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SOME ASPECTS OF THE ECOLOGY OF THE STINK ANT PALTOTHYREUS TARSATUS (FAB.) IN UGANDA

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RÉSUMÉ

Quelques aspects de l'écologie de la fourmi puante Paltothyreus tarsatus (FAB) en Ouganda.

Les activités ravageuses et fouisseuses de la « fourmi puante », *Paltothyreus tarsatus*, furent suivies, de novembre 1970 à décembre 1971, à deux stations situées dans les environs de Kampala en Ouganda. Les deux types d'activités sont significativement influencés par la température et l'humidité. La chasse est effectuée individuellement, au hasard ; la vue ne constituant vraisemblablement qu'un des sens utilisés. Cette activité prend habituellement place au crépuscule et pendant la nuit. L'observation directe ainsi que celles des tas de nourriture indiquent la prédominance des insectes (81,8 %) dans l'alimentation. Les principaux groupes sont dans l'ordre les Hyménoptères, les Dictyoptères, les Isoptères et les Coléoptères. Les Millipèdes (Diplopodes) sont encore importants (15,1 %) tandis que les groupes non arthropodes sont de faible importance. L'alimentation montre peu de variations saisonnières. Le fouissement du sol (203 g/m2/an) est spectaculaire et comparable à celui de deux espèces de termites édificateurs de monticules. Il est faible en pleine saison des pluies et en pleine saison sèche.

ABSTRACT

The foraging and soil excavation of the large and common ' Stink Ant ', *Paltothyreus tarsatus*, were studied from November, 1970 to December, 1971 at two sites in the vicinity of Kampala, Uganda, in the Lake Victoria zone. Both activities were significantly affected by temperature and humidity. The ants hunt singly, by randon search in which sight is probably only one of the senses used. Foraging was usually, concentrated to crepuscular and nocturnal times. Food midden and direct observations indicated that insects, with 81.8 % predominated in the diet. Hymenoptera, Dictyoptera, Isoptera and Coleoptera in that order

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were the main groups. Millipedes (Diplopoda) were also important (15.1 %) but non-arthropods were of little significance. Diet composition showed no large seasonal differences. Soil excavation (203 g/m2/yr) was striking and comparable to that of two species of mound-building termites. There was very little soil excavation during both the wet and dry seasons.

INTRODUCTION

Ants, like termites, comprise a ubiquitous, large and significant component of the fauna of tropical soils. In spite of this fact, however, the study of their ecology in Africa has been relatively neglected, presumably because the majority of the species that are commonly encountered have no obvious pest status. Their role in the soil ecosystem has, nevertheless, been often stressed by various authorities, albeit in vague and general terms (BANAGE, 1966). Among the major ecological activities performed by ants in the soil are the following :

1. They move large quantities of soil and create favourable conditions for its aeration and the percolation of water through it and possibly for the retrieval of nutrients.
2. They consume animal and plant remains which are then incorporated into the soil for humification processes, unlike termites which partly remove these products from circulation by incorporating their faeces into their consolidated mounds.
3. They act as regulating agents for populations of noxious and other organisms through their predation, although in some cases they also herd undesirable organisms and so themselves act as pests.
4. They form a food source for a considerable number of insectivorous animals, particularly certain vertebrates but also invertebrates.

It was with some of these activities in mind that a study was initiated on the ecology of the common Stink Ant, *Paltothyreus tarsatus* (Fab.). The investigation concentrated on environmental factors responsable for its activities, and on aspects of its feeding biology, with the hope that these investigations would form the basis, later on, for detailed studies on the role of this ant in the energetics of the soil ecosystem.

THE ANT

The most comprehensive account of the biology of *Paltothyreus tarsatus* was given by WHEELER (1922) in his compendium on the ants of the then Belgian Congo, now Zaïre. It is a monotypic Ponerine entirely restricted to the Ethiopian Region in its distribution. It does not extend beyond 15°N, but elsewhere it is a most characteristic and often, locally very abundant, ant. The workers are large, black and monomorphic, measuring about 1.5— 2.0 cm in length. They possess massive, triangular mandibles whose apical borders have denticles and are lined on the inner side with fine, presumably sensitive hairs. In addition, the ant is armed with a powerful sting with which it immobilizies its prey and, when disturbed or excited, emits an alarm substance with a foetid odour (SUDD, 1962) which has been variously described as like an 'appalling smell of bad eggs' (CAPENTER, 1920) or 'the juice of a foul tabacco pipe' (ARNOLD, 1916). Its common name of 'Stink Ant' refers to this smell which has been reported to be due to sulphur compounds (CASNATI *et al.* 1967). The ants have large, compound eyes and a well-developed sense of sight although how much of this is used in foraging is not known.

Of the other castes, the queen is more or less similar to, but slightly larger than the worker for which it may be mistaken in the field. The winged males have small, conical heads with mandibles which are less developed than those of the females. The head also has long, slender antennae unlike those of the females. Males are short-lived. These castes have been described by WHEELER (1922).

THE STUDY SITES

The work was done at two sites in the vicinity of Kampala, Uganda (0°19''N, 32°35''E). The first and the major one was at Kabanyolo University Farm which lies about 18km to the north of Kampala, in an area of a dissected mid-tertiary peneplain now forming a series of rounded hill and ridges and coalescent pediments sloping towards slow-draining papyrus swamps. The University Farm is at an altitude of 1317m above sea level and the soils on the hills and ridges are generally acid, red clay loams (latosols). The original vegetation was dominated by Elephant Grass (*Pennisetum purpureum*) and was clearly a post-cultivation community as described by LANGDALE-BROWN *et al.* (1964). Details of the soils and the climate of the area have been given by BANAGE & VISSER (1967) and VISSER & BANAGE (1974). Between 1970 and 1974 several colonies and one in particular, Colony K-B, on the side of a farm road bordering a coffee plot, was studied intensively.

The second site was at Kaazi on the shores of Lake Victoria, about 13km to the south of Kampala and at an altitude of about 1066 m above sea level. The area has typical shallow lake-side sandy loam soils overlying lateritic outcrops on quartzite rocks. The vegetation consists of patches of lake shore forest interspersed with swards of edaphic grassland dominated by *Loudetia kagarensis*. There are also thickets on termitaria and clearings in the forest. The area is heavily grazed by native cattle (LIND & MORRISON, 1974). Nests of *Paltothyreus* were very abundant in the grassy patches and forest clearings and on the termite hills.

Both these sites experience rainfall throughout the year but with a bimodal pattern characteristic of the Lake zone of Uganda. The peaks usually come in April-June and September-November with July-August and January-February being the driest periods. Kabanyolo has an average rainfall of 1400mm per anum while Kaazi has about 1270mm.

METHODS

1. Meteorological Methods

HUXLEY & BEADLE (1964) studied the effect of the topography on the diurnal microclimatic conditions on Kabanyolo University Farm and the fluctuations in the annual soil moisture and soil temperature were investigated by BANAGE & VISSER (1967). The Farm has a metereological station from which daily and mean rainfall data were obtained but for the purposes of this investigation a special micrometereological unit, with a standard East African Stevenson screen, was set up. Air and soil temperatures at three levels: ground level, 5cm and 10 cm below the surface, were measured with mercury in glass thermometers, while a continuous record of temperature and humidity was obtained with a 24-hour self recording thermohygrograph. Soil moisture at 15, 30, and 60 cm levels was measured at 3-day intervals with nylon/stainless steel electrical resistance units (FARBROTHER & HARRISON, 1957). When 24-hour observations were made on the ants, light intensity in watts, was simultaneously measured by means of a specially designed photo-electric light meter. Weather factors were measured at 30 minute interval.

2. Biological Methods

Foraging activity and the kind of food organisms captured by the ants were studied by direct observation of the ants leaving and returning to the nest holes. On four occasions, 24-hour watches were carried out at the main study colony at Kabanyolo (Colony K-B). All the ants foraging over the whole of 700m2 area covered by the colony were counted at hourly intervals by two people traversing the area slowly. Each count took about 10min. and at night powerful torches were used. In this way foraging activity could be correlated with the changes in the daily environmental factors.

Another method used to study the food eaten by *Paltothyreus* was to examine the remains of the organisms thrown out at midden heaps. The ants use regular holes for communal refuse including pupal cases and food remains and at the main study site there were five such middens from which the food remains were collected about twice a week. The weekly samples were bulked and spread out thinly on a perspex tray with graduated sides. After removing any large items, five random sub-samples were taken and analysed. The remains of the different food organisms examined under the microscope were identified as far as was possible. At the same time, for comparative purposes, litter samples were taken, the organisms hand sorted and rated according to their abundance into four classes : very many, many, few or absent. Each month 5 litter quadrats, each 1m2, were taken for this purpose, except in October when 10 quadrats were taken. Handsorting, the number of qnadrats taken and the qualitative method of presenting the results, although sufficient for this work, may nevertheless be open to criticism. These were decided on as a matter of convenient compromise in the light of other work that had to be done at the same time. The automatic extraction with Tullgren funnels was intially tried but abandoned because it did not work for organisms like *Limicolaria martensiana* (Mollusca) nor for large arthropods such as millipedes whose egress was prevented by the wire mesh.

Nesting activity was studied by mapping the nest holes which were open and noting those which were active or abandoned. Soil from the holes was collected with a brush and trowel every three days during the dry season or regularly before the storms during the rainy season. In the laboratory a 5gm sub-sample of this was oven-dried to constant weight at 80°C and from this the dry weight of the sample was estimated.

The nomenclature adopted for the insects was according to IMMS (1957) and that for other arthropods was according to CLOUDSLEY-THOMPSON(1958).

THE RESULTS

1. Foraging Methods

Although some reports have been made of *Paltothyreus* carrying out group raids, for example by WILSON (1971) among many others, no evidence of this behaviour was found during this work. Instead, all the foraging was found to be done by lone ants. Such congregation at a food source as was seen occasionally appeared to be entirely fortuitous and to be due to ants locating the same prey site independently or possibly by recruitment. This happened, during the wet season, at termite tunnels.

In order to find out the pattern of foraging, individual ants were followed and timed from the moment they left the nest hole to the moment they returned, with or without prey, and Fig. 1 shows a number of such tracks. Ants carried out random searches for prey usually fairly close to their nest holes, althought sometimes they could traverse quite considerable distances. Each ant feels its way as it moves slowly touching the ground with its antennae. All the ants observed stopped now and again, waved their antennae and tapped the ground or often doubled on their paths and re-oriented before moving on again. Although the ants have well — developed eyes, they did not seem to hunt by sight entirely as they often bumped into or startled arthripods but did not pursue them or orient to them particularly. They appear, however, to use their sight in returning to the nest hole, for unlike ants that lay trails, *Paltothyreus* does not return by the same route as that taken on the outward journey. The return is usually quicker and more direct. Most foragers, especially when laden, often show no hesitation in their returning to the nest hole.

Once located, the prey is grabbed and bitten with the powerful jaws but larger prey or that which continues to struggle is also stung by the ant doubling its gaster under itself while holding the prey with the mandibles. During the transport, the ant holds the prey with its longest or largest part underneath its gaster. Heavy items are dragged backwards, but then the ants are seen to stop and drop the prey periodically and then scout or explore the way before proceeding again. Some-

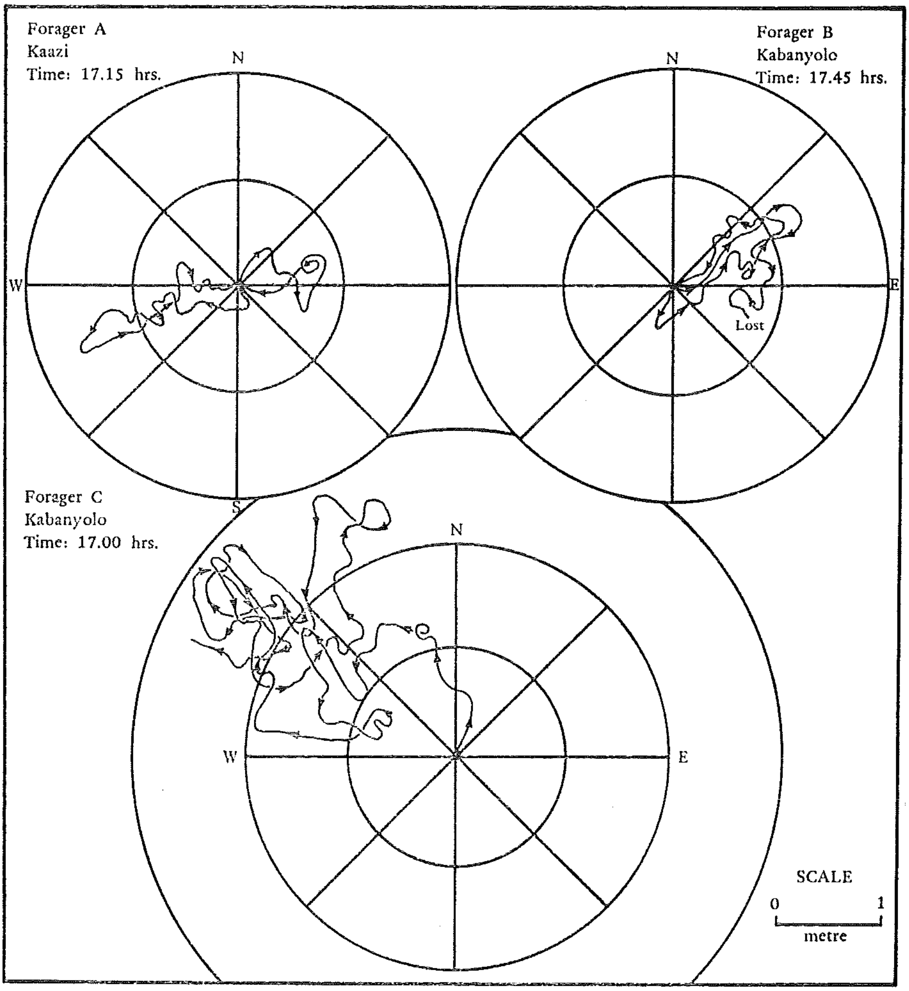

Fig. 1. Foraging tracks of three *Paltothyreus* individuals.

times co-operation between a group of workers occured in killing and dragging large prey organisms. Such co-operation was particularly noted in artificial formicaria when, offered large prey organisms like grasshoppers, more ants appeared to be drawn to the prey by the foetid, alarm scent of the previous attackers.

2. Foraging Rhythm and Factors affecting it

Workers of *Paltothyreus* are usually seen foraging during the hours of early morning, evening and at night — During the wet seasons individuals may be seen in varying numbers throughout the day. The factors which control the foraging rhythm were investigated by 24-hour observations on four occasions at the Kaba-

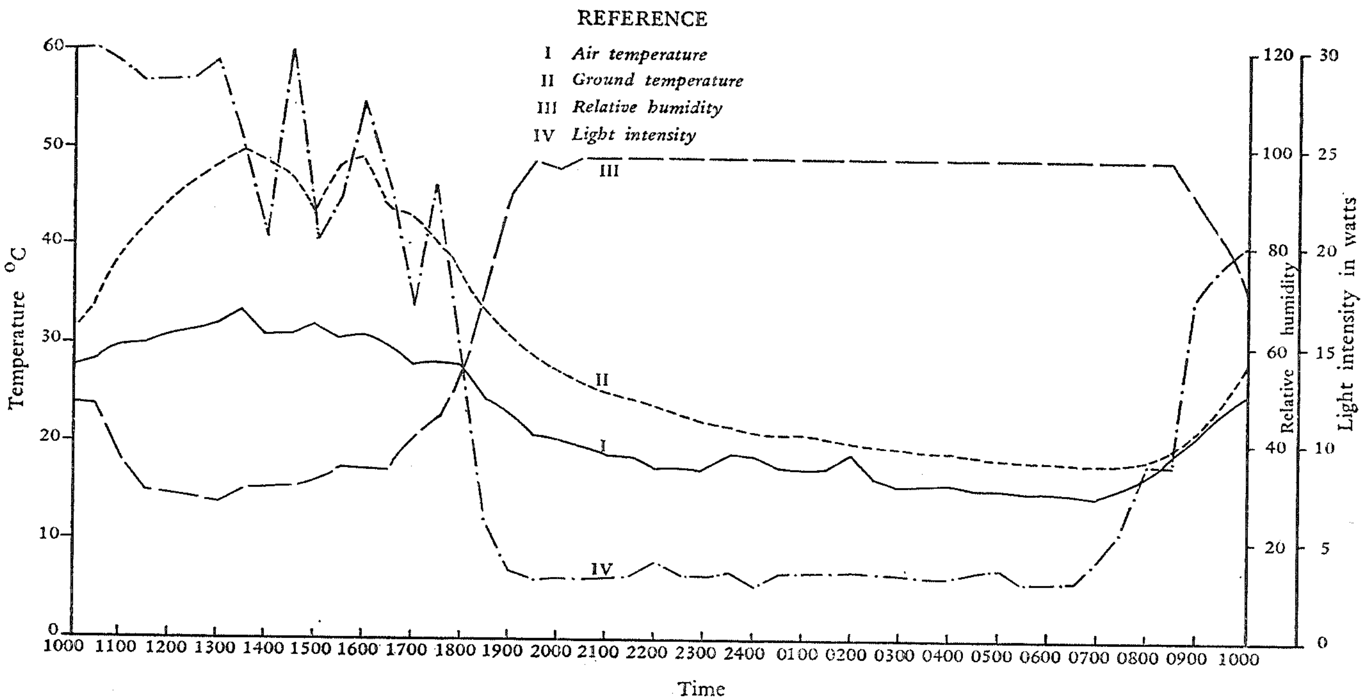

Fig. 2. Mean weather conditions at Kabanyolo on Days I, III and IV.

nyolo K-B colony. Two of the occasions were during the dry periods and the other two during the wet. To test for the possible effect of moonlight the seasonal observations were timed to coincide with full moon and dark phases alternately, but moonlight was not found to have any significant effect on the foraging activity. The other weather factors thought to affect activity : air and ground temperature, relative humidity and light intensity, were measured as already indicated.

On three of the occasions there was a consistent pattern in the results of the micro-climatic factors and the mean of the factors was taken in each case (Fig. 2). It could then be seen that the day divided into four time periods which are summarised in Table 1. On the fourth occasion (Day II) which was a humid, warm

Table 1. Summary of average micro-climatic factors at Kabanyolo. (1)

Time Interval	N° of Hours	Conditions
10.30-16.30 hr	6	Daylight conditions : A.T. > 30°C, G.T. > 40°C R.H. < 30 %, L.I. > 17.5W
16.30-19.30 hr	3	Evening Transitional conditions (before and after sunset) : A.T. 20°—30°C, G.T. 30°—40°C R.H. 30 %—95 %, L.I. 2.5—17.5W
19.30-07.30 hr	12	Night conditions : A.T. 15°—20°C, G.T. 20°—30°C R.H. > 95 % L.I. 2.5W
07.30-10.30 hr	3	Morning Transitional conditions (immediately after sunrise) ; A.T. 15°—23°C, G.T. 15°—30°C R. H. 70 %— 95, % L. I. 5-20 W

and cloudy day, relative humidity remained above 60 % during the daylight period. As for the temperature, whilst the minima of the air and ground temperature were similar to the other occasions or only slightly depressed, the maxima were depressed by as much as 10°—20°C, thus creating uniformly warm conditions during the daylight hours (Fig. 3).

The mean numbers of ants foraging over a 24-hour period is given in Fig. 4 for the three more normal conditions and in Fig. 5 for the anomalous fourth occasion (Day II). Evidently, from Fig. 4, the ants started foraging during the evening transitionnal period while the temperature and light conditions were rapidly decreasing and relative humidity was rapidly increasing. These apear to have become optimal around 23.30 hr. There was then a main peak of ant activity, succeeded by a smaller one at 02.30 hr and foraging then decreased as air

(1) Key : A.T. = Air Temperature, G.T. = Ground Temperature
R.H. = Relative Humidity, L.I. = Light Intensity.

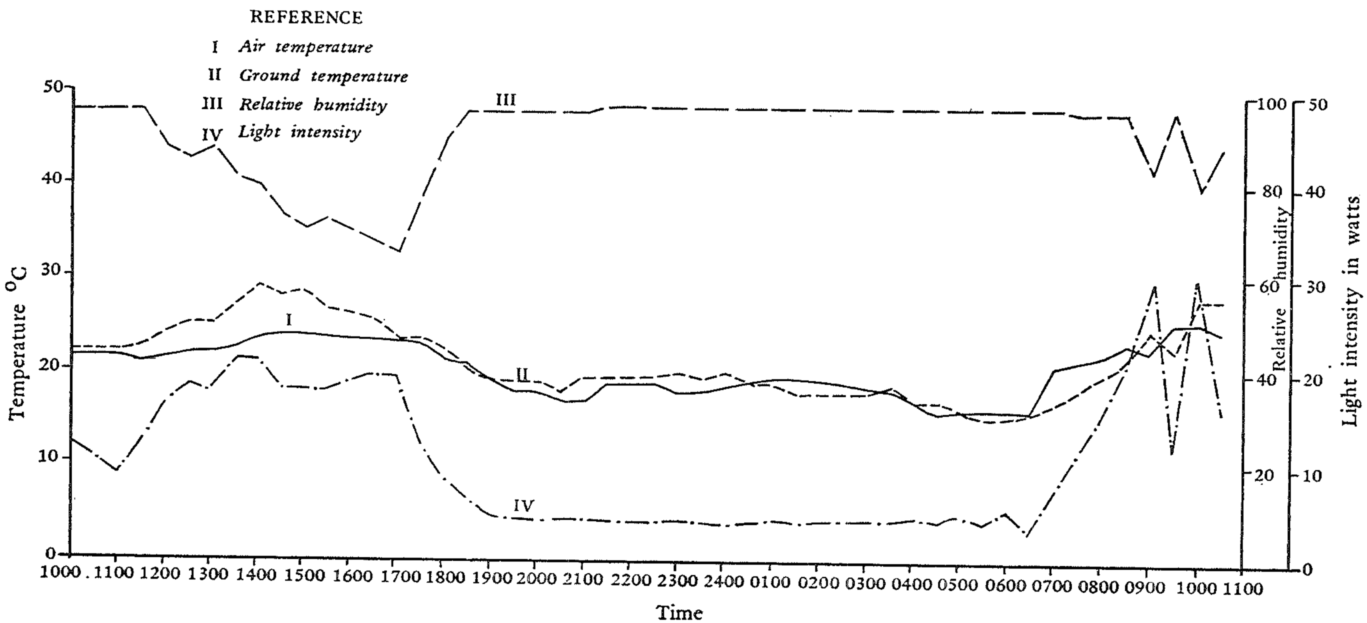

Fig. 3. Weather conditions at Kabanyolo on Day II.

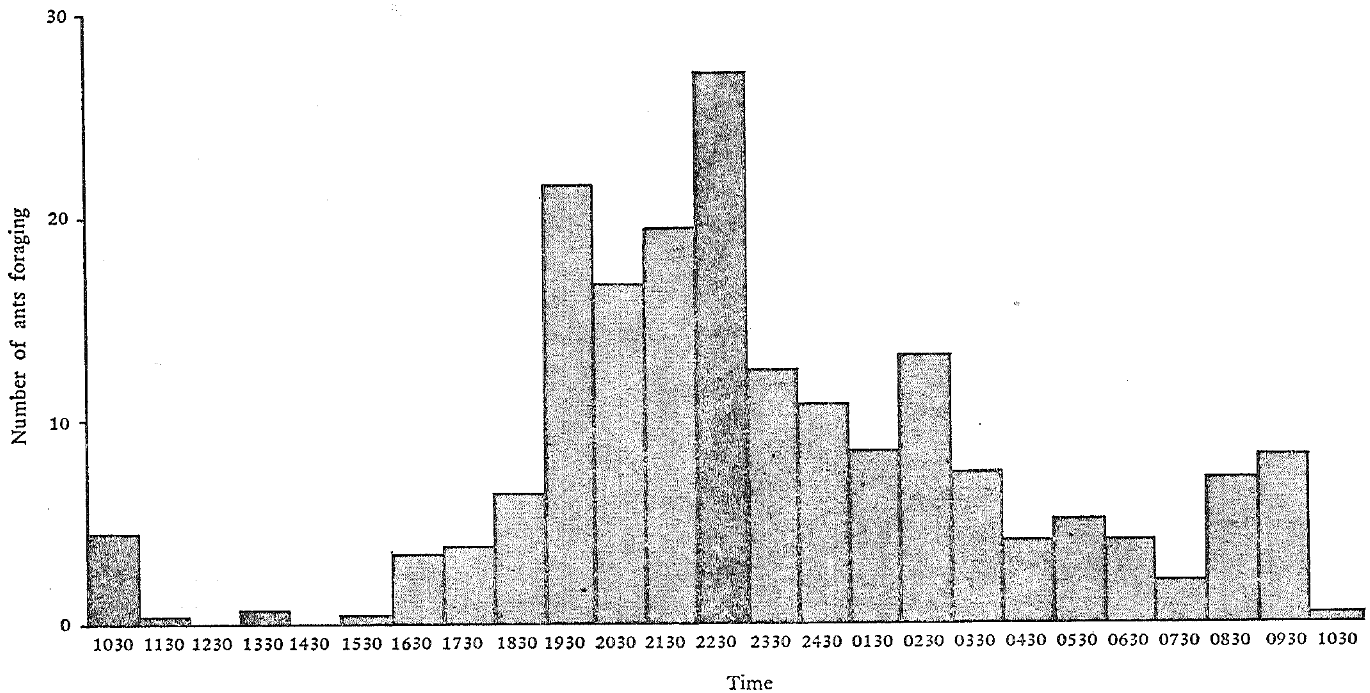

Fig. 4. Mean number of ants foraging on Days I, III and IV.

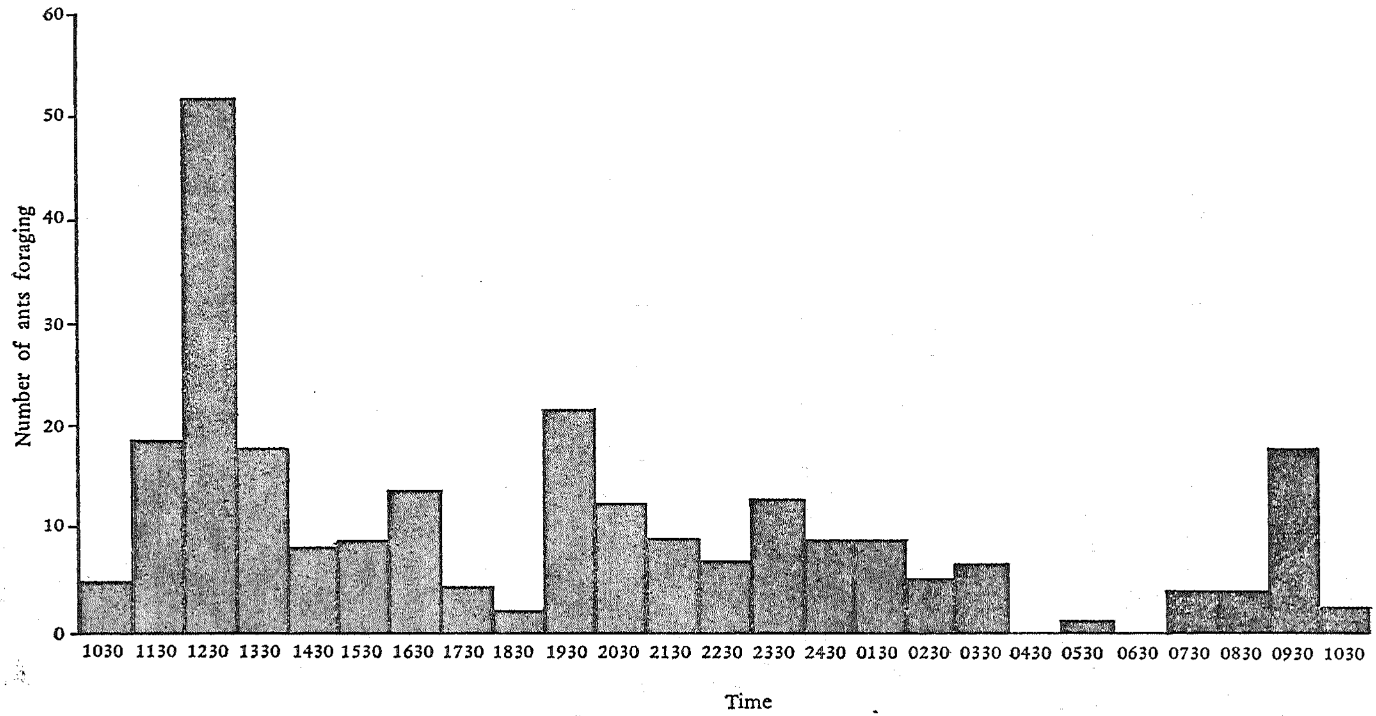

Fig. 5. Number of ants foraging on Day II.

and ground temperature fell to their lowest level just before sunrise. Another and lower peak of activity occurred at around 09.30 hr, during the morning transitional period following sunrise. On the 'freak' Day II, given a high relative humidity, the main foraging activity peak occurred at 12.30 hr (Fig. 5) when air and ground temperatures, at 21.5°C and 24°C respectively, were comparable to those at 23.30 hr in Fig. 4. This day also indicated further activity peaks of decreasing magnitude at 19.30 hr and 23.30 hr besides the morning peak at 09.30 hr It is intersting to note that this periodicity was shown in spite of the rather uniform weather conditions experienced for most of the day, indicating that it was probably inherent in the ants.

3. **Food Organisms**

While there are several reports to the effect that *Paltothyreus* feeds largely or exclusively on termites (e.g. WHEELER, 1922 ; SKAIFE, 1953 ; GLOVER, 1967 and WILSON, 1971), these have usually been based on casual or brief observations. Other writers have stated that the ant is a general scavenger and carnivore ; (CARPENTER, 1920 ; BOLTON 1973) and yet others have found it utilizing food of plant origin (SUDD, 1967). The objective of the present study was to try and provide some systematic information on the composition of the ants diet in one situation against which investigations elsewhere might be compared and also to find out any differences which might be due to season.

A. — Analysis of Food Middens

Between November 1970 and December 1971, 50 weekly midden samples were collected from the Kabanyolo K-B site and analysed for their content of food remains. In order to compare with what was available as prey for ants, litter samples were taken from the neighbouring coffee mulch. Table 2 indicates that

Table 2. Composition of 50 food midden samples from Kabanyolo Colony K-B, 1970-71.

Food Organisms	% Occurrence
Orthoptera	6.4
Dermaptera	0.8
Dictyoptera	11.9
Isoptera	11.5
Hemiptera	5.5
Lepidoptera	0.4
Diptera	0.8
Hymenoptera	16.8
Coleoptera	11.0
Other Insecta	16.8
Total Insecta	81.8
Diplopoda	15.1
Crustacea	1.1
Mollusca	2.0
Total Other Organisms	18.2

insect remains predominated in these food middens, occurring in 81.8 % of the samples. Hymenoptera, Dictyoptera, Isoptera and Coleoptera, in that order, formed the bulk of the insect groups, together having a total occurrence of 51.2 %. The Hymenoptera were almost entirely made up of ants. Several species of *Camponotus* nested in the ground in the area. Individuals of *Paltothyreus* was seen to raid their nests and remains of *C. flavomarginatus* Mayr, *C. acvapimensis* Mayr, *C. chrysurus* Gerst. and, occasionally *C. maculatus* Emery, were identified in the food middens. Remains of Dorylines, swarms of which were to be seen during the wet seasons, and of *Odontomarchus* spp. also occurred.

All Dictyoptera were cockroaches (Blattidae). The common Isoptera were *Macrotermes subhyalinus, Pseudacanthotermes* spp. and *Cubitermes* spp. although there were other unidentified subterranean forms also raided. Most of the Coleoptera were ground beetles (Carabidae) while Orthoptera were represented by wings and limbs of crickets (Gryllidae) as well as both Acrididae and Tettigonidae. Micro-lepidopteran moths were common in the coffee mulch and they were found in the middens as so were caterpillars and wings of butterflies and other moths.

One of the most constant non-arthropod, and apparently favoured item of diet, was the Diplopoda (15.1 %). These appeared to be small millipedes measuring 2-6cm in lenght and belonging to the families lulidae, Blaniulidae and Strongylosomidae. The terrestrial Isopods (Crustacea) and the Molluscan snails were other but smaller items found. The snails all belonged to the common *Limicolaria martensiana.*

A few middens were also collected from Kaazi and from Namulonge Cotton Research Station, the latter some 4.8km to the north of Kabanyolo, fut these revealed no new items of diet except that termites appeared to occur more frequently in the Kaazi middens. As the samples were too few, they were not analysed further.

B.— Direct Observations

The results of food middens may be regarded as biased in favour of showing only prey with hard remains. Direct observations were, consequently, carried out to find out what sorts of soft-bodied invertebrates were captured by the ants. The only organisms of such kind noted were slugs, which were often taken and, occasionally, earth-worms. This indicated that the Mollusca were probably underestimated in the midden samples (Table 2), but it is unlikely that earth-worms formed anything but occasional prey during the rainy seasons.

C.— Litter Samples and Food Middens compared

The workers of Kabanyolo K-B colony foraged on the colony floor and in the litter of the coffee mulch adjacent. This mulch was also probably the source of invertebrates wandering into the colony area at night. The seasonal abundance of these invertebrates was assessed throughout the year, except for the driest months, when the litter was very dry and contained hardly any organisms (Table 3). In Table 4 the data from this assessment are re-arranged to show over-all abundance of the organisms in the litter in a form in which a comparison can be made with Table 5 showing their importance and regularity of occurrence in the food middens.

Table 3. Seasonal abundance of invertebrates in the litter, 1971 (1)

Groups of Organisms	I WETTEST MONTHS	II	III	IV DRIEST MONTHS
	Apr. Oct. Sept.	May July Nov.	Jan. June Aug.	Dec. Feb. Mar.
Orthoptera	O	O	x	—
Dermaptera	xx	x	x	—
Dictyoptera	xx	xx	x	—
Isoptera	O	O	O	—
Hemiptera	O	x	x	—
Lepidoptera	xx	x	x	—
Diptera	xx	O	x	—
Hymenoptera	xx	xx	xx	—
Coleoptera	xx	O	x	—
Other Insecta	xxx	O	x	—
Diplopoda	xx	xx	x	—
Chilopoda	O	x	x	—
Crustacea	xx	x	x	—
Arachnida	xx	x	xx	—
Annelida	xx	x	xx	—
Mollusca	xx	O	xx	—

Table 4. Organisms in the litter grouped in decreasing order of abundance.

Group No.	Organisms
1	Hymenoptera
2	(Dictyoptera (Diplopoda (Arachnida (Mollusca
3	(Dermaptera (Lepidoptera (Unidentified Insecta (Crustacea
4	(Diptera (Coleoptera (Hemiptera (Chilopoda Orthoptera

N.B. The bracketed groups were of equal abundance

Table 5. Importance and regularity of organisms in food middens.

Major and regular organisms (In 10 % of samples)	Minor and regular organisms (In 10 % of samples)	Irregularly found organisms
Hymenoptera	Orthoptera	Crustacea
Diplopoda	Hemiptera	Dermaptera
Dictyoptera	Mollusca	Diptera
Isoptera		Lepidoptera
Coleoptera		Annelida
Unidentified Insecta		

(1) Key : xxx = Very many, xx = Many, x = Few, O = Absent, — = No Sample

First, in both Tables 4 and 5 three of the most important food organisms : Hymenoptera, Diplopoda and Dictyoptera, rank very high. Secondly, predominantly nocturnal arthropods (Coleoptera, Hemiptera and Orthoptera), or those which are hypogaeic (Isoptera), are either entirely absent from, or lower down in the litter sampe list (Table 4) because these samples were taken during the day, whilst the ants are largely nocturnal foragers. Thirdly, Arachnida and Chilopoda, not found in the middens, were probably too active or venomous for the ants to feed on. Fourthly, apart from what has already ben said about slugs, the greater prominence of the Mollusca in the litter samples was dus to the abundance of the snail *Limicolaria martensiana* of which only the smaller ones could be transported by the ants.

It is fair to conclude, therefore, that the results of the food midden analysis, as modified by direct observation (Table 5), trully reflected the diet of *Paltothyreus* in this environment.

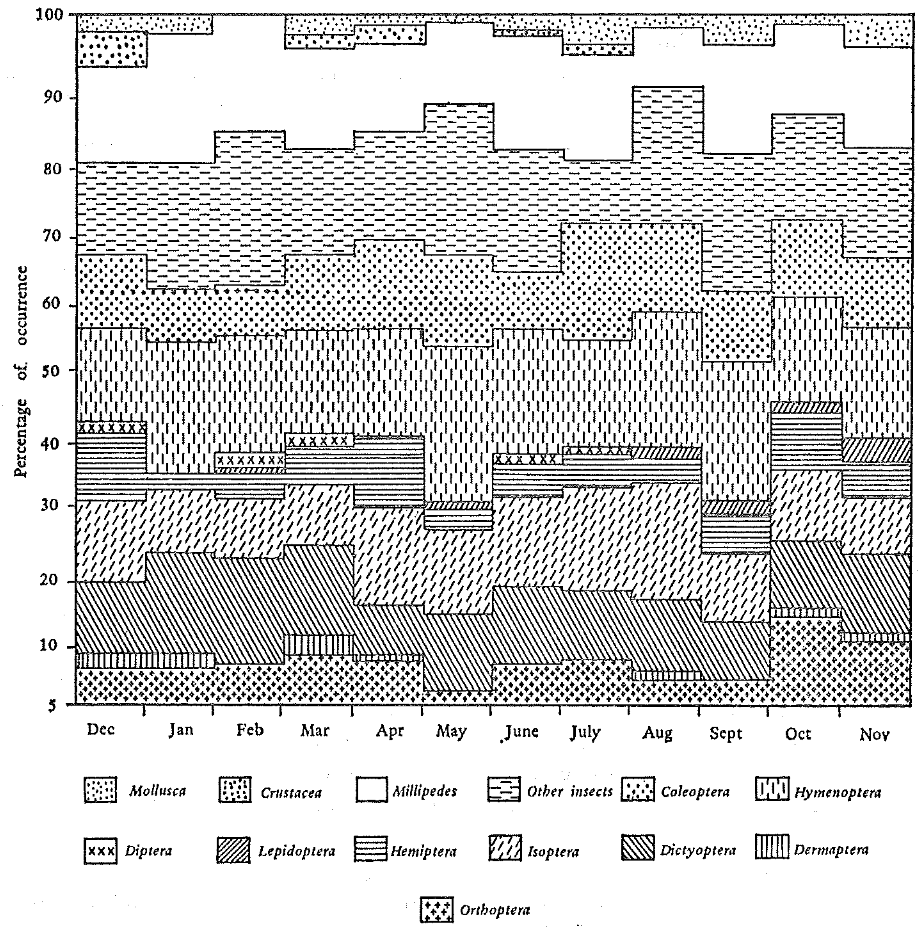

Fig. 6. Composition of monthly food midden samples from Kabanyolo.

D.— Seasonality of the *Paltothyreus* diet

The monthly food midden samples from Kabanyolo, plotted in Fig. 6, revealed a surprising lack significant seasonal differences in the major, regular prey taken by *Paltothyreus.* Groups like Isoptera and Hymenoptera whose active aundance in the fied is so obviously related to the rains might have been expected to be more numerous in the food middens of the wet seasons.

4. Soil Excavation and Movement

The nests of *Paltothyreus* have been previously described by LEVIEUX (1965). At Kabanyolo and Kaazi the nests were constructed in warm, exposed, short grass areas or on the periphery of plantation crops (like coffee and bananas), forest or thicket into wich, however, the ants made short distance foraging trips. They did not nest deep in the forest and were not usually found in area of thick elephant grass. The nests consist of extensive, interconnecting underground tunnels and chambers at different levels within the upper 1-1.5m of the soil profile. The subterranean excavations are connected to the outside by a number of nest holes, 1-1.5 cm in diameter, around which are piled loose earth pellets and small stones removed from the excavations and, in a few cases, the food middens, dead bodies and pupal cases. The debris form small craters the shape and size of which depend very much on the topography and nature of the soil. During the dry season and, in dry climates apparently, these craters are dissipated or not built and the nest holes are not easy to detect. Quite often the ants nest in termite mounds and then, too, no soil craters are made.

The excavating activity is a striking feature when and where it occurs and during 1970-71 at Kabanyolo investigations were made into the nesting activities and soil movement by *Paltothyreus.* Three plots, each 81.7m2 in area, were demarcated from the middle, northern and southern ends of the 700m2 area covered by the colony K-B. The three plots had initially 16,24 and 24 nest holes respectively. From these and those that were subsequently opened the amount of soil excavated was collected, dried and weighed as already described above. The combined results are presented in Fig. 7.

The graph shows that the number of nest holes in use was not related to the amount of soil excavated, but was negatively correlated with the rainfall, so that during the very wet months many of the holes were closed, presumably to reduce flooding of the nest tunnels and chambers. In fact, over 60 % of the holes were closed about two months after the rainfall began to exceed a weekly average of 20mm. Consequently, there was very little soil excavated during this period. Similarly, during the dry months, although many hols were re-opened, there was little excavation. The maximum excavation activity occurred during the moderately wet months of May to August. At the height of this period the amount of earth moved by the ants was 60g/m2/month compared with 17g/m2/month in January, 1971 and about 2.5g/m2/month in November, 1971, all figures being

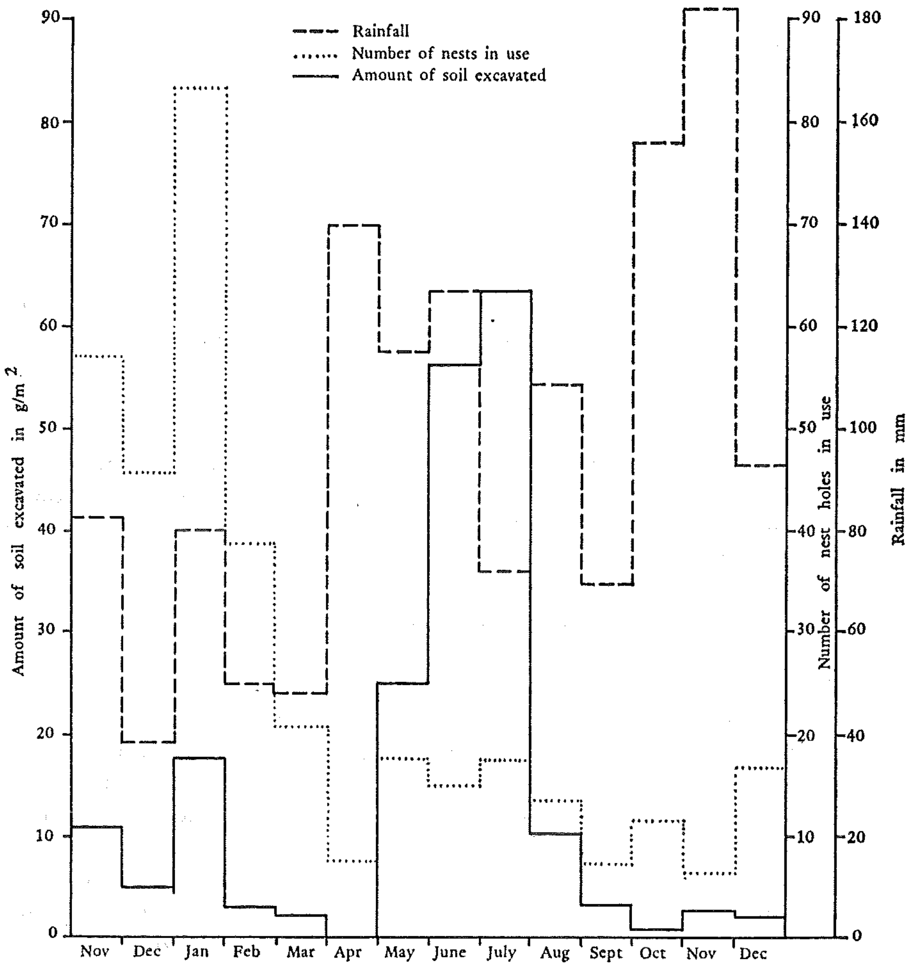

Fig. 7. Relationship of excavating activity to rainfall.

dry weights. Little soil was moved therefore during both very dry and very wet seasons.

The possible interaction of various climatic factors in controlling soil excavation activity was tested for by a multiple regression using values for number of factors and the average amount of soil excavated in the three plots. The factors that were obviously less important were eliminated leaving only four that showed apparent effects on the activity in the first set of analyses. These factors were : ground at 09.30 hr, relative humidity, rainfall and air temperature, in that order of importance. After three sets of selection, each time eliminating the least important factor, the two that remained as the most important were ground temperature at 09.30 hr (t-values —2.854, $p < 0.01$) and relative humidity (t-value = — 2.352,

$p<0.05$). Ground temperature and relative humidity have already been shown to be significant factors in the foraging activity of the ants.

DISCUSSION

This study has sought to clarify a number of points about the behaviour and ecology of *Paltothyreus tarsatus* under a bimodal rainfall regime such as is found over the greater part of Uganda. It has shown that the major environmental factors controlling the activity of *Paltothyreus* were temperature and humidity. Both its daily foraging and its seasonal soil excavation activities were signiticantly affected by the level of ground temperature and relative humidity. The ant was usually most active at temperatures between 20° and 25°C when relative humidity was high (over 90 %). Results for the foraging activity under apparently optimal conditions did, however, indicate activity peaks, which were probably inherent in the ant, which need to be further investigated. This work confirmed the observations of GLOVER (1967) that *Paltothyreus* hunt individually and do not practise group raids as has been indicated by WILSON (1971). It is not, therefore, an army ant. Foraging is done by random search of the area and the prey is located purely by chance. Some workers were seen to traverse considerable distances and spend a lot of time but return without prey while others quickly found prey within a short distance of the same nest hole. The possession of large compound eyes suggests that these ants depend mainly on their sense of sight and SUDD (1967, p. 95) has reported that '*Paltothyreus tarsatus* is attracted from a distance of several inches to strike at the moving feet of giant millepedes ! It is doubtful, however, that sight alone is used in hunting particularly as, under the usual conditions of humidity, the ants forage more under crepuscular or nocturnal than under diurnal conditions. Also, like another nocturnal forager, *Camponotus maculatus aegyptiacus* Emery, studied by KASCHEF & SHEATA (1969), moonlight had no effect on foraging activity. These facts and field observations of foraging individuals suggest that *Paltothyreus* depends on more than one sense when hunting its prey.

Under Ugandan conditions, also, *Paltothyreus* is apparently one general carnivore. At Kabanyolo, the main single prey groups (Table 2) were active arthropods (Hymenoptera, Diplopoda and Dictyoptera) while termites (Isoptera), comprising 11.5 % of the diet, were fourth in importance and soft-bodied invertebrates were insignificant. The ant was never seen to take any plant food as reported by SUDD (1962) in West Africa. On the other hand, while it no doubt carried out some scavenging, it was not possible to estimate the extent of this. The results reported here, from both the food midden analysis and direct observations, dispose of the idea, formed from insufficient observations, that *Paltothyreus* feeds mainly or exclusively on termites. This is probably true only where, as in the arid areas of Somalia examined by GLOVER (1967), termites form the only abundant prey invertebrates. It is interesting that under the same conditions, GLOVER reported *Paltothyreus* being attracted to a bait of condensed milk.

An unexpected finding here was that the ant did not show any seasonal shifts in its diet to correspond to the changes in abundance of the various prey arthropod groups. The fact that this did not happen was probably because of the absence of a severe drought in this area. Alternatively, it might indicate a certain degree of discrimination in the selection of prey organisms by these ants.

Unlike those of termites, the soil-forming activities of ants have hardly been studied. It is, consequently, difficult to make useful comparisons with the results obtained in this investigation. MORLEY (1953, p. 115) quoted unsupported figures for Brazil which indicated that there ants, probably of all species, excavated about 3.23 kg/m2/yr. Assuming 20 % water content this would be equivalent to about 2.58 kg/m2/yr against which may be compared the 203 g/m2/yr excavated by *Paltothyreus* at Kabanyolo. More significant, however, is the comparison in Table 6 of the amount of soil excavated by two species of mound-building termites

Table 6. Amounts of soil excavated by *P. tarsatus* compared with two mound-building termites in 1974.

Species	Locality	Amount of soil (g/m2/yr)
P. tarsatus	Kabanyolo	203
Termites :		
Macrotermes bellicosus :	Natete	230
	Naluvule	78
Pseudacanthotermes sp. :	Natete	24
	Naluvule	200

found in the same general area (D.E. POMEROY, unpub.) Unfortunately, events in Uganda did not permit further work on the mechanical and chemical properties of the soil excavated.

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