 1934).

(vii) In S. rufecep{s} and Z. angusticolitis the females do most of the initial boring, while in Kalotermes spp. both sexes share in this work.

Activities of Dealates in the Wood

It has been stated above that in the somewhat haphazard behaviour during entry into suitable wood one to several individuals may occur within any suitable cavity. As already observed, most often at least a pair enter each cavity. In the other instances observations indicate that single individuals eventually die after excavating a small chamber, while where there individuals occur together a pair may result and the extra one remains for some time as a supernumerary. Though no evidence is available for the assumption, it is nevertheless possible that, should the corresponding sex of the mated pair die, the supernumerary could fulfil an important function in the survival of the species. Other entomologists (Light, 1934) have always considered that the original dealates are inseparable except by death and that promiscuous matings between several individuals do not occur in the termite world. However, on the death of one or both of the royal pair, neotines are developed, and it seems likely that should an extra dealate be present in a young colony it would probably take up its reproductive role.
Where two pairs of dealates enter the same hole, two colonies result from a separation of their respective royal cells by a frass wall or plug. The normal sequence of events concerning reproductive pairs after entry of wood is that the female appears to be more industrious and does most of the work of establishment. The boring rate is constant but the amount of work completed in a given time depends to some extent on the state of the wood, the presence of other insect workings, and the severity of the winter climate of the locality. When a cell about 25 mm by 12 mm by 8 mm has been constructed, mating takes place. Copulation has been observed in laboratory-kept dealates and consists of the reproductive pair touching the tips of their abdomen together and remaining thus for an indefinite period, usually two minutes but varying from 30 seconds to at least 7 minutes. Castle (1934) reports a copulation period of from 1 to 4 minutes in Zootermopsis.

Six months after swarming, the galleries (Text-fig. 1, Fig. 1) constructed by reproductive pairs of *S. ruficeps* consisted in basic plan of a main gallery 50 mm to 75 mm long by 6 mm to 12 mm wide, plus a lateral gallery 12 mm to 40 mm long in which the first egg was deposited. Boring followed the direction of the longitudinal axis of the log. In 15 months a new colony of *K. minor* removes 0.50 to 2.5 cc of wood by its activity (Harvey, 1934).

In laboratory-kept *S. ruficeps*, the first egg was laid in October by a pair that had swarmed the previous April. Egg laying was initially sporadic, and after 12 months only 24 eggs had been laid in three or four batches with rest periods alternating with laying. Eggs are laid by *Z. angusticollis* 14 to 18 days after copulation, but in the case of *Z. nevadensis* Hagen, the period between copulation and egg laying is in excess of five months, the eggs being laid the spring following the autumnal swarm (Castle, 1934) *In S. ruficeps* four to seven eggs were laid over a period of eight days and then a resting period ensued during which the reproductive pair tended the eggs, moving them about, picking them up and cleaning them with the mouthparts. The eggs (Text-fig. 3, Fig. 1) when laid are 1.00 to 1.35 mm long and 0.59 to 0.87 mm wide, are white, bean-shaped, and are enclosed in a smooth membrane or chorion. They are usually lightly cemented together in clusters of varying numbers.

**Incubation of Eggs**

To determine the incubation period, all eggs were removed from an active colony so that subsequent layings could be dated. As eggs were laid they were removed to containers in which nymphs to the fifth instar had been placed. The containers were covered to reduce moisture loss. One was left on a table in the laboratory, while others were placed on top of an oven maintained at 37.5°C.

Temperatures inside the containers were checked twice a day, and a few drops of water were added when necessary to maintain humidity. Egg counts were made at intervals of seven days to ensure that nymphae reproduction had not commenced. Dates of hatchings were recorded, and the incubation period was found to vary between 33 and 54 days, at an average temperature of 18°C, and 26 to 44 days at an average temperature of 20°C.

If a young colony with nymphs up to the second and third instars is opened, often no eggs will be observed in the galleries, and side galleries from the main two bored by the young king and queen will have been commenced by the nymphs. As the first nymphs are cared for by the reproductives up until the second or third stage, the queen does not appear to lay eggs during this time and following it undergoes a short rest period. The nymphs take over the menial tasks of the colony at about the third instar and in effect represent a worker caste. At about this time (from three to four months after the first egg was laid) the second batch of eggs, usually from 6 to 12 in number, is laid. As the eggs are laid, they are picked up by the nymphs and stored in the end of a gallery. The eggs are again usually lightly cemented together in clusters of from 2 to 12. In such clusters they are moved.
about each day by the nymphs Castle (1934) refers to this care of eggs in Z. angusticollis, stating that the daily movement of the eggs allows for aeration and the changing of the eggs to the most suitable part of the gallery. The movement may also prevent adhesion of the embryo to non-embryonic surfaces, which is probably as important to the successful incubation of termites' eggs as it is to the incubation of eggs of other animals, notably birds. By the time the second batch of eggs has hatched, the first nymphs are caring for the colony, and the royal pair, if isolated, will die in 48 to 96 hours. These times were recorded in laboratory tests carried out to ascertain at what stage reproductives lose the power to feed themselves.

**Instars**

The number of instars was determined by following the development of individuals from the hatching of the first eggs in young colonies. Seven instars were recognised and each stadium was found to vary slightly. There was an increase in length up to the fifth stage (Table II). Stage 3 may be very long in young colonies where the fifth instar represents a temporary worker caste due to a period when development ceases, temporarily. It can be as short as 14 days in older colonies preparing for an autumnal swarm. Stages 6 and 7 are sometimes of short duration but may last from one November to the next. Unpigmented imagines may be found from December to February and fully pigmented adults from late December to May. Swarms may occur from March to May.

Variation in the later stadia is probably related to the age and constitution of the colony, and to the ecological conditions prevailing at critical times. Caste balance seems to be an important factor in the length of time each stage occupies. It is known that no alates are produced by S. ruficeps for at least the first 3 years of development. Thus the few nymphs produced in that time are all required to do the colony tasks and so promote the stability of the infestation. In other cases where a colony has a reduced food supply many alates are produced, leaving only the reproductives and soldiers of the parent colony to perish from starvation.

The average measurements for each instar are given in a later section describing the external morphology and outline drawings are included in Text-fig. 3, Figs. 2 to 8.

**Table II**

Variation in the Length of the Stadia in the Development of Nymphs of Stolotermes ruficeps Compared with those of Zootermopsis angusticollis as reported by Castle (1934)

<table>
<thead>
<tr>
<th>Instar</th>
<th>Length of Stadium in Days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S. ruficeps</td>
</tr>
<tr>
<td>1</td>
<td>8 to 11</td>
</tr>
<tr>
<td>2</td>
<td>18 to 21</td>
</tr>
<tr>
<td>3</td>
<td>21 to 24</td>
</tr>
<tr>
<td>4</td>
<td>42 to 48</td>
</tr>
<tr>
<td>5</td>
<td>14 plus</td>
</tr>
<tr>
<td>6</td>
<td>10 plus</td>
</tr>
<tr>
<td>7</td>
<td>6 plus</td>
</tr>
</tbody>
</table>

** Colony Structure - Castes **

In a colony of S. ruficeps there is a division of labour among its members correlated with a specialisation of structure and behaviour. Thus any colony when examined will be found to consist of individuals which can be divided up into several morphologically different types called castes. All castes when examined are found to contain both females and males, and represent fairly definite proportions of a colony at any one time, though variation occurs with changes in the needs of the colony as a whole. The ratio of each caste to the colony has been studied in respect of S. ruficeps. Caste typically refers to an end line of development and is not properly
Fig 1—Antenna of a third instar nymph of Stolotermes ruficeps showing characteristic features. Fig 2—Soldier, ventral view. Fig 3—Lateral view of the abdomen of a sixth instar nymph (not to scale) showing tergites 1 to 10 (T1-T10), Sternales 2 to 10 (S2-S10). Spracral (B represents abdominal spraca 1) and the intersegmental membrane (A). Fig 4—Lateral view of head and thorax of a sixth instar nymph (not to scale). Fig 5—Labrum, 2, Anteclypeus, 3, Postclypeus, 4, Basal segment of antennae, 5, Brorns, 6, Pigmented eye, 7, 8 and 9, Episternum of prothorax, 10, Pronotum, 11, Epimeron of prothorax, 12, Cova (i), 13, Spracral (i), 14, Episternum of mesothorax, 15, Epimeron of mesothorax, 16, Mesonotum, 17, Spracral (ii), 18, Episternum of metathorax, 19, Epimeron of metathorax, 20, Metanotum, 21, Merum (ii), 22, Cova (ii), 23, Merum (ii), 24, Cova (i), 25, Trochantin (i), 26, Laterosternite (ii), 27, Labrum, 28, Labial palp, 29, Maxillary palp, 30, Left mandible. Fig 5—Head of slate, dorsal view (not to scale). A, antennae, B, Antenna, C, to scale. Fig 6—Head of slate ventral view (not to scale). A, antennae, B, Antenna, C, to scale. Fig 7—Mandible. Fig 8—Ventral view of thorax of slate (not to scale). 1, Ventral cervical sclerite, 2, Anterior lateral cervical sclerite, 3, Prosternum, 4, Posterior lateral cervical sclerite; 5, Episternum (i), 6, 7, Trochantin (i), 7, Sternum (i), 8, Epimeron (i), 9, Cova (i), 10, Episternum (ii), 11, Epimeron (ii), 12, Sternum (ii), 13, Laterosternite (ii), 14, Trochantin (ii), 15, Furca, 16, Cova (ii), 17, Sternum (iii), 18, Episternum (iii), 18A, Epimeron (iii), 19, Furca, 20, Merum (iii), 21, Cova (iii), 22, Abdominal Sternum. Fig 9—Ventral view of mandibles of fourth instar nymph (A) and sixth instar nymph of Stolotermes ruficeps (B) with grinding surfaces shaded (not to scale). Fig 10—Dorsal view of mandibles of soldier. Fig 11—Ventral view of maxilla and labium of sixth instar nymph. 1, Maxillary palp, 2, Galea, 3, Lancina, 4, Subpalp, 5, Cardo, 6, Culicidentum, 7, Labial palp, 8, Paragatoma, 9, Glossa, 10, Prementum. Fig 12—Soldier (dorsal). Fig 13—Heads of soldiers from same colony showing sequence of development. A, soldier head after moult from nymph; B, head of intermediate stage; C, head of mature soldier. Fig 14—Emergency soldiers from same colony, showing head variations. Fig 15—Soldier from laboratory colony inhabiting wood with moisture content of 20.5 per cent.
used to describe immature forms. In *S. ruficeps* there are only two castes, the soldiers and reproductives, though the latter may be sub-divided into primary and supplementary forms which carry out a similar function but which are morphologically distinguished from one another. Except for certain neoteinecs no definite caste seems to have been determined up to and including the fifth stage, where a static period in development may occur that is significant to the colony as a whole. From individuals retained in the fifth stage, emergency reproductives and soldiers may be developed as demanded by colony requirements.

**Soldier Caste**

Soldiers are characterised by their large pigmented heads and long mandibles. Due to these specialisations they cannot chew wood and must be fed by the nymphs. They also eat faecal pellets and fungal spores (Hendee, 1934). They may vary in number in any colony dependent on the time of year, frequency of disturbance, and needs of the colony. Under normal conditions they represent about 7 per cent of the colony. As the colony grows the numbers of soldiers increase, but the percentage decreases sometimes to less than 2 per cent. Several forms are distinguishable by the difference in body size and head shape (Text-fig 2, Figs 12 to 15). All forms may be found in one colony, but usually the typical form is that shown in Text-fig 2, Figs 2, 7, and 12.

The strength in the closing movement of the mandibles is such that an individual may be picked up by placing a sliver of wood between its mandibles and allowing the insect to bite it. The pressure exerted is sufficient to bite off legs and other appendages of insects. If a soldier is disturbed sufficiently, it will attack other termites in its own colony, leaving the injured insects to be partially eaten by nymphs or to be destroyed by fungal agencies. In one observed instance, a soldier had been greatly disturbed during an examination of a colony, and finally attacked some members of its own colony, biting the queen in two through the second thoracic segment. The soldiers never reach sexual maturity.

At swarming time in *S. ruficeps* and about 48 hours after a colony has been considerably disturbed, soldiers may represent up to 30 per cent of the colony, though this proportion does not last long due to the burden of extra feeding placed on the nymphal stages. After the swarm, all the smaller soldiers, here called "emergency soldiers" (Text-fig 2 Fig 14), are killed off by the nymphs or die of starvation. In this way the caste balance within the colony is restored. The greater numbers of emergency soldiers appear to be derived from fifth instar nymphs, are smaller, and vary in head shape considerably from soldiers that develop under normal conditions from sixth instar nymphs. Observations indicate that individuals in stage 5 undergo an ecdysis, after which the head is slightly longer than wide, and the mandibles are slightly elongated at their bases, giving a definite first stage of development into a soldier (Text-fig 2, Fig 13A). In one instance observed only one such individual could be so distinguished in a young colony. I examined the colony again after 22 hours and noted that the same individual was almost through a second moult, and the head and mandibles were almost fully developed to the stage of a mature soldier though there was a total absence of any pigmentation on the head (Text-fig. 2, Fig 13B). A count of the individuals of the colony was made, and proved that the individual was the same one that had passed through a moult from the fifth instar 22 hours before. Unfortunately, this observation was not subsequently repeated, nor was the cause of emergency development apparent. It was noted that, in previously observed ecdyses, individuals became isolated within the galleries for some hours before commencing to moult. When other nymphs came in contact with such individuals there was a rapid movement away from them. However, after the moult, nymphs appeared from the connecting galleries and groomed and fed the newly moulted termite. I noted that when the termite had been thoroughly groomed it was fed either food regurgitated from the mouth or excreted from the anus, of an
older nymph. This may have some bearing on the future development of the individual, for in the case of emergency soldier formation already discussed above, only regurgitated food was given between the molts. It is reasonable to assume that food regurgitated from the mouth will contain saliva and gastric secretions, though most digestion probably takes place in the hind gut where the flagellates and their bacteria are located. It would be much more concentrated in such secretions than food that had passed through the alimentary tract. Thus food rich in glandular secretions may play an important role in the development of castes from various instars.

**REPRODUCTIVES**

(1) Normally only a small percentage of a colony are reproductives, but neotenic is more numerous than primary reproductives in a compound colony or one having several reproductive centers. In nature neotenic reproductives are only distinguishable from nymphs when they are sexually mature. No special group of nymphs is set aside within the colony from which neotenics develop as required. They occur commonly in *S. ruficeps*, where they comprise from 1 per cent to 4 per cent of the complement of compound colonies. Apterous neotenics (Text-fig. 3, Fig. 10A) are most common, but brachypodous forms (Text-fig. 3, Fig. 10B) are frequently found. The latter are of rare occurrence in *Z. angusticollis* (Castle, 1934). When immature they are called nymphs and may help with the tasks of the colony. When mature they take on the form of a royal pair, differing in not being fully pigmented and in having no wing stumps. As in *Zootermopsis* (Light and Illg, 1945) and *Kaloterme* (Harvey, 1934), the neotenic reproductives of *S. ruficeps* may be matured from nymphs of all instars from the fourth to the early seventh, both inclusive. Neotenics developing from third instar nymphs have been recorded for *Zootermopsis* sp. (Castle, 1934). Under natural conditions colonies of *S. ruficeps* are usually of the compound type, the primary reproductives being found near the point of original infestation, and brachypodous and aperures reproductives occurring at points throughout the rest of the colony workings. Some colonies opened in the field have been found to have functioning reproductives within 100 mm of each other, and in one instance I extracted three apterous queens from a piece of wood 150 mm long by 100 mm wide by 40 mm thick. Neotenics have a significant effect on colony growth (Castle, 1934; Heath, 1927). Pseudo-soldier-nymphs are described by Castle in fifth instar nymphs of *Z. angusticollis* and it is probable that he is referring to individuals "retained" at this stage for emergency development into soldiers or reproductives. As has already been stated, neotenics develop from individuals of the fourth to early seventh instars. Only primary reproductives develop further than the early seventh stage.

In experiments designed to test the instar/neotenic relationship, the relative rapidity of sexual maturation was gauged by the length of time taken to produce the first egg. This is shown in Table III.

**Table III**

<table>
<thead>
<tr>
<th>Instar</th>
<th>No of Isolated Termites</th>
<th>Days Till First Egg Laid</th>
<th>Instar of Neotenics</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>20</td>
<td>65</td>
<td>4</td>
<td>Development into 4th stage</td>
</tr>
<tr>
<td>4</td>
<td>20</td>
<td>38</td>
<td>4</td>
<td>No 5th stage termites</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>30</td>
<td>5</td>
<td>No 6th stage termites</td>
</tr>
<tr>
<td>6</td>
<td>20</td>
<td>32</td>
<td>6</td>
<td>No 7th stage termites</td>
</tr>
<tr>
<td>Early 7</td>
<td>7</td>
<td>57</td>
<td>Early 7</td>
<td>No late 7th stage termites</td>
</tr>
<tr>
<td>Late 7</td>
<td>20</td>
<td>No eggs produced</td>
<td>None produced</td>
<td>Developed to alates</td>
</tr>
</tbody>
</table>
The two distinct forms of supplementary reproductives are distinguishable, the apterous (Text-fig. 3, Fig. 10A) and brachypterous (Text-fig. 3, Fig. 10B). The wing buds, commencing development in the late sixth stage, become visible to the naked eye on the seventh instar nymph as dorsal backwardly directed buds projecting from under the lateral edges of the mesonotum and metanotum (Text-fig. 3, Fig. 10B). Thus the brachypterous neotenic, which develops at a later stage, has wing buds and the apterous neotenic has none. Light and IIlg (1945) report sixth instar brachypterous neotenics and seventh instar apterous nymphs in Zootermopsis. The above tests with S. ruficeps (Table III) showed that neotenics are formed readily by fourth, fifth and sixth instar nymphs but not nearly as readily by seventh instar nymphs. Late seventh instar nymphs failed to produce neotenics, but continued development to imagines.

(u) Primary Reproductive These individuals are often called the royal pair, and are the most important reproductives in the termite world. They are specially important in the dampwood and drywood groups as they are the only means of spreading the infestation from one site to another through their ability to fly varying distances during the alate stage. Brachypterous and apterous reproductives are important both in spreading the colony throughout the available habitat and also in increasing the rate and extent of colony growth, but they still do not spread the species to different and distant sites.

The female primary reproductive or queen has an indeterminate period of existence that on my own observations seems to be controlled more by changes in ecological conditions than by the presence of a definite life span. No records of reliable ages of old queens are available, but by the study of colony growth and development, fairly reliable estimates can be made on the ages of colonies still having a primary queen. Escherich (1911) on Macrotermes bellicosus found that while queens of new colonies were under an inch in length, queens from really old colonies of the same species measured up to 5 inches long. The increase in length is due to the expansion of the abdomen in conjunction with the increase in size of the ovariess. This phenomenon is called physogastry. Light (1934) quotes Fuller as recording that old queens in certain tropical species lay an estimated 4,000 eggs per day, Emerson as reporting a count of 7,000 eggs laid on one day by a queen of the South American termite Anoplotermes silvestris, and Bugnon as estimating that the ovaries of a queen termite from Ceylon contained at any one time 48,000 eggs. These old queen termites of the subterranean group reach a size where they can no longer move around and become stationary. In the dampwood termites this never happens. Queens that could not move around freely have not been observed in colonies of S. ruficeps. Physogastry and consequently egg production is restricted within fairly definite limits. Old queen termites in S. ruficeps never appear to reach more than one and a half times the length of the alates, but the abdominal width of an old queen is nearly twice that of the alate. The laying capacity of an old queen would probably reach a maximum rate of 60 eggs per day over short periods with resting periods between the laying periods.

Other observations showed that eggs are laid at night and during all seasons of the year. In colonies of Zootermopsis spp. eggs are also deposited for from six to eight months. The remainder of the time is spent in a resting stage for recuperation (Castle, 1934). A laying rate for apterous neotenic queens of from 30 to 40 eggs in a few days has been recorded by Castle. It may be possible that the rate of egg production is slower in such queens in Zootermopsis than in S. ruficeps for an apterous neotenic queen of the latter species has been observed to lay 24 eggs in a period of 20 hours.

Factors limiting the life span of a termite queen include:

(i) The loss of food supply

(ii) The excess or paucity of available moisture
(iii) Upset of balance between fungal activity and fungal control by the termites
(iv) Successful attack by predators
(v) Extreme conditions of heat or cold
(vi) Damage from other sources.

The primary male reproductive or king is initially as important as the primary queen, for without the male alate, survival of the species would not be possible. After the colony is established the primary king may be replaced by a neotenic. Only one case was observed where the primary female was replaced and the male retained in *S. ruficeps* though on occasions both primaries are lost and replaced by neotenics.

In laboratory-bred colonies of *S. ruficeps* primary kings were regularly lost from colonies in their third year of development. In colonies opened in the field, the absence of the primary king was one of the most common features noticed in older colonies, and it seems that in *S. ruficeps* colonies of more than 200 individuals seldom have the primary king present. Heath (1927) found colonies of *Zootermopsis sp.* containing 3,500 individuals which still had the primary reproductives present.

The primary males in *S. ruficeps* have in many cases, therefore, a relatively short life span. They are initially important to the successful distribution of the species and establishment of the young colony, though they appear to offer little help in the formation of the royal cell after swarming. They are easily distinguished from queens by their narrower abdomen and the presence of styles.

**DISCUSSION**

There are thus two well defined castes in *S. ruficeps*, the reproductive caste and the soldier caste. The reproductives are divided into two distinct kinds, primaries and supplementaries (neotenics), the latter group being divisible further into brachypterous (with rudimentary wings) and apterous (without wings) types.

**NYMPHS**

These individuals do not represent a caste as they are forms passing through stages of development. They comprise 80 per cent to 90 per cent of every colony except just before and just after swarming. They take the place of the worker caste in species of the Family Kalotermitidae, which has no true worker caste (Light, 1930). They feed the reproducing pair, the young and the soldiers, apart from doing other menial labours of the colony such as caring for the eggs, colony hygiene, boring the galleries, grooming, and cleaning the members of the colony. It is highly probable that they play an important role in the development of neotenic reproductives through specialised feeding. This may be combined with a biological pressure or need for a colony to have a reproducing pair. It is a feature of the continual maintenance of a caste balance necessary to the existence of the colony. Neotenics arise only when required, and only among groups of nymphs that have lost the dominating influence of a reproductive pair. The reason why neotenics are inhibited from maturing in a colony with a reproductive pair has long been considered to be due to the presence of an inhibiting factor in the exudates groomed from the reproductive (Pickens, 1932; Castle, 1934). Keene and Light (1944), however, have demonstrated that the feeding of exudates from reproductives does not inhibit the formation of neotenics in isolated groups of nymphs. When neotenic reproductives are required, there must be more than the maintenance of the caste balance responsible for their development; otherwise more than one pair could conceivably mature in any one group of nymphs. It would be possible for all the nymphs to mature into neotenics at the same time, but different instars take different lengths of time to develop neotenics (Light and Ilg, 1945). This may have a bearing on the situation, though it does not explain why a group consisting of only one instar produces only a single reproductive pair.
In *S. ruficeps* neotenes are formed among nymphs in from 28 to 65 days of being isolated, and it appears that the extent to which neotenes are produced in this species is at least partly governed by the composition of the group (i.e., the need for a reproducing pair in any group of nymphs is an incentive to the development of neotenes).

The rate of development of neotenic reproductives by instars in *S. ruficeps* appears to be faster in the fifth and sixth instars than in the fourth and early seventh instars, while in the third and late seventh instars reproductives may not be formed at all. The experimental evidence available cannot however be considered conclusive, as it is not based on sufficient data, but the trend is similar to that reported by Light and Illg (1945) for *Zootermopsis*. In large mixed groups, however, Light and Illg found that the neotenes formed were from one of the comparatively young instars present.

An experiment carried out on a mixed group containing sixth and seventh instar nymphs of *S. ruficeps* resulted in the production of neotenes, the female of which commenced laying eggs 30 days after isolation. These reproductives were sixth instar nymphs. The queen was of the late sixth instar and was brachypterous, while the king was of the early sixth instar and was apterous.

There still seems to be some justification for assuming that specialised feeding plays a part in the development of neotenes, and as nymphs collect food and feed the reproductives, soldiers, and very young nymphs that cannot feed themselves, the sexual maturity of neotenes may conceivably be directly related to such activity. This theory involves a selection of a pair of individuals by the other nymphs which then invoke their specialised feeding techniques, which ostensibly cause the sex organs to mature in the pair selected. That younger nymphs are fed by older nymphs may be related to the fact that it is usually the younger nymphs present that become reproductives in isolated groups. This could be taken as additional evidence for the specialised feeding theory of the development of supplementary reproductives. The matter of selection is not difficult to understand when it is realised that nymphs are invariably used to feeding a particular pair in the colony probably with specialised food. It would be normal behaviour for them to continue to feed a pair among any group that is isolated.

While there is not a true worker caste, present observations on *S. ruficeps* show that alates are not produced in laboratory-reared colonies for up to three years. This suggests that the first batches of nymphs produced in a colony of this species develop as far as either soldiers or neotenes, though they may be retained almost indefinitely at the fifth instar as essentially a worker caste. Within 7 days of reaching the imago state a noticeable darkening of the tips of the mandibles and the head of each individual is observed. The thoracic and abdominal segments dark in that order and the appendages follow the parts of the body to which they are joined. Thus the legs, the abdomen and the wings become pigmented at about the same time. Immediately after the moult the alate is pale and almost translucent. A gradual change to an opaque creamy white colour follows, which continues to deepen to a light coppery brown, gradually darkening until the fully pigmented alate is dark brownish black. This state of complete pigmentation is reached during December in some localities, but flight may not occur until March, April or May.

It seems probable, from field observations, that all sixth and seventh instar nymphs and possibly some of the nymphs of the late fifth instar present in old colonies in the early spring (September) develop into imagines and fly together the following autumn.

Hill (1942) records taking mature alates from rotten wood at Days Bay in December and January. Colonies opened at this time do show fully pigmented alates though whether or not they are fully mature is debatable. Swarming has not been observed in the Wellington district during December or January.
After attaining full pigmentation the alates apparently undergo a period of rest during which food and energy is stored for the strenuous period ahead. For though the alates bore the initial cell, then mate and care for eggs and young, it is reasonable to assume from the slow rate of boring that young reproductive pairs are not gross feeders. At this time it is possible that food stored during their pre-flight rest is utilised in conjunction with normal feeding. This stored food may conceivably last until the nymphs take over the feeding of the reproducitives. Harvey (1934) notes a resting period sometimes lasting over nine months with young reproductive pairs of K. minor and reports that many of these pairs do not survive the resting period before egg laying. This suggests that previous food storage was insufficient to tide the individuals over the resting period.

In S. ruficeps many of the alates are non-flyers or weak flyers, while few are strong, powerful flyers that reach good distances from the parent colony. This may be accounted for in three ways:

(i) Alates that are weak flyers may be immature or matured from fifth or sixth instar nymphs, thus lacking the strength of those matured from seventh instar nymphs.

(ii) The weak flyers may not be as well nourished as the strong flyers.

(iii) The weak flyers are damaged during release from the wood, thereby making it impossible for them to fly at all or capable of flying short distances only.

Harvey (1934) considers that the alate potential of K. minor consists of two types, viv, those fully mature and those not fully mature. In S. ruficeps alates of the late seventh instar which in the spring reach the imago state have a relatively long period for rest and food storage before the autumnal flight. This permits them to fly long distances when released. Late sixth instar and early seventh instar nymphs may reach the imago state somewhat later and have a shorter period of food and energy storage. These alates fly, but fly only relatively short distances. The alates arising from late fifth and early sixth instars comprise the most immature alates at swarming time and fly but a few feet or not at all. I do not suggest that the food stored as fat in the termite body could be utilised as energy on the flight. It is the shorter period of rest and energy conservation that is considered significant. These differences in lengths of flight by alates are biologically important, for the reproductive potential of the colony is thus spread over the available landscape, giving a possible better range of infestations and also a better chance of survival against predators and overpopulation of each available piece of wood.

Field observations of colonies supported this view, for whereas the number of immature alates present in colonies in the spring reach a figure of from one to three hundred, and sixth and late fifth instars were present in normal proportions, by late summer the numbers of pigmented alates had doubled or trebled, and at swarming only nymphs to the fifth instar remained, except where development of a small number of seventh instar nymphs had been so recent that they could not participate in the swarm. Such nymphs with wingbuds cease further development until the next spring.

**Moulting**

Ecdyses were examined in connection with the determination of the stadia, and there seems to be little variation in the method throughout the various instars. There is a distinct slowing of the activity of the individual for some 10 minutes before it rolls on its side to commence the moult. In all moults observed the insect was lying on its right side. The body of the insect becomes more translucent, probably due to the activity of the ectodermal glands which play an important role in the moult. There is very little movement during the first stages, when activity appears to be confined to an almost imperceptible contraction and expansion of the body, followed by a relatively quick splitting of the exoskeleton along the middorsal line from the anterior edge of the pronotum to the third or fourth segment of the abdomen.
Immediately following this, the insect becomes very energetic, pulling the head down under the thorax and flexing and unflexing the abdomen and thorax in the dorso-ventral plane. Gradually the exoskeleton is slipped off towards the posterior of the body, and as the legs become partially freed, they are brought into action in a bending and stretching motion which considerably helps the process. As the exoskeleton is pushed off the surface of the body is wet and glistening. If the body surface is at this stage touched with the finger, it will be found to be covered with a somewhat greasy secretion. The exoskeleton is gradually slipped backwards until it remains attached to the posterior segment of the abdomen.

Activity then shifts to the head region, where a split occurs from the dorsal edge of the large foramen of the head anteriorly along the middorsal line of the head to a point about midway between the eyes. The head is again bent under the thorax and the two anterior pairs of legs are used to push the head capsule anteriorly towards the mouthparts. As the antennae become partially freed, they are used in a flailing movement and eventually the old head capsule is attached to the head only at the mouth.

The head is now brought into contact with the tip of the abdomen and the head capsule in some way adheres to the eighth and ninth sternites. The body is then straightened and the pressure exerted pulls off the old head capsule and with it what appears to be a part of the lining of the pharynx and oesophagus.

The whole exoskeleton which is now attached to the posterior segments of the abdomen is removed by bending the tip of the abdomen ventrally towards the posterior legs, which are used to push off the exoskeleton.

The newly moultered insect is colourless and has a glabrous transparent appearance. Within a matter of seconds after ridding itself of the old exoskeleton, it stands up on to somewhat unsteady limbs and may fall and stagger about for a short while, flexing and expanding itself to allow for future growth inside the newly forming exoskeleton. At about this time nympha, which have until this moment shown no interest in the individual, appear in numbers of about five or six and commence a vigorous grooming of the newly moultered insect. During grooming the insect flexes itself in various ways to permit the groomers to complete a thorough cleaning off of the ectodermal secretion. After grooming the mouth parts, the nympha feed the newly moultered insect on stomodeal or proctodeal fluids. In a short time the insect is relatively strong and takes its normal place in the society.

Times were noted as follows and were found to be fairly constant:

<table>
<thead>
<tr>
<th>Event</th>
<th>Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>From moment of lying down to splitting of</td>
<td>12 mins</td>
</tr>
<tr>
<td>the body exoskeleton</td>
<td></td>
</tr>
<tr>
<td>From splitting of exoskeleton of body to</td>
<td>60 mins</td>
</tr>
<tr>
<td>attachment of exoskeleton to posterior</td>
<td></td>
</tr>
<tr>
<td>abdominal segments</td>
<td></td>
</tr>
<tr>
<td>Removal of head exoskeleton</td>
<td>50 mins</td>
</tr>
<tr>
<td>Removal of exoskeleton from posterior</td>
<td>20 mins</td>
</tr>
<tr>
<td>abdominal segments</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2 hrs 22 mins</td>
</tr>
</tbody>
</table>

Features of the moulting process appeared to be:

(i) The fundamental constancy of the method.
(ii) The activity of the ectodermal glands and their function in the process.
(iii) The strong flexing movement of body and appendages which greatly aid the process.
(iv) The after-moult grooming and feeding which apparently has not been described for other termites.

**Colony Growth Rate**

The rate at which a colony flourishes, expanding its workings and increasing its numbers of individuals, depends to a large extent on the infrequency of major disturbances. Castle (1934) has shown that prolonged extremes of dry or wet conditions are unfavourable and each slows, ceases or reverses any progress the colony may
previously have made. My study on *S. ruficeps* has shown that prolonged disturbances of the colony's galleries will eventually lead to the death of all the termites through their inability to maintain normal environmental conditions. Paucity of available food or strong competition for available food, parasites, predators and disease, all affect to varying degrees the progress of the termite colony. Finally, extremes of temperature, either heat or cold, may inhibit reproduction, incubation, or development, or may kill out part or whole of the colony.

The growth of new colonies of *S. ruficeps* has been studied over the first three years, and, while different colonies progress at different rates, the following table shows the average rate of development in laboratory colonies:—

**Table IV**

The Average Increase in Numbers of Individuals as Shown by Counts made at Intervals in Young Colonies of *S. ruficeps*

<table>
<thead>
<tr>
<th>Age of Colony</th>
<th>Type of Individual and Numbers Present</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Reproductives</td>
</tr>
<tr>
<td>Six months</td>
<td>Primaries</td>
</tr>
<tr>
<td>One year</td>
<td>Primaries</td>
</tr>
<tr>
<td>Two years</td>
<td>Primaries</td>
</tr>
<tr>
<td>Three years</td>
<td>Primary Queen</td>
</tr>
<tr>
<td></td>
<td>and neotenic king</td>
</tr>
</tbody>
</table>

Similar rates have been recorded for *Kalotermes minor* (Harvey, 1934) and *Zootermopsis angusticollis* (Castle, 1934). Field observations have been made on young and old colonies of *S. ruficeps* and seem to support the above figures. The largest colony found in nature headed by the primary pair had a complement of three soldiers and 57 nymphs, one of which had reached the seventh instar. Young colonies with the male primary reproductive missing have been found to consist of from 50 to 250 individuals. However, after a colony reaches a complement of several hundred individuals, neotenic reproductives begin to appear. Though a colony may have less than 50 members at three years, reproduction seems to increase in rate after this time, and at the end of four years at least 100 individuals may be present. After the fourth year supplementary reproduction may increase reproduction enormously, and so-called compound colonies are formed. The supplementary reproductives and their nymphal stages are more or less separate units, but observations indicate that their workings are not actually separated from the parent colony, and that there is no distinct separation of sub-colonies from each other. Alates matured and released from old compound colonies of *S. ruficeps* appear to be released from the same exit hole and moreover, as they reach the imago state, they may congregate in a part of the compound colony workings common to all centres of reproduction.

Field observations on *S. ruficeps* consisted of counts of individuals in the immediate proximity of both primary and neotenic reproductives. These showed that in a mature compound colony, the supplementary colony may vary in number of individuals from 37 to 220, the larger sub-colonies being nearer the primary colony while the smaller sub-colonies occur at the extremities of the workings. The original primary colony was found to consist of from 150 to 210 individuals.

These examinations of supplementaries suggest that reproduction rate of neotenics is faster in the initial stages than that of the young primary reproductives. As stated earlier the interconnecting reticulation of galleries does not appear to be interrupted when sub-colonies are formed. It is, however, very difficult when opening termite workings to ascertain whether the sub-colony is truly isolated from both the primary colony and other sub-colonies, for in some instances they may be less than 4 inches apart throughout the length of the infestation. The galleries are usually excavated
parallel to the longitudinal axis of the log (i.e., with the grain of the wood) with short connecting passages at intervals across the grain. In the workings of S. ruficeps there is usually no definite attempt to keep to the spring wood of the annual rings. This is probably due to the decayed condition of the wood infested by S. ruficeps. The state of the wood and type of working by this termite make doubly difficult any attempt to obtain evidence on whether sub-colonies are isolated.

Primary colonies (without sub-colonies) of S. ruficeps do not appear to reach a size of more than 200 to 300 individuals, but compound colonies have been found with a complement of 2,800 to 3,000. This compares with Z. angusticollis (Heath, 1927). In other groups much larger colonies are common, such as 11,000 in K. minor (Harvey, 1934), and 3,000,000 in Nasutitermes (Emerson v Light, 1934). During the examination of infestations to determine the size of compound colonies it was most noticeable that, even though conditions in the centre of the log appeared to be quite suitable, the termites rarely established sub-colonies at depths greater than 4 to 5 inches from the surface. Indeed, the main termite activity was always between 2 and 6 inches from the surface of the log, but exploratory or foraging galleries were often found to have been excavated at intervals into the centre of the log when that part of the log was suitably decayed. Such a habit of exploring the depths of the habitat may be associated with moisture requirements. Termites in logs frequently exposed to the sun were found to have deeper workings than those in shade. Moreover, during the sunny part of the day few termites remained in the outer warmer galleries, the main body either moving into deeper, cooler galleries or being already established there. This type of "temperature migration" has been reported in Zootermopsis spp (Castle, 1934) though in Z. angusticollis and S. ruficeps it is evidently not as well developed as in other species.

Habitat

Stolotermes ruficeps inhabits most decaying wood, does not construct termittaria, but houses eggs and casts in the ordinary galleries excavated by the nymphs. The species has not been observed infesting sound wood during this study, though it has been recorded from relatively sound wood bordering on the decayed areas in which the main body of the colony was established. Hill (1942) took the species from Nothofagus spp at Days Bay, Wellington, and reported an infestation in Pinus radiata.

I have taken S. ruficeps from the following species: Metrosideros robusta, Agathis australis, Pinus radiata, Nothofagus spp, Griselinia littoralis, Podocarpus spp., Dacrydium cupressinum, Salix sp., Eucalyptus obliqua and Larix decidua.

In each case the wood infested was decaying. In many cases the site of the infestation was in a forest, but in other cases the infested logs and stumps were far from the forest in open farm land.

Nurse (1944) records S. ruficeps from Podocarpus spp, Griselinia littoralis and Metrosideros lucida at Banks Peninsula, Nelson and Westland. My observations indicate that any decaying wood may be successfully attacked by S. ruficeps.

Infestations in living trees, or sound green or dry wood, have not been observed, but attack in decayed parts of living trees has commonly been recorded. To determine the suitability of certain food sources, attempts were made to establish S. ruficeps in sound wood and to keep colonies on a diet of filter paper. In each case the temperature and moisture content of the wood, were maintained as near as possible to the environment from which the termites were taken. The procedure consisted of removing 10 individuals, ranging from stage 3 to stage 5 in development, from two parent colonies, one in Dacrydium cupressinum and the other in Nothofagus sp. Each lot of 10 was placed in a petri dish containing a piece of sound timber or variously moistened filter paper. The moisture contents of the two parent woods were 100.9 per cent and 109.9 per cent respectively. The pieces of sound timber were Pinus radiata, Nothofagus fusca and Eucalyptus saligna, and their moisture contents
TABLE V
Tests with Small Numbers of Nymphs of *Stolotermes ruficeps* to Indicate the Suitability of Sound Wood and Filter Paper as Food Sources

<table>
<thead>
<tr>
<th>Test</th>
<th>No. of Nymphs</th>
<th>Food Supplied</th>
<th>Deaths Recorded After</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>12hrs</td>
<td>24hrs 36hrs 48hrs 72hrs 96hrs</td>
</tr>
<tr>
<td>A</td>
<td>10</td>
<td><em>Pinus radiata</em></td>
<td>—</td>
<td>2 2 6 — —</td>
</tr>
<tr>
<td>B</td>
<td>10</td>
<td><em>Euc. saligna</em></td>
<td>—</td>
<td>2 3 — — —</td>
</tr>
<tr>
<td>C</td>
<td>10</td>
<td><em>Nothofagus fusca</em></td>
<td>—</td>
<td>1 — — — —</td>
</tr>
<tr>
<td>D</td>
<td>10</td>
<td>Damp filter paper</td>
<td>—</td>
<td>2 — — 8 —</td>
</tr>
<tr>
<td>E</td>
<td>10</td>
<td>Three lots of filter paper (variously moistened)</td>
<td>2 3 1 2 2 —</td>
<td>Two deaths at 12hrs due to drowning in excess moisture.</td>
</tr>
<tr>
<td>F</td>
<td>10</td>
<td>As in E</td>
<td>—</td>
<td>1 4 — 2 3</td>
</tr>
<tr>
<td>1</td>
<td>200 approx</td>
<td>Rotted <em>Dacrydium spp</em></td>
<td>—</td>
<td>— — — — —</td>
</tr>
<tr>
<td>2</td>
<td>400 approx</td>
<td>Rotted <em>Nothofagus sp</em></td>
<td>—</td>
<td>— — — — —</td>
</tr>
</tbody>
</table>

were 94.3 per cent, 67.2 per cent, and 64.7 per cent respectively. In the tests with filter paper one dish contained damp material and one three lots of paper variously moistened from half damp to very wet, with much free moisture. A further test repeated the latter but used termites from a different colony. Results are shown in Table V.

The results of these experiments indicate that:

1. *S. ruficeps* taken from decaying wood will not exist on rot-free wood, and the progress of invasion is constant for all woods tested.
2. Individuals cannot exist for longer than 96 hours on a filter paper diet, and deaths occur regularly after 24 hours. It was noted that the younger instars were affected first and died within 24 to 48 hours. The older nymphs take from 36 to 96 hours to die.

A further series of experiments was carried out to ascertain whether the invasion rate varied with the species of wood. In each test 10 termites of stages 3 to 6 were used, and similar conditions were maintained to those in the previous experiment.

**METHOD**

Three pieces of decaying wood from different species were placed in each culture dish so that all were separated from each other, and the termites were placed in the centre of the dish equidistant from the pieces of wood. The culture dish was examined every 24 hours, and a few drops of water added when necessary to maintain humidity. In Dish G the pieces of wood were (a) *Nothofagus sp.*, (b) *Pinus sp.* and (c)
Dacrydium sp. The first examination showed all termites working on (a). They were removed to (b) and at the end of the second day they were still on (b). They were removed to (c), where they were still located at the end of the third day. Three were removed back to (a) and three to (b), and there was no change on the fourth day when examined. All pieces of wood were placed together, and the termites continued to feed on all three species. Dish H was set up in the same way as G, using Nothofagus sp., Eucalyptus sp. and Agathis australis. The result was the same as that for Dish G, though similar transfers were made.

The experiment showed that no particular species of the woods used were preferred by S. ruficeps.

In further series of tests designed to ascertain the nutritional value of filter paper when combined with rotten wood, moistened filter paper was wrapped around pieces of damp decayed wood and then subjected to attack by nymphs of S. ruficeps. Ten nymphs were placed in one petri dish and 20 were placed in each of five other petri dishes. Drops of water were added occasionally to the paper and wood to maintain humidity.

Observations were made at intervals of 24 hours on Dish 1, and 7 days on Dishes 2 to 6. In all tests the paper was attacked and entry gained to the wood where feeding was confined. When the wood was almost depleted the paper was attacked again, but this attack was spasmodic and very little paper was eaten. The longevity of individual nymphs varied from 7 to 37 days (Table VI) depending on the amount of wood present. In each test the first deaths recorded were in the younger stages. The mortality recorded in the two controls (Table VI) in the 37 days was insignificant and due to cannibalism. The mortality recorded in the test groups was therefore apparently due to starvation following the depletion of the wood supply. The tests when compared with the controls indicate that:

(i) There is apparently no nutritional value in filter paper when used in conjunction with decayed wood for nymphs of S. ruficeps.

(ii) The period of survival for individual nymphs is proportional to the amount of decayed wood present with no effect from the amount of paper present.

(iii) The decayed wood must contain some feature of nutritional value not found in damp filter paper.

<table>
<thead>
<tr>
<th>Dish</th>
<th>No of Termites</th>
<th>Grams of Wood</th>
<th>Grams of Filter Paper</th>
<th>Maximum Termite Longevity in Days</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10</td>
<td>13.1</td>
<td>5.9</td>
<td>37</td>
<td>2 dead by 30th day</td>
</tr>
<tr>
<td>2</td>
<td>20</td>
<td>11.6</td>
<td>5.9</td>
<td>28</td>
<td>5 dead by 21st day</td>
</tr>
<tr>
<td>3</td>
<td>20</td>
<td>9.2</td>
<td>5.9</td>
<td>28</td>
<td>11 dead by 21st day</td>
</tr>
<tr>
<td>4</td>
<td>20</td>
<td>5.8</td>
<td>5.9</td>
<td>22</td>
<td>7 dead by 14th day</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>7.2</td>
<td>5.9</td>
<td>24</td>
<td>6 dead by 14th day</td>
</tr>
<tr>
<td>6</td>
<td>20</td>
<td>5.2</td>
<td>5.9</td>
<td>15</td>
<td>1 dead by 7th day</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td></td>
<td></td>
<td>17</td>
<td>17 dead by 14th day</td>
</tr>
<tr>
<td>A</td>
<td>200</td>
<td>Unlimited</td>
<td>—</td>
<td>—</td>
<td>2 deaths in 37 days</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No deaths</td>
</tr>
</tbody>
</table>

The presence of wood-rotting fungi in wood attacked by dampwood termites has received a good deal of attention in other studies (Koford et al., 1934; Cook, 1935). It has been considered that decay aids attack by softening the wood, and also that
the fungus could fulfill the protein and vitamin requirements of the insects as their main food, cellulose, is a carbohydrate.

From the above series of tests it seems probable that the presence of wood-rot fungi in wood is necessary to the successful existence of nymphal stages of S. ruficeps. This is important to any preventive measures used for the protection of timber in service. It also appears probable that S. ruficeps will attack decaying wood regardless of the species.

It is of interest to note that a whole colony of S. ruficeps deprived of food did not show unusual mortality until the third week. After this time a rapid peak was reached and all individuals had succumbed by the fifth week. It would, therefore, appear that, provided humidity and temperature are satisfactory, a whole colony can exist much longer without food than a few individuals separated from that colony as indicated in the above tests.

**Habitat Moisture Variations as an Indication of Termite Tolerance Range**

Actively infested wood was collected from various sites and was brought into the laboratory. Samples free of termites were taken, numbered, their respective moisture contents determined as a percentage of their oven dry weights.

The method of sampling the infestations was to examine the cross section of the workings, then starting at one extremity blocks were marked in parts of the outer surface of the log, the innermost areas of the infestation, and areas intermediate between but overlapping into these two extremities. In this way a fair representation of the moisture content of each infested wood was obtained.

The range of moisture contents obtained varied between 30.5 per cent and 186 per cent, average 97.9 per cent. The lower moisture contents were above ground level and near the outside of the log, while the higher readings came from samples nearer the centre of the log, on the surface nearest to the ground, and from wood below the surface of the ground.

In the greater proportion of infestations observed, free water was present in many of the galleries, the ceilings of which were used for access by the termites. The decayed sapwood of some infested logs when squeezed released free water. Infestations of wood below ground level invariably showed much free water in the galleries. On the other hand, S. ruficeps was found infesting relatively dry wood with no free water in the galleries. In several cases where alates were observed they were located in the drier situations. In one case, the alates were all located on the ceilings of galleries in which there was much free water. The whole habitat of this particular colony was extremely wet. It is significant that, regardless of the moisture content of the actively infested woods, the respective colonies appeared to be healthy.

Obviously this species has a wide range of tolerance to the moisture content of its environment. This holds true for other dampwood termites, but definite limits have been described. Extended periods of extremes of either very dry or very damp conditions apparently cause considerable upset in the economy of Zootermopsis spp., for after long droughts colonies were reduced to the reproductive pair and last instar nymphs, while excessively wet conditions led to a high mortality rate due to attack by certain fungi (Castle, 1934).

A series of experiments on S. ruficeps were carried out over three years to determine the effect of reduced moisture content of the environment. Nine young reproductive pairs obtained from a flight in the laboratory on April 19, 1948, were set aside in large culture dishes with an ample food supply. These dishes permitted slow evaporation of moisture and no water was added to maintain the humidity. Excess fungal activity was carefully removed from time to time, but the young colonies were disturbed as little as possible.

Three other reproductive pairs were set aside in culture dishes as controls, and in these, moisture lost by evaporation was replaced by adding a few drops of water
every four or five days. In other respects these colonies were treated the same as in the nine tests. The moisture content of each piece of infested wood was taken by removal of a sample at the beginning of the experiment and again when the colony was exposed for examination.

<table>
<thead>
<tr>
<th>Test Lot</th>
<th>Initial MC of Wood (per cent)</th>
<th>Period of Development in Days</th>
<th>Present MC of Wood (per cent)</th>
<th>Number of Individuals and Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>126.7</td>
<td>192</td>
<td>72.0</td>
<td>Healthy reproductive pair, 1 egg</td>
</tr>
<tr>
<td>2</td>
<td>100.0</td>
<td>192</td>
<td>64.6</td>
<td>Healthy reproductive pair only</td>
</tr>
<tr>
<td>3</td>
<td>141.7</td>
<td>360</td>
<td>51.5</td>
<td>7 (healthy average size)</td>
</tr>
<tr>
<td>4</td>
<td>146.7</td>
<td>360</td>
<td>67.1</td>
<td>10 (healthy average size)</td>
</tr>
<tr>
<td>5</td>
<td>146.2</td>
<td>570</td>
<td>42.9</td>
<td>15 (healthy average size)</td>
</tr>
<tr>
<td>6</td>
<td>120.0</td>
<td>570</td>
<td>35.0</td>
<td>12 (dead)</td>
</tr>
<tr>
<td>7</td>
<td>120.0</td>
<td>1089</td>
<td>25.7</td>
<td>17 (healthy but small)</td>
</tr>
<tr>
<td>8</td>
<td>105.2</td>
<td>939</td>
<td>20.5</td>
<td>19 (healthy but small)</td>
</tr>
<tr>
<td>9</td>
<td>100.0</td>
<td>1059</td>
<td>17.7</td>
<td>23 (dead)</td>
</tr>
<tr>
<td>C1</td>
<td>127.2</td>
<td>1089</td>
<td>130.4</td>
<td>22 (healthy, average size)</td>
</tr>
<tr>
<td>C2</td>
<td>131.7</td>
<td>939</td>
<td>115.6</td>
<td>38 (healthy, average size)</td>
</tr>
<tr>
<td>C3</td>
<td>131.7</td>
<td>570</td>
<td>136.9</td>
<td>20 (healthy, average size)</td>
</tr>
</tbody>
</table>

The decreases in moisture content of the wood and the development of the young colonies over the various periods are shown in Table VII. In Test Lots 1 to 5, 7 and 8 and the controls, no difference in the activity of individuals was observed on examination. In the controls, C1 showed a slower rate of development than the others. In C2 and C3 the numbers of individuals were similar relative to the respective periods of development. Test Lots 5 and 6 both lost considerable moisture in 570 days, while in the same time C3 gained slightly. There were fewer numbers of termites in these test lots than in C3, and in Test Lot 6 the colony appeared to have been killed by some disease. Another explanation is that the evaporating moisture condensed on the upper surface of the chamber and may have sealed it. In this case the termites could have been asphyxiated.

There was no difference in the size of individuals, stage for stage, between Test Lot 5, C3 and field collected specimens. There was only one soldier in C3 compared with three in Test Lot 5, which had been disturbed for removal of excess fungal growth a week before examination. C2 lost a small amount of moisture compared with that lost by Test Lot 8. This is reflected in the smaller number of individuals and their smaller size in the latter. However, the number of instars present in each group were the same, and a primary reproductive had been replaced by a neotenic in each colony indicating that some cannibalism had occurred. The same remarks are applicable to the two colonies in Test Lots 7 and C1. Except for the unexpected small population in C1 there was similar development in these two colonies to that in Test Lots 8 and C2.

The tests indicated that colonies of *S. ruficeps* can tolerate considerable reductions in the moisture content of the wood that they inhabit. Reduced moisture eventually affects the termites in two ways:

(i) The rate of reproduction is slower when the moisture becomes critically low

(ii) The size of individuals is smaller at moisture contents below 30 per cent of the oven-dry weight
However, stadal development in the colony does not appear to be interrupted by low moisture conditions, and activity of individuals is not affected. It was apparent from these tests that optimum conditions were present when the moisture content of the decayed wood was above 50 per cent. Test Lots 7 and 8 indicated that development will continue at very much lower moisture contents, but it would appear that the minimum moisture content at which wood-rot fungi continue activity is closely related to the limit to which individuals of S. ruficeps will exist.

Provided that the galleries are not damaged or opened up, S. ruficeps can survive in wood with a moisture content of 20.5 per cent for a period. While the galleries are intact, the termites appear to be able to control the temperature and humidity within them to some degree. Evidence for this may be obtained by opening the galleries of laboratory-bred termites living in a limited wood supply and dependent on free water for humidity. It will be seen that the surfaces of the galleries appear significantly more damp than the fresh split surfaces of the wood. This is possibly due to the confined space of the galleries and the moisture given off from the bodies of the termites. It was found that if termites were unable to seal themselves off from the larger environment of the culture dish the loss of moisture from their bodies was eventually lethal, unless free water was added regularly.

In certain cases where a natural high moisture content was maintained excessive fungal activity caused rapid death of part or whole of the colony. This happened in C2, where the whole colony perished a few days after examination. The wood had lost only 16.1 per cent of moisture in the two years seven months, but apparently conditions were suitable for the disease to flourish.

Causes of Mortality

There appears to be no obvious indication as to how or when diseases attack colonies. But colonies brought in from the field and kept in culture dishes often contract diseases which, while having no appreciable effect on the appearance of the termites, certainly lack nothing in ability to cause rapid and widespread mortality within the colony. In some cases some proportion survives. It is difficult to determine whether, in the latter cases, the termites regain control of the disease or whether certain members of the colony become naturally immune from previous mild attacks of it.

Grassi and Sandias (1893) reported deaths in laboratory-kept Kalotermes flavicollis due in the first place to a very dry environment and in the second place to one that was too damp. In the latter, a distinct edema accompanied by the presence of a bacterium was recorded. I have not observed such a disease in colonies of S. ruficeps. I found that this species is not tolerant of frequent disturbances, but when left alone with an ample food supply the termites seal themselves either inside the wood or between the floor of the container and the wood. In such circumstances, they can control their environment within certain limits of moisture because of the restricted area of the habitat. Light and Illg (1945) refer to this in discussing laboratory kept termites and point out that the termites live essentially as in nature. They further mention unavoidable disturbances of termites being used in research, and report mortality, the cause of which is unknown to them. Some deaths in termite colonies have been attributed to the edema referred to by Grassi and Sandias while others are caused by a bacterial disease which colours the termite's head black (De Bach and McOmie, 1939), and some have no apparent causal agent.

Deaths in S. ruficeps are seldom accompanied by a visible external change and it is my opinion that such deaths are due to frequent disturbances, which prevent attempts by the termites to set up a controlled environment normal to their existence. While such an inadequate environment may suffice for a time, in certain instances the colony may decline in a short period.
In order to test this hypothesis, five groups of termites were selected at random from stocks on hand. Each was given a food supply that was sufficient to last some months, and moisture and temperature conditions were the same for all examples. Three were regularly disturbed while the other two were not. In one of the three examples that were regularly disturbed, all termites died rapidly. The first death occurred after four days when it was also noted that the survivors were segregating individually and remaining inactive for unusually long periods. Movement was sluggish compared with the normal activity of other termites. All termites in the example were dead on the fifth day with no apparent cause of death. The next example to show mortality seemed perfectly healthy until the twenty-fifth day when three termites died in a manner similar to the previous example. On the twenty-sixth day only one termite remained alive and normally active. This termite was still alive and active on the thirtieth day when the termites in the third example commenced to separate from one another and became inactive. On the thirty-first day, all termites except the solitary survivor of the second example were dead.

The undisturbed examples were opened and were thriving. No deaths or cannibalism had occurred and the colonies were living as if in nature. In one, no teneinics had developed and an egg had been laid.

The tests supported the hypothesis previously described indicating that *S. ruficeps*, kept under laboratory conditions, cannot tolerate indefinitely the regular disturbance of their controlled environment.

It was also noticed in the first stages of the experiment that the termites continually attempted to seal off a cell within which they could live. After having this cell broken up for several consecutive days, such efforts ceased and individuals commenced to dwell a nomadic existence between the pieces of wood present. The disturbances had therefore prevented the establishment of normal colony existence and had undermined the social way of life inherent in these insects. Such disturbances may be the cause of mortality in laboratory-kept termites under research conditions.

The effect of varying temperatures on individuals and colonies of *S. ruficeps* was studied as follows:

1 *Field tests*

Colonies were carefully opened in the field and 0° to 200° C mercury-in-glass thermometers were inserted as far into the galleries as possible. Readings were taken and correlated with air temperatures taken at the same time with similar thermometers.

2 *Laboratory tests*

(a) Two groups of 20 nymphs, each from different colonies were placed in petri dishes with damp decaying wood. The nymphs used in the experiment ranged from the second to the seventh instars both inclusive. Both dishes were placed in an electric thermostat-controlled oven with an inserted thermometer. The thermostat was adjusted to give increased temperatures and the termites were observed every five minutes. Observations and significant changes in activity of the termites were noted.

(b) Two other lots from the same colonies as those in the previous test were set out in the same manner as in (a).

In this test the oven was allowed to reach certain temperatures and the two lots of termites were then placed in the oven for five minutes after which time, observations were made and results noted in each case.

(c) Termites from two other stocks were set up in petri dishes in the same way as in (a) and (b). They were subjected to certain temperatures for 60 minutes, observations were made, and results noted.

(d) Two colonies or part colonies inhabiting wood (*Nathofagus sp.*) were placed inside glass containers. A 0° to 200° C mercury-in-glass thermometer was
placed inside the container and another similar thermometer was inserted 75 mm into the infested wood. The containers were covered with paper so that the ends of the thermometers protruded through two holes in the paper thus minimizing air exchange between the atmosphere in the container and that outside it. The containers were placed under bell jars and located in a part of the laboratory least affected by day/night temperature fluctuations. Temperatures were taken three times a day over a period of 15 days and correlated with room temperatures taken at the same times. The infested wood samples measured approximately 150 mm long with an average diameter of 50 mm, and no water was added during the experiment.

In the field tests, readings were taken on colonies inhabiting wood in different sites such as in shaded gullies, on sunny spurs, and from wood both above and below the ground. Temperatures inside the galleries of the termites, on the surface of the wood, and 150 mm from the surface of the wood were taken and the trends for each habitat variation were as follows:

(i) In the sunny positions or where sun penetrated to the infested wood at some time during the day the mean readings of all tests were:
Air 17.9°C, Surface of wood 17.8°C, Galleries 18.5°C

(ii) In total shade but on the sides of spurs the corresponding means were:
Air 17.2°C, Surface of wood 17.2°C; Galleries 17.7°C

(iii) In shaded valley bottom (infestations above ground level):
Air 17.0°C, Surface of wood 17.0°C; Galleries 17.5°C.

(iv) In shaded valley bottoms (infestations below ground level)
Air 16.8°C; Surface of wood 16.5°C; Galleries 17.5°C.

The limits of such tests were well realized as, no matter how carefully the colonies were exposed and how quickly the thermometers were inserted, the effects of exposure on the gallery temperatures must have affected the results obtained. The thermometers were inserted at last 50 mm into the galleries in each test; in this way it was hoped to minimize exposure effects. The trends shown in the tests are significant. They show a variation correlated with the source of the sample tested in that shaded habitats had lower gallery temperatures than exposed habitats. The gallery temperatures were consistently higher than the air temperatures which suggests that the termites have some control over the temperatures of their immediate environments. Laboratory test (a) showed that temperatures between 17°C and 24°C had little effect on the termites. At 25°C, the termites showed increased activity which reached its peak at 28°C. Activity commenced to drop off at 30°C, and the first deaths occurred at 38°C, when all termites were inactive. Deaths continued in increasing numbers and only five showed signs of life at 42°C. All were dead at 45°C. Test (b) showed that increased activity occurred at 26°C. At 35°C, deaths occurred in both colonies. Further deaths occurred at 40°C, and no termites survived exposure to 42°C. Test (c) showed that S. ruficeps can exist for 60 minutes at 28°C, only one death being recorded. At 35°C, only five termites survived the exposure period and these did not recover when returned to a room temperature of 19°C.

These tests showed that maximum activity of individuals of S. ruficeps is reached at about 28°C which in the case of one termite was lethal after 60 minutes’ duration. Temperatures above 30°C have an inhibitory effect on termite activity while 35°C is generally lethal, though some termites survived 60 minutes exposure to this temperature. Temperatures ranging between 17°C and 24°C have no abnormal effect on S. ruficeps.

In test (d), readings were taken at 9 a.m., noon, and 4 p.m. The daily ranges of temperatures within room, container and galleries showed inconsistent variations. These variations were most noticeable in the room and container temperatures, and it was concluded that the room temperatures affected the container temperatures. The room was centrally heated, the heating being on during the week and off during the
week-end, when a marked drop in the room and container temperatures was recorded means of all readings taken for the three times of day were as follows—

<table>
<thead>
<tr>
<th></th>
<th>9 a.m</th>
<th>Noon</th>
<th>4 p.m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Room</td>
<td>17 1°C</td>
<td>18 2°C</td>
<td>19 5°C</td>
</tr>
<tr>
<td>Container A</td>
<td>17 1°C</td>
<td>17 9°C</td>
<td>18 6°C</td>
</tr>
<tr>
<td>Container B</td>
<td>17 3°C</td>
<td>18 1°C</td>
<td>18 7°C</td>
</tr>
<tr>
<td>Galleries in A</td>
<td>17 2°C</td>
<td>18 0°C</td>
<td>18 3°C</td>
</tr>
<tr>
<td>Galleries in B</td>
<td>17 7°C</td>
<td>18 2°C</td>
<td>18 5°C</td>
</tr>
</tbody>
</table>

As considerable condensation occurred on the interior walls of the containers, the humidity within the containers was considered to be satisfactory to the termites and much higher than that of the room. As was expected, because of the fact that the termites were in partially sealed containers, the temperatures within the termite galleries were greater at the morning reading, when the room temperatures were low, than the temperatures outside of the wood. This was reversed as the room temperatures rose to their peak in the afternoon.

The trends shown in this experiment indicate that the temperature within the galleries varies throughout the day the variation being more restricted than that shown by room temperature. The temperature variation within the containers was intermediate between the two extremes.

The range of the variations between 9 a.m and 4 p.m. on any one day were:—

<table>
<thead>
<tr>
<th></th>
<th>Min Variation</th>
<th>Max Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Room Temperature</td>
<td>1° C</td>
<td>3° C</td>
</tr>
<tr>
<td>Container Temperature</td>
<td>0° C</td>
<td>2° C</td>
</tr>
<tr>
<td>Galleries Temperature</td>
<td>0° C</td>
<td>1° C</td>
</tr>
</tbody>
</table>

Such a trend suggests a more stable temperature range in the galleries of *S. ruficeps*, and therefore that these termites are capable of some control over the variations of temperature within their galleries.

It is most difficult to obtain a reliable measure of the temperature within the galleries of termites as many factors influence the results obtained. For one thing, the colony must be opened up to some degree to obtain any results at all. The difficulties I have met in trying to obtain data on this factor may explain the paucity of reported researches to date. Although writers frequently stress the importance of temperature, actual readings are rare. Luscher (1949) showed a series of temperatures recorded from a mound (termite nest) of *Macrotermes bellicosus* Sneatham. These temperatures were taken in the course of efforts to find the significance of fungus gardens in the termitaria of the family Termitidae. The figures recorded show that the temperature within the termitarium is very constant at about 30°C while air temperatures vary between 27°C and 31°C. These temperatures were taken from the termitaria in the shade of trees. Luscher points out that in termitaria exposed to the sun, the variation of temperature may be as much as 2°C to 3°C. The work was carried out in Tanganyika, and the temperature cannot be compared with those normal to New Zealand. However, the variations and trends in the case of the shaded termitaria give results that are in some measure in agreement with those obtained in my tests.

Kofoid et al (1934) refer frequently to the controlled environment in which termites dwell. Most entomologists seem to accept the idea that temperatures remain relatively constant within termite workings, but, as Williams (1934) points out, the temperature factor, which may be very important, has not been greatly studied as a factor limiting the distribution of termites.

The results of the above tests tend to support the view that termites control the temperature within their workings to some degree and also that there is a large range of temperatures suitable to *S. ruficeps*. The range shown is from 17°C to 24°C for usual activity. At 28°C increased activity with almost harmless results occurs.
Temperatures over 35°C. are increasingly lethal, and those over 30°C. considerably reduce activity and completely change activity patterns that appear to be normal to individuals examined in the field.

The minimum temperature requirements were not studied. However, field observations show that frost will quickly kill exposed nymphs. Provided they remain sealed off in wood away from the outer atmosphere, *S. ruficeps* may endure relatively severe winter conditions. This is evident from the fact that they survive and flourish in parts of New Zealand where winter temperatures of 22°F. are common. In the Wellington District, *S. ruficeps* was found thriving at approximately 1,700 feet above sea level where snow is often experienced in winter.

**Humidity Within Galleries**

Under optimum conditions the environment in which dampwood termites live appears to be saturated. That is to say, the relative humidity of that environment is approximately 100 per cent.

Though it is almost impossible to measure the humidity within the galleries of *S. ruficeps*, there is much evidence to indicate that the humidity is very high. It has already been reported that free water is often present in the galleries and that, when squeezed by hand, actively infested decayed wood releases free water. Such conditions could hardly occur if the relative humidity in the termite galleries was less than 100 per cent. It is of interest that the fibre saturation point of wood is the point where no free water exists in the cell cavities of the wood, but the cell walls remain saturated (Tiemann, 1906). At this point the relative humidity of the cell cavities approximates 100 per cent, otherwise the cell walls could not be saturated. The fibre saturation point varies with the kind of wood. In softwoods it occurs at moisture contents (M/C's) ranging from 23 per cent to 30 per cent, depending on the species. For general purposes it is deemed to occur at 25 per cent M/C. In hardwoods the M/C range is 26 per cent to 38 per cent and for general purposes it is deemed to occur at 30 per cent M/C (Wilson, 1932). It can be seen from this that all wood with an M/C of more than 38 per cent can be deemed to have a relative humidity in the cell cavities of 100 per cent. It seems likely, therefore, that because the great majority of infested samples tested had moisture contents of over 90 per cent and the lowest recorded in *Dacrydium sp.* (a softwood) was 30.5 per cent, the relative humidity within the cell cavities and likewise in the termite galleries of those samples must have been 100 per cent.

If samples of wood actively infested by *S. ruficeps* are placed in covered glass containers, it will be noticed that within 12 hours under room temperatures of from 18°C to 20°C, condensation will occur on the insides of the walls and lid of the container. Such condensation would not occur unless the air within that container was saturated. It seems probable, therefore, that the air within the wood in the container and likewise in the galleries in that wood would be saturated also.

It would appear that, as in the case of habitats of *Zootermopsis*, where the humidity is presumed to be 100 per cent (Castle, 1934), a saturated environment is usual for *Stolotermes ruficeps*. It may also be possible, in view of the lowest recorded moisture contents of actively infested wood in nature being within 5 per cent of the fibre saturation point of the timber infested, that the fibre saturation point may prove a limiting factor to successful colonisation by *S. ruficeps* and, indeed, other termites. In the laboratory, as has already been shown, *S. ruficeps* was found existing in wood with a moisture content of only 20.5 per cent. Williams (1934) has shown that very little moisture is necessary to create a saturated environment where the air is confined in a limited space. There can be little doubt, therefore, that wherever *S. ruficeps* thrives the humidity of the environment in which it lives, is a saturated one.
HYDROGEN-ION CONCENTRATION OF INFESTED WOOD

The hydrogen-ion concentration of termite infested wood does not appear to have been studied. In the present work, the pH of 24 infestations all from different sites was measured by surface contact, using a Macbeth electric continuous recording pH meter. Two readings, taken in different parts of the galleries of each sample, were recorded and averaged. The pH of the habitat was found to be acid. The lowest pH recorded was 4.4, the highest 5.4, giving a range of ± 1.0. The range mean was 4.9.

FUNGUS-TERMITE RELATIONSHIP

Fruiting bodies growing on infested wood were collected and identified. Many of the commoner wood-rotting fungi, the fructification bodies of which are well known to me, were merely noted when found on wood infested by S. ruficeps. Tests to determine whether these termites preferred one kind of rotting wood over another, together with field observations, lead me to conclude that S. ruficeps has no specific relationship with any particular fungus. This view is held by Kofoid (1934) regarding Zootermopsis spp. and Reticulitermes hesperus. Banks and Hendee (1934) found that the groups Phycomycetes, Ascomycetes, Basidiomycetes, and Fungi Imperfecti were all represented in the workings of termites from all the ecological groups.

Fruiting bodies of Agaricaeae (Cortinarius sp.) and Polyporaceae (Fomes sp. and others) have been observed on wood infested by S. ruficeps. In addition, Pencillus sp. and Mucor sp. have been identified on the bodies of dead termites in the laboratory.

These fungi constitute a common element in the termite diet, as records from the faecal pellets of termites demonstrate (Hendee, 1934). The faecal pellets are commonly eaten by the termites. Fungi have been isolated from the gallery walls which were being eaten by the termites S. ruficeps, as has been demonstrated, cannot successfully establish itself in wood that is not decayed to some degree. In many cases, fructification bodies of fungi have developed from infested wood in the laboratory during the course of this investigation. It is therefore probable that S. ruficeps has a diet rich in fungal spores and hyphae. Efforts to keep this termite on a diet of filter paper proved unsuccessful, and experiments with sound timber also failed. This seems to support the view that the fungus forms a necessary part of the diet of S. ruficeps. Cook (1933) suggests that fungi probably fulfill the protein and vitamin requirements of termites, their normal food (cellulose) supplying only carbohydrate. Beckwith and Rose (1929) have shown that bacteria occur in the gut of termites and that certain of these bacteria aid the digestion of cellulose. Hendee has demonstrated that termites are capable of transporting fungal spores and hyphae, and that fungi are more abundant on the surface of the galleries of the termites than within the wood away from the galleries.

It is therefore probable that:

(i) While fungi are commonly present in the diet, no particular fungus is preferred by a particular species of termite.

(ii) Bacteria in the alimentary tract may be symbiotic and aid in the digestion of cellulose.

(iii) Fungi in the diet may fulfill certain nutritional requirements, and hence be necessary to the continued existence and economy of S. ruficeps.

(iv) Fungi associated with the wood which termites are inhabiting belong to a wide range of families from all the main classes of fungi, so that it is unlikely that there is any specific relationship between a given termite and a particular fungus.

(v) Termites may be a distributing agency for fungal spores and hyphae.
RATE OF WOOD DESTRUCTION BY *S. ruficeps* RELATED TO NUMBERS OF INDIVIDUALS FEEDING

It is interesting to note that in six months the young royal pair dispose of about 6.4 to 16.0 cc of wood. In one year a young colony of six individuals may destroy about twice as much as this, and if the year-old colony contains 10 individuals, from 31 to 60 cc of wood may be destroyed, while 17 individuals may account for from 40 to 110 cc of wood. All figures given depend on the degree of decay present in the wood. Harvey (1934) stated that a reproductive pair of *K. minor* removes from 0.5 to 2.5 cc of wood in 15 months. The slowness of this boring rate compared with that of *S. ruficeps* may be due to...

(a) The longer resting period before egg laying commences in *K. minor*.
(b) The fact that *K. minor* works in sound wood compared with *S. ruficeps* infesting decayed wood.

ECONOMIC SIGNIFICANCE OF *S. ruficeps*

Miller (1925) attributes considerable damage to buildings and bridge timbers to this termite, but Hill (1942) suggests that Miller’s report requires confirmation. Kelsey (1946) reports the species as having been found once in buildings, and also mentions two reports of the insect being found in sound timber. The species of wood concerned were *Pinus radiata* and *Agathis australis*, and both were in situations where the sound wood was in contact with decayed wood, or wood that was very damp. Kelsey points out that conditions in many New Zealand homes are admirably suitable for attack by *S. ruficeps* and considers it merely a matter of time before further reports of this termite from buildings will be recorded.

My own work on this species suggests that sound timber is not liable to attack and that therefore its economic significance is reduced, as any timber attacked has already been deprived of much of its strength and usefulness by the activity of wood-rotting fungi. Additional support for this viewpoint comes from another characteristic of this termite species—namely, the small size of the compound colony compared with the colonies of other ecological groups.

Castle (1934) considers that dampwood termites, once thought to be of no economic importance, must now be regarded as having a potential economic significance through their ability to attack sound timber under certain conditions. This is particularly so where a copious supply of moisture is available to the termites. Poles, sleepers, and a building are reported to have been extensively damaged by *Zootermopsis* sp.

AFFINITIES

*Stolotermes ruficeps* has near relatives in the Australian region. According to Hill (1942), the winged adult differs from all other described species by having the posterior margins of the mesonotum and metanotum markedly conical. *S. brunneicornis* Hagen occurs in Tasmania, *S. australicus* Mjoberg, and *S. queenslandicus* Mjoberg in Queensland, and *S. victoriensis* Hill, in Victoria, Queensland, New South Wales and the Australian Capital Territory.

There seems little doubt that the *Stolotermiteidae* reached New Zealand via Australia. The present distribution of this group, according to Ahmad (1950), conforms to Matthew’s theory of the distribution of primitive forms. This concept includes the belief that South Africa, Australia and South America project southwards like great peninsulas and as the primitive forms entered them at the north, they have necessarily accumulated in these continents from successive waves of dispersal and evolution. The Mastotermiteidae, the most primitive termites, are confined today to Australia, but by fossil record once had a much wider distribution in Europe and North America. The Porotermiteidae are recorded from Australia, Tasmania, New Zealand (introduced), South Africa, and Chile, and the Stolotermiteidae are recorded from Australia, Tasmania, New Zealand and South Africa. These three groups are among the most primitive of the Isoptera (Ahmad, 1950).
ASSOCIATED ANIMALS

Except for gut protozoa (Helson, 1935; Nurse, 1945) there is no indication from my observations that any of the other animals which associate with S. ruficeps show symbiotic or commensal tendencies, though Sinella termittum (O Collembola) is a commensal in the galleries and nests of many termite species. For the most part, associating animals are found in the wood or disused galleries surrounding the actual termite workings, though on occasions mites and springtails invade the termite nest. One mite was found to be ectoparasitic on these termites, but it does not appear to affect the termites to any great degree.

The following list gives animals that will be found inhabiting wood infested with Stolotermes ruficeps:

**PHYLUM ARTHROPODA**

(1) Cl. Crustacea.

O Isopoda (inhabit damp decayed wood; on one occasion taken from termite nest).

Fam Trichoniscidae

*Trichoniscus otakensis*

(2) Cl. Mysanapoda

(a) S Cl. Chilopoda (inhabit disused termite galleries).

O Scolopendromorpha

Fam Cryptopidae

*Cryptops zelandicus.*

(b) S Cl. Diplopoda (inhabit decaying vegetation and sometimes very rotten wood never actually associated with termites).

(3) Cl. Arachnida

(a) O Chernetidea (found in decaying wood).

Fam Cheliferidae

Possibly *Chelfer sp.*

(b) Acarina. Two species found in termite nests.

(i) Fam Oribatidae (vegetarian round bodied mites found in termite galleries)

(ii) Possibly Fam. Discozerconidae (ectoparasitic on termites).

(4) Cl. Insecta

(a) O Collembola Found in decaying vegetation; sometimes enter termite galleries

*Sinella sp.*

*Mydonius sp*

(b) O Orthoptera.

Fam Tettigoniidae.

*Hemideina megacephala* Found in decayed wood—not actually associated with the termites.

(c) O Isoperta

Fam Kalotermittidae

*Kalotermes browni* Found in drier parts of decayed wood. Never actually associated with S. ruficeps though often inhabiting the same log

(d) O Diptera. Numerous larvae found in damp decayed wood

(i) Fam Tipulidae

*Tipula spp*

(ii) Fam Empididae

(iii) Fam Mycetophilidae

(e) O Coleoptera Numerous larvae found in dead and decayed wood

(i) Fam Cucujidae
MORGAN—Ecology, Etc., of Stolotermes ruficeps Brauer

Possibly *Dryocora sp*

*Ochosternus zelandicus.*

(iii) Fam. Cerambycidae
Sub Fam. Prioninae

*Pronoplus reticularis*

Sub Fam. Cerambycinae

*Ambeodontus tristis* (in sound dry parts of infested wood).

(iv) Fam. Pselaphidae

Possibly *Pselaphus sp*

(v) Fam. Tenebrionidae

*Uloma tenebrionoides*

*Cilbe otagoensis.*

(vi) Fam. Cistelidae

*Tanychulus sophorae.*

(5) Cl. Onychophora

O Peripatoida  Found in decaying wood; never actually associated with termites

Of the above orders only three have been found within the actual termite galleries currently in use. Of these, the O Isopoda may possibly be excluded, due to the fact that *Trichonisus* was usually found in old damp disused insect workings. On the only occasion on which this isopod was found within the termite galleries, they had been broken open for some time and the termites were in fact living on the wood, not within enclosed galleries.

The O Acarina is probably the only important group, as one mite is commonly ectoparasitic on *S. ruficeps.* The O Collembola, however, includes a commensal in *Sinella termitum* which is commonly found in termite nests in Australia and New Zealand.

The gut protozoa, which are truly symbiotic and occur specifically in termites, were identified after Helson (1935) and Nurse (1945). Two distinct species were observed.

Cl. Mastigophora

(i) O. Hypermastigina

*Spartrichosoma magna* Helson  (Text-fig. 3, Fig. 11)

(ii) O. Polymastigina

Fam. Joenididae

*Cyclojoenma australis* Nurse  (Text-fig 3, Fig 12.)

EXTERNAL ANATOMY OF STOLOTERMES RUFICEPS BRAUER

The segmented body is elongate with a lightly sclerotised exoskeleton variously covered with fine short to moderately long bristles. The head bears the mouth and biting mouth parts, a pair of moniliform antennae, and a pair of compound eyes. The fenestrae are distinct in mature insects but ocelli are lacking in all stadia and castes. Each thoracic segment subtends ventrally a pair of jointed legs, and in the perfect insects the mesothorax and metathorax each support a pair of dorsal membranous veined wings approximately 1.5 times the length of the body. The prothorax and mesothorax each contains a pair of lateral spiracles. The abdomen consists of ten segments: the first eight each having a pair of spiracles, while the ninth segment may bear ventrally a pair of styles (absent in females) and the tenth segment bears latero-ventrally a pair of jointed cerci. The sclerites of the body which are separated by soft membranous intersegmental areas are shown in Text-fig 2, figs. 3, 4, 5, 6 and 8. The legs each consist of five distinct segments called from the proximal segment, the coxa, trochanter, femur, tibia and tarsus. The tarsus (Text-fig. 1, Fig. 11B) is further divided into four segments: the distal one bearing a pair of claws without an empodium. The tibia distally bears two or three spurs.
Text-fig 3—Fig 1—Eggs  Fig 2—First instar nymph, dorsal view  Fig 3—Second instar nymph, dorsal view  Fig 4—Third instar nymph, dorsal view  Fig 5—Fourth instar nymph, dorsal view  Fig 6—Fifth instar nymph, dorsal view  Fig 7—Sixth instar nymph, dorsal view  Fig 8—Seventh instar nymph, dorsal view  Fig 9—Alate  Fig 10—A, aperous neotenic, B, brachypterous neotenic  Fig 11—Spyrotrichomus magna Helson  Fig 12—Cyclopoecia australis Nurse
BRIEF DESCRIPTION AND MEASUREMENT OF NYMPHAL INSTARS FROM
DORSAL ASPECT

Note. Measurements of head length always taken to clypeofrontal suture
Measurements of labrum length includes the clypeus. All measurements are in milli-
metres to the nearest second decimal place.
1 The First Instar Nymph. Text-fig 3, Fig. 2

Head 0.55 to 0.70 wide by 0.42 to 0.55 long, labrum tongue-shaped, 0.20 long
by 0.25 wide; mandibles with teeth pigmented (orange to red); antennae with
6 to 8 segments 0.50 to 0.65 long, thoracic segments of almost equal length; pronotum
little modified but narrower than head; thorax 0.40 to 0.50 long; abdomen 0.90
to 1.05 long, and 0.50 to 0.80 wide, cerci usually with 4 segments. Total length of
animal 1.90 to 2.30 Colour, white.

2 The Second Instar Nymph Text-fig. 3, Fig. 3

Head, 0.80 to 0.85 wide and 0.60 to 0.72 long; labrum 0.30 long by 0.32 wide;
mandibles with teeth pigmented (reddish) antennae 9 or 10 segments 0.70 to 0.82
long; thoracic segments slightly modified in shape, thorax 0.70 to 0.85 long; abdomen
1.20 to 1.40 long by 0.85 to 0.96 wide Total length of animal 2.80 to 3.30. Colour
creamy white.

3 The Third Instar Nymph Text-fig 3, Fig 4.

Head 0.90 to 0.95 wide by 0.75 to 0.79 long; labrum 0.35 to 0.36; antennae
11 or 12 segments 1.00 to 1.15 long, thorax 1.00 to 1.10 long abdomen 1.72 to 2.15
long by 1.00 to 1.15 wide Total length 3.90 to 4.50 Colour rich cream, abdomen
darker, due to wood particles in gut

4 The Fourth Instar Nymph Text-fig. 3, Fig 5

Head 1.00 to 1.35 wide by 0.80 to 0.83 long, pigmented compound eyes present
0.15 to 0.19 in longest diameter; labrum 0.45 to 0.50 long by 0.45 wide Antennae
12 segments, 1.65 long; thorax, pronotum now characteristic of species with anterior
dege slightly concave with median indentation, lateral edges slope sharply to small
posterior edge, which has a median indentation Pronotum 0.47 long by 0.75 wide;
has median longitudinal depression, thorax length 1.57 to 1.69; abdomen 2.30
to 2.64 by 1.47 to 1.63 wide Total length 5.10 to 5.76 Colour same as third instar

5 The Fifth Instar Nymph Text-fig 3, Fig 6

Head 1.35 to 1.49 wide by 0.90 to 1.02 long, eyes as in fourth instar nymph;
labrum 0.46 to 0.50 long by 0.47 wide, antennae 14 to 16 segments 1.70 to 1.85
long, thorax, pronotum 0.47 long by 0.75 wide: thorax length 2.05 to 2.15 long,
abdomen, 3.00 to 3.15 long by 1.75 to 1.90 wide Total length 6.15 to 6.85 Colour
as in third instar

6 The Sixth Instar Nymph Text-fig. 3, Fig 7

Head 1.50 to 1.52 wide by 1.05 to 1.15 long; eyes 0.20 to 0.25 in longest
diameter, labrum 0.50 long by 0.50 wide, antennae 14 to 16 segments 1.80 to 1.95
long, thorax, pronotum 0.50 long by 0.90 wide; thorax length 2.15 to 2.20; abdomen
3.25 to 4.45 long by 1.35 to 2.15 wide Total length 6.90 to 8.40 Colour as in third
instar

7 The Seventh Instar Nymph Text-fig 3, Fig 8

Head 1.55 to 1.60 wide by 1.15 to 1.20 long, eyes 0.30 in longest diameter,
labrum 0.50 long by 0.50 wide, antennae 14 to 16 segments 1.85 to 2.20 long; thorax,
pronotum same as sixth instar mesonotum and metanotum (with wing buds) and
posterior edges bluntly conical; thorax length 2.75 to 2.85; abdomen 3.75 to 4.50
long by 1.95 to 2.20 wide Total length 8.02 to 8.95. Colour as in third instar

N
**Detailed Descriptions with Measurements of Alate and Soldier**

**Alate. Text-fig 3, Fig. 9.**

Colour: Dark brownish black except the labrum, which is a lighter brown, and the clypeus, which is white. Head as in nymphs, width 1.55 to 1.60, length 1.00 to 1.20. Length including labrum 1.45 to 1.65; labrum 0.45 to 0.47 long by 0.41 wide; clothed with fine short bristles with longer bristles on the anterior edge; clypeus (Text-fig 2, Fig 4, number 2); membranous but with a few fine short hairs; mandibles (Text-fig. 2, Fig. 9, B), the left mandible is 0.57 long by 0.54 wide and has 4 sharp, conical teeth and a basal grinding area about one-third the length of the total grinding face of the mandible. The right mandible is 0.45 long and 0.51 wide and has 3 prominent conical teeth, the second one with a very small tooth on its upper surface near the base. A grinding area is present on the basal third of the mandible. Maxilla and labium (Text-fig 2, Fig 11) Maxilla: Cardo 0.3 long with very few hairs on outer surface; stipes 0.35 long with few hairs on outer surface. Palp with 5 segments becoming progressively longer towards the distal segment, which is longest. All but the basal segment are profusely bristled. The lacinia is 0.50 long and has 12 to 28 stout bristles on its inner face and distally it terminates in two sharp points. The galea is 0.52 long and consists of a basal segment subtending a long distal segment. Labium: glossae 0.25 long without bristles, paraglossae 0.26 long with very short bristles. Palp of 3 segments progressively longer towards the distal segment, which is longest. All segments are profusely bristled. Prementum 0.4 long and covered with very short bristles. Gulaementum oval-shaped 0.93 long by 0.52 wide with moderately long bristles. Hypopharynx (Text-fig 1, Fig. 10) anteriorly clothed with very short bristles. Antennae 15 to 17 segments (commonly 15), third segment very small. Segments progressively larger from the fourth towards the distal end, profusely bristled, largest bristles towards the centre of each segment. Frons with two median depressions; fenestrae large, conspicuous and slightly crescent-shaped; epicranial suture distinct; eyes large (0.47 in longest diameter) and prominent; ocelli are absent, head with few fine bristles. Thorax: Pronotum with anterior edge slightly concave, a small median depression, and clothed with moderately long bristles. Lateral edges slope back to a somewhat rounded posterior edge much shorter than the anterior one and having a small median depression. The longitudinal midline of the pronotum is slightly grooved; length, 0.55 to 0.65, width 0.86 to 0.93. Mesonotum and metanotum with posterior edges bluntly conical and each sclerite laterally recessed for the wing stumps when the wings are folded. Thorax length 2.38 to 2.53. Ventrally and laterally the thoracic segments are protected by sclerites (Text-fig 2, Figs 4 and 8). Forewing (Text-fig 4, Fig. 3B): Subcosta rudimentary, radius about one-third the length of the wing and extending beyond the second branching of the radial sector, radial sector parallel to the anterior margin of the wing and having 6 to 9 short diagonal branches to the costa, the distal one usually terminating just above the extremity of the wing, the media slightly above the mid-line of the wing with 3 to 7 diagonal branches, 2 to 4 of which branch again before meeting the posterior margin of the wing distal to the cubitus. The last branch of the media terminates below the distal extremity of the wing, the cubitus almost as long as the radius and having 3 to 6 diagonal branches to the posterior margin, anal rudimentary. The wing membrane is clothed with minute stellate microstars. Spines are widely spaced except towards the wing extremity, where they occur closer together on the wing margin. Spines are situated on the veins of the wing. The basal suture is concave. The anterior wing stump is 0.80 long on the anterior margin and 0.53 long on the posterior margin. Full length of wing with wing stumps 10.72 to 11.15, width 2.85 to 3.20. Hindwing (Text-fig. 4, Fig 3A): Subcosta as in forewing, radius as in forewing but typically gives rise to media just distal to the basal suture, media as in forewing but only 1 to 3 of its branches branch again before meeting the posterior margin of the
wing; cubitus often longer than in forewing with 3 to 6 branches running to the posterior margin of the wing. In other features the hindwing resembles the forewing, except that spines are fewer and more widely spaced. Length 9·92 to 10·75, width 2·56 to 2·85. The abdomen (Text-fig. 2, Fig. 3) consists of 10 segments, the first 8 each having a pair of lateral spiracles (B) near the postero-lateral edges of the tergites. The 10 tergites are distinguishable. The first sternite is lacking. In the male alate the remainder of the sternites are visible and easily distinguished; the ninth subtends a pair of subanal styles (Text-fig. 4, Fig. 12B), and the tenth subtends a pair of five-jointed cerci (Text-fig. 4, Fig. 12A). In the female, sternites 2 to 7 are distinguishable, the eighth and ninth are reduced and modified, being covered by sternite 7 (Text-fig. 4, Fig. 12B). Sternite 10 is visible and subtends a pair of five-jointed cerci as in the male. The majority of the thoracic and abdominal sclerites have short to moderately long bristles or hairs, the greater numbers of which occur towards the posterior margins of the sclerites. Text-fig. 4, Fig. 12A shows a ventral view of the 7th, 8th, 9th and 10th abdominal segments of a male alate with ventral subanal styles and latero-ventral cerci. Text-fig. 4, Fig. 12B shows the corresponding part of a female alate with sternites 6, 7 and 10 visible, the absence of styles and the presence of the jointed cerci. Abdomen length 3·25 to 4·25; width 1·46 to 1·83. The legs (Text-fig. 1, Fig. 11A) are short, stout, and covered with fine, moderately long bristles. Spines occur at the extremities of the tibiae, 3 on each of the prothoracic and mesothoracic legs and 2 on each of the metathoracic legs. Tarsi are four-jointed, the distal segment having a pair of claws without empodia.

Size of dealates: Length from anterior margin of the labrum 7·05 to 8·32.

The Soldier. Text-fig. 2, Figs. 7 and 12.

Colour, rich creamy white thorax and abdomen, head reddish brown, large, parallel-sided and dorso-ventrally flattened with dorsal and ventral surfaces parallel. Head broadly oval in transverse section, very dark reddish brown anteriorly, gradually shading back to a yellowish posterior. More profusely bristled than in alates and nymphs. Length toclypeofrontal suture 1·75 to 2·15, length to tip of mandibles 3·05 to 4·89, width 1·18 to 1·59. Labrum (Text-fig. 1, Fig. 8): 0·73 long by 0·51 wide, truncate anterior margin with 8 to 12 long bristles, lateral margins sloping outwards for about three-quarters their length then turning sharply in to the basal margin, which is about 1·3 times as long as the anterior margin. The dorsal surface has short, fine bristles. Clypeus (Text-fig. 1, Fig. 8): Membranous and without bristles. Mandibles (Text-fig. 2, Fig. 10), stout and elongate, almost black at the apices, shading back to dark reddish brown at their bases. The outer margins slightly convex, inner margin of the right mandible distinctly more concave than that of the left mandible. The right mandible has an apical tooth, a second broadly conical tooth situated about one-third the length of the mandible from the apex, a third broader topped tooth about half-way along the mandible and a basal grinding area. The left mandible has 3 large conical teeth, one at the apex, another just above one-third the length of the mandible from the apex, and another just above half-way. A smaller conical tooth occurs just below half-way, followed by a long basal grinding area. Mandible length: 1·50 to 1·85, width 0·61 to 0·68. Maxilla and labium (Text-fig. 1, Fig. 7): Maxilla as for alates; labium differs from alate pattern in the shape of the gulaementum, which in the soldier is narrower and more elongate. Labium length from the apex of paraglossa to the base of the gulaementum 2·20 to 3·12; gulaementum 1·77 to 2·70 long, 0·51 to 0·73 wide at widest point. Usually without bristles. Hypopharynx as for alates. Antennae: 14 to 19 segments (usually 15 or 16), form as in nymphs (Text-fig. 2, Fig. 1), with a light band of brownish pigment encircling central region of each segment from the third to the distal one. The segments are clothed in bristles of varying length. Frons almost parallel to the ventral surface of the head; epicranial suture distinct, eyes small and pigmented; ocelli and fenestrae absent. Thorax as in fifth and sixth instar nymphs. Pronotum 0·65 to 0·75 long,
Text-fig 4—Fig 1—Three year old queen A, dorsal view, B, ventral view of head and thorax. Fig 2—Ventral view of posterior abdominal segments of first instar nymph. Fig 3—Dorsal view of right wings of alate B, forewing, A, hindwing, showing basic pattern of venation. 1, Basal suture, 2, Subcosta, 3, Radius, 4, Radial sector, 5, Media, 6, Cubitus, 7, Anal. Fig 4—Ventral view of right forewing. Fig 5—Ventral view of right hindwing. Fig 6—Ventral view of left forewing. Fig 7—Ventral view of left hindwing. (NB—Wings in Figs 4 to 7 are from one alate which came from the same colony as that from which Fig 3 wings were drawn.) Fig 8—Dorsal view of left anterior wing stump. Fig 9—Dorsal view of left posterior wing stump. Fig 10—Dorsal view of section of leading edge of the distal part of the forewing, showing spines and stellate micrasters. Fig 12—Ventral view of posterior abdominal segments of alates—(A) the male and (B) the female. Fig 13—(A) cercus, (B) style.
0.98 to 1.21 wide, always much narrower than the head. Abdomen as in alates, with the same differences in the posterior sternites of male and female soldiers (Text-fig. 4, Fig. 12, A and B). Legs, cerci, and styles as in alates. Length of soldier 8.02 to 10.05. All castes and stadia have the majority of the exoskeletal sclerites of the body clothed with short to moderately long bristles. Thoracic and abdominal appendages are similarly bristled. The head has relatively few bristles except on the palps, laciniae, paraglossae, labrum and gulalementum of the mouthparts. The gulalementum of the soldier caste lacks bristles.

**Emergency Soldiers**  Text-fig 2, Fig. 14A and B.

They are essentially the same as the soldiers described above, but usually much smaller (5.71 to 7.22 in length). The head sometimes varies, having the sides slightly convex instead of parallel. The mandibles follow the characteristic pattern. Soldiers from the same colony may show all ranges of variation.

**Primary Female Reproductive.** Text-fig. 4, Fig. 1.

Form as in the female alate without wings. The abdomen enlarges with age and increased egg-laying capacity. Size range: Length, 10.00 to 11.00 (same as alate for first year after swarm). Width, 2.24 to 2.65 (same as alate for first year after swarm). Color: Brownish black except for labrum (brown) and clypeus (white).

**Primary Male Reproductive.**

Form and size range as in male alate already described.

**Brachypterous Female Reproductive**  Text-fig. 3, Fig. 10B

Form as in seventh nymph. Wing buds usually rudimentary, scale-like, and small. Abdomen as for primary female reproductive. Size range: Length, 9.65 to 11.25. Width, 2.10 to 2.65. Color: Creamy white.

**Apteron Female Reproductive.** Text-fig. 3, Fig. 10A.


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