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Colony structure, seasonality and food requirements of the crazy ant, *Anoplolepis longipes* (Jerd.), in the Seychelles

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ABSTRACT. 1. In Seychelles, *A.longipes* nests on the ground and in trees, underground nests do not occur, possibly because soils are too hard or unstable.

2. Nest density approached 700 ha^{-1} in some areas and nests contained, on average, about 4000 ants. The total population (including foragers) in heavily infested areas may exceed 10 millions ha^{-1}.

3. On average, each nest contained about forty queens and fifty males, although only 50% of nests contained males. A few nests contained up to 300 queens, 1000 males, 36 000 workers and 23 000 brood.

4. Production of sexual adults and brood was related to the wet season, most being produced shortly before or after the heavy rains from November to March.

5. Natural spread is probably by budding of colonies which, during an expansive period, may advance 1 m day^{-1}.

6. Food collected by the colony included sugary substances from fruits, honeydew-producing insects and plant exudates, and proteinaceous material, mainly in the form of insect prey and carcases. A forager collected, on average, 1.2 mg of liquid or 2.8 mg of solid material on each foraging trip.

7. Foraging occurred at fluctuating intensities throughout the day and night, but was limited by heavy rain, strong winds and substrate temperatures above 30°C. Maximum activity occurred at ground temperatures of 25–30°C and ceased about 44°C.

8. Availability of food and nest sites proably have the greatest influence on population size.

Introduction

Anoplolepis longipes (Jerd.) has spread by commerce throughout the tropics. It is regarded as a pest in the Seychelles, where it is known as the crazy ant, but elsewhere it may occur as a pest or a beneficial species, depending on circumstances (Haines & Haines, 1978).

The history of the crazy ant infestation in the Seychelles up to 1973 and preliminary attempts to devise control methods based on toxic baits and sprays were described by Lewis *et al.* (1976). Subsequent attempts to improve control required more basic information on the biology, ecology and behaviour of the ant in this habitat. This paper describes the nesting habit, seasonal trends in population, and food requirements of *A.longipes* on the island of Mahé.

Observations

Nest sites

In Seychelles, *A.longipes* nests on the ground and in trees. Perhaps the most common arboreal site is in the crowns of coconut palms

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TABLE 1. Nest cover, occupancy and mean distance between 100 potential nest sites of three study areas

Study area	Suitable cover available for nests (% occurrence)			Size of cover (m^2) ($\bar{x} \pm$ SE)	% occupancy by *A.longipes*	Distance between sites (m) ($\bar{x} \pm$ SE)	Estimated nest density ha^{-1} (using 95% limits)
	Rocks	Fallen vegtn.	Other				
Union Vale	94	5	1	0.24 ± 0.06	41	3.72 ± 0.40	123–291
Les Mamelles	78	22	0	0.14 ± 0.02	72	2.37 ± 0.22	317–671
Maldive	87	8	5	0.14 ± 0.02	97	3.78 ± 0.73	92–457

but nests also occur in raffia (*Raphia ruffia* Beauv.). Probably other tree species provide suitable shelter and are used for nesting (we have observed, for example, queens and workers with brood ascending the pillar-roots of *Ficus benghalensis* L., and the trunks of *Premna obtusifolia* L. and other trees).

On the ground, *A.longipes* nests in or under almost any material which provides shelter. Rocks and fallen vegetation provide the most common nest sites, the latter being generally less permanent. A survey of the suitable cover available for nests in three areas on Mahé showed that rocks provided more than 78% of the potential sites present at ground level (Table 1). Up to 22% of cover was provided by fallen vegetation (especially palm fronds, rotting palm trunks, coconut husks and leaf litter) and the rest by miscellaneous debris. Nests built in litter were often stratified, with egg masses, larvae and pupae in different layers; other nests were usually unstratified.

Underground nest chambers were not observed in the field (cf. Way, 1953; Baker, 1976) but, when the soil was moist under certain nest covers, shallow pits (up to 15 mm deep and 25 mm wide) sometimes occurred. *A.longipes* did, however, construct underground chambers in artificial nests based on Freeland's (1958) design.

In three field study areas, the size of nest cover (based on 95% limits) was generally between 0.1 and 0.35 m^2. Based on nearest neighbour measurements, average distances between covers (including those vacant but potentially habitable) varied from around 1.9 to 5.2 m, equivalent to an estimated density of 92–671 nests ha^{-1} if all nests covers were occupied (Table 1). There was some indication that the spatial disposition of nest covers was aggregated (Fig. 1), so estimates of nest density based on nearest neighbour may not be reliable (Southwood, 1966). Vacant covers were included in the estimate because occupancy of covers was often transient, some remaining occupied for months and others for only about a week. Mean distances between covers (Table 1) should therefore be regarded as minimum mean distances between nests.

The rate of evacuation of covers was estimated by recording the disappearance of ants from marked covers in two study areas, Les Mamelles and Maldive. Observations were made at monthly intervals and, although the

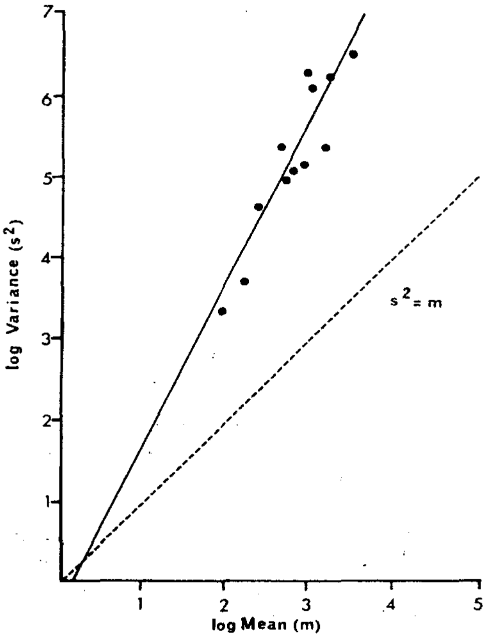

FIG. 1. Spatial disposition of nest sites of *A.longipes*. Variance (s^2) X mean (m) plots for density of sites in twelve regions. (Variance accounted for by regression = 84.6%; log s^2 = –0.3 + 2.04 log m.)

lifting of covers may have disturbed ants, any disturbance was minimal and thought unlikely to lead to vacation of nest sites. The average occupancy (expressed as time taken for 50% of nest covers to be vacated) was around 70 days at Les Mamelles and 110 days at Maldive, the rate of vacation of covers being 0.7% and 0.45% day^{-1} respectively, indicating a shifting population. Nests under small covers were generally less persistent than those under larger ones.

Colonies were ill-defined: individuals from different nests showed no aggression towards each other, nor was there aggression (after an initial period of excitement) when whole nest contents from different areas were brought together.

Contents of nests

From October 1974 to July 1976, seventy-five nests were collected from the field and the contents sorted into stages. An aerosol knockdown insecticide was used to immobilize ants before nest contents (with some soil and debris) were brushed or scooped on to trays. Large samples were estimated by sub-sampling.

Nine stages: alate queens, dealate queens, alate males, workers, queen pupae, queen larvae, other pupae, other larvae and 'egg' masses (which included some early instar larvae) were separated and counted.

Mean content and percentage occupancy of nests for each stage were determined (Table 2), and the weight of each stage estimated. Weighings made on torsion balances were of fresh and preserved (in 70% industrial spirit) specimens from various sources.

A range of one to 320 queens per nest was observed, but most nests contained between twenty-seven and fifty-six (based on 95% limits) queens. The number of workers varied generally between 2553 and 5206, but the maximum number observed in a single nest was 36 000. On average forty-nine males per nest were found but they were present in only about 50% of nests. The greatest number recorded in a single nest was 1296. Each egg mass contained, on average, 24.5 SE ± 3.5 eggs and 4.9 ± 0.8 early-instar larvae, and the highest numbers recorded were 121 eggs and twenty-four larvae.

Workers made up more than 80% of the individuals in nests, and 75% of the total mean biomass of nearly 10 g. Based on the maximum number of workers and queens found in nests, total nest biomass may approach 90 g in some instances.

There was little relationship between the size of nest cover and the number of ants in nests. The linear regression of worker number on cover size accounted for 16.2% of the variance and that of queen number on cover size for only 6.9% of the variance. This result was unexpected because nest observations made in the field gave an impression that there was a closer relationship.

TABLE 2. Mean content and percentage occupancy of seventy-five nests collected in the field between October 1974 and July 1976 (average nest cover size 0.29 m^2 comprising 75% rocks, 16% fallen vegetation and 9% other debris), with an estimate of unit weight of stages and biomass

Stage	Number in nest $\bar{x}$ ± SE	% of total number	% occupancy	Unit wt (mg) of stages $\bar{x}$ ± SE	Mean biomass (g)	% of total biomass
Alate queens	2.05 ± 1.04	0.05	36	23.70 ± 0.97	0.049	0.51
Dealate queens	39.47 ± 6.47	0.87	100	21.24 ± 0.29	0.837	8.67
Males	49.23 ± 24.16	1.09	52	1.07 ± 0.08	0.053	0.55
Workers	3789 ± 645	83.78	100	2.55 ± 0.13 (fed) 1.32 ± 0.07 (unfed)	7.332	75.92
Queen pupae	10.93 ± 7.25	0.24	27	28.07 ± 1.37	0.307	3.18
Queen larvae	12.56 ± 8.84	0.28	35	17.74 ± 0.64	0.223	2.31
Other pupae	556 ± 311	12.29	92	1.46 ± 0.04	0.812	8.41
Other larvae	33.0 ± 12.52	0.73	55	0.19 ± 0.01	0.006	0.66
'Egg' masses	30.52 ± 14.16	0.67	16	1.29 ± 0.17	0.039	0.40
Total	4522.76				9.658	

Population assessment

Assuming a nest density of 92–671 ha^{-1} when all the available cover is occupied (as at Maldive, see Table 1) and taking 3880 as the mean number of ants per nest (Table 2), the density of the ant population (excluding foragers and brood) would be 0.4–2.6 millions ha^{-1}. This range is extended to 0.2–3.5 millions ha^{-1} using 95% limits about the means. Numbers of foragers were estimated in different ways and at various times, except around noon when foraging was reduced. Estimates based on quadrats were perhaps the most reliable, though this method was restricted to areas where the ground was reasonably flat. With quadrats (of area 0.25 m^2, with tall sides to retain ants – a knockdown insecticide sometimes being used to facilitate counting), mean counts of 97.9 ± 26.3 (95% limits) ants m^{-2} at Les Mamelles were recorded, equivalent to about 0.25–1.25 million foragers ha^{-1}.

Independent assessments, based on subjective scores of abundance (abundant 5, common 4, frequent 3, occasional 2, rare 1, or none 0) were made over larger areas. Comparisons between quadrat counts and the above scores gave numerical equivalents of roughly 500, 250, 125, 50, 5 and 0 ants m^{-2} respectively. Average scores of around 3.2 at Maldive and Les Mamelles and 1.5 at Union Vale indicated foraging populations of about 1.5 million ants ha^{-1} at the first two sites and 0.25 million ha^{-1} at Union Vale.

Populations were also assessed using filter paper discs soaked in 2 M sucrose solution to attract ants. Mean counts of forty-nine ants per set of five discs were obtained at Maldive, thirty-seven at Les Mamelles and twenty-two at Union Vale. In terms of ants ha^{-1} these are roughly equivalent to 1.3 million, 0.9 million and 0.5 million ha^{-1} respectively, the equation $y = 4 + 0.36x$ being determined graphically by fitting a regression line to plots of counts against numbers m^{-2} obtained from quadrats.

Based on overall estimates of maximum numbers of foragers, and of ants in nests (upper 95% limits), the total ant population (excluding brood) may reach 5 millions ha^{-1} in areas of high nest density, and in areas of maximum abundance up to 10 millions ha^{-1}. These are probably underestimates because no account was taken of ants foraging or nesting in vegetation when assessments were made. Comparable estimates for other monospecific populations vary, but densities of around 1 million ha^{-1} are recorded for *Formica subnitens* Creighton, 5 millions ha^{-1} for *Dorylus wilverthi* Em. and *Lasius niger* L., 6 millions ha^{-1} for *Oecophylla longinoda* Latr., 7 millions ha^{-1} for *F.rufa* L., and up to 150 millions ha^{-1} for *L.flavus* Fab. (in Brian, 1965). Clearly, nuisance caused by *A.longipes* is not solely related to density; its exploratory behaviour is also an important factor.

Seasonality

Observations on the seasonality of *A. longipes* were made at Maldive, Les Mamelles and Union Vale from April 1975 until August 1976. At monthly intervals (or weekly at Union Vale), 100 nest covers at Maldive, eighty at Les Mamelles and thirty at Union Vale were carefully lifted and nest contents assessed. Queens and queen brood were usually counted directly, but this procedure was not possible for other stages because of their small size and, often, their great abundance. For these, and for queens and queen brood when counts were difficult, a scoring system was used. Numerical values were given to the scores based on their approximate relationship to real counts made on a sample of fifty nests collected from the field (Table

TABLE 3. Subjective scores and their approximate numerical value for each stage

	Approximate numerical value					
Subjective score	Queens	Queen larvae and pupae	Males	Workers	Other larvae and pupae	Egg masses
Few	10	10	10	1000	50	50
Some	20	20	25	2000	200	200
Many	50	50	100	3000	1250	1250

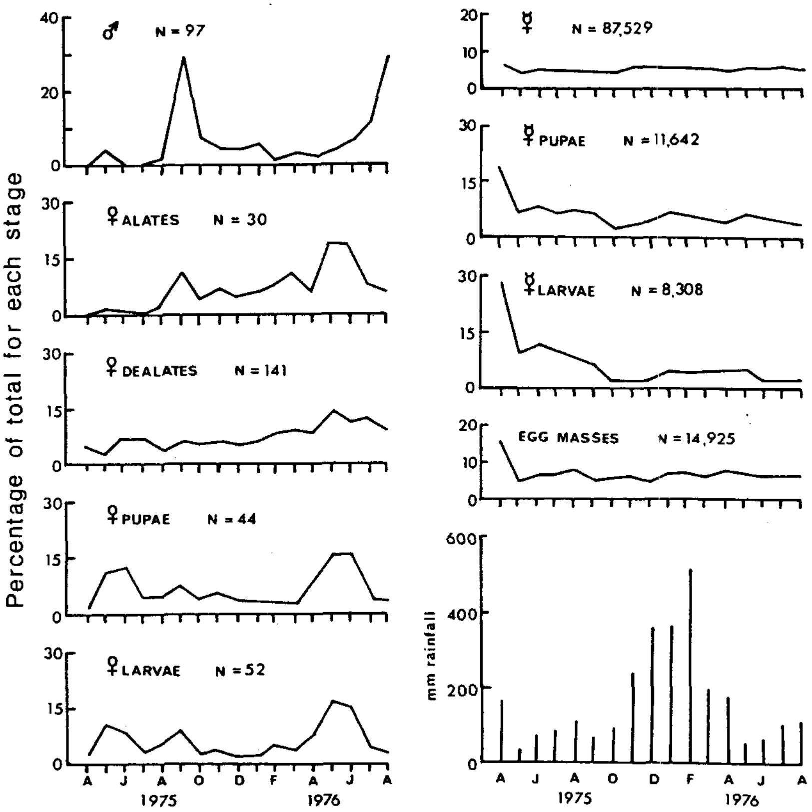

FIG. 2. Seasonality of *A.longipes* (expressed monthly as mean percentage of totals (N) from two sites). Average monthly rainfall was estimated from rainfall contour maps provided by the Meteorological Office in Seychelles.

3). Nests observed in the field on each occasion were not necessarily the same as those observed on other occasions, but the number observed at each site was constant. Seasonal trends were similar at each site and best illustrated by combining observations from Maldive and Les Mamelles (Fig. 2).

In all sites, most of the sexual adults and brood were produced shortly before or shortly after the rainy season, with smallest numbers generally observed in the middle of the wet season. Sexuals occurred throughout the year, but males, alate queens, queen larvae and pupae were not seen at some sites during certain months of the dry season.

Most males were produced shortly before the rainy season. The rapid decline in their numbers at Maldive and Les Mamelles between September and October in 1975 may indicate dispersal from nests and subsequent death at this time. A second and more prolonged period of production and dispersal, from December to March, was indicated at Union Vale but the reason for this not occurring at other sites is uncertain. Perhaps it was associated with the steady decline of *A. longipes* at Union Vale at this time.

During observations in 1975, decreases following peak production of alate queens occurred from September to October at Les Mamelles and Union Vale, but at Maldive the peak was ill-defined. In 1976, decreases after peak numbers occurred in different months at the three sites: between April–May at Union Vale, May–June at Les Mamelles and June–July at Maldive. These decreases may indicate dispersal of alate queens and, if so, it seems likely that there are one or, more generally, two periods of dispersal (before and after the wet season) each year, although production of alates is continuous. In nests, no seasonality of workers was observed at any of the sites (cf. Baker, 1976), but this result may have been partly due to the subjective scoring. Worker larvae and pupae, and egg masses were produced throughout the year, but there was no clear seasonality.

Dispersal

Both alate stages of *A.longipes* are able to fly (cf. Lewis *et al.*, 1976). In 2 years of light trapping at Union Vale, using a Rothamsted trap, 131 males were caught (most between August and November in 1974) and eleven queens. The only time males and queens occurred together in the trap was on 6 July 1976, when two males and four queens were found. Mating flights were not observed. A swarm of queens (which we were unable to confirm) was reported to us in September 1976. Possibly, mating flights do occur (cf. Dammerman, 1929) but the most common method of natural spread in Seychelles is probably by colony budding. During field observations between March 1974 and April 1975, sixty queens were seen walking in the open: forty-four were alates accompanied by several workers, three were unaccompanied alates, eleven were accompanied dealates and two were unaccompanied dealates.

Rate of spread

Attempts were made to determine the rate of natural spread of *A.longipes* by marking boundaries of populations and by mapping. The procedures were not highly successful because of difficulties in defining boundaries and because boundaries tended to advance and retreat unpredictably. Nevertheless, some measurements of boundary movement were obtained and rates of spread indicated.

At Glacis (in the northern region of Mahé), where there were reports of the ants advancing rapidly, boundaries advanced 75 m in 68 days, giving an overall rate of movement of 1.1 m day^{-1}. Other measurements in different parts of Glacis indicated boundary movement at a rate of 0.1–0.3 m day^{-1}. At Union Vale, when *A.longipes* populations were declining, the rate of retreat was, on average, 0.4 m day^{-1} over a period of 10 months.

Assuming that *A.longipes* was introduced to Mahé around 1962 and that, from the village of Maldive (its first place of discovery on Mahé), it spread to the east and west coasts of the northern peninsula (distances of approx. 1.25 km) in about 10 years (see Lewis *et al.*, 1976), colonies advanced at an overall average rate of 0.34 m day^{-1}. This rate is within the range of those determined by marking boundaries.

Food requirements

Field and laboratory observations show that *A.longipes* foragers collect liquid sugary substances and solid proteinaceous material throughout the year. Seasonal changes in the proportion of liquid : solid food collected were not detected, but detailed studies were not made.

Sugary foods were obtained from the juices of fruits, from honeydew-producing insects and from plant exudates. The weight of fed and unfed workers (Table 2, incoming and outgoing foragers for liquid food) indicate that a forager collects 1.23 SE±0.13 mg of liquid food on each occasion.

The bodies of dead or dying invertebrates, especially of insects, provided most of the solid material collected (Fig. 3, i). In culture, living victims (cockroaches, centipedes and others) were also attacked and either dragged or carried beneath nest covers, or dismembered (over several days) *in situ*. Ants of other species, and corpses of their own species, provided much of the insect material collected by foragers (Fig. 3, ii). *Camponotus maculatus* Forel gp., *C.grandidieri* Forel, *Odontomachus troglodytes* Sant., *Technomyrmex albipes* (Smith), *Paratrechina vividula* (Nyl.) and *Plagiolepis madecassae* Forel were amongst those species collected, but is is not known whether *A.longipes* had attacked live individuals or found them as corpses; some bodies were obviously dry when collected, but others were in a reasonably fresh state. In laboratory observations of ants in crystallizing basins, ten workers of *A.longipes* attacked and sometimes overcame a single soldier of *C. maculatus* gp., but then the proportion of crazy ants was reduced to 5:1, the attacks were less persistent and the ants failed to overcome the solitary ant of the other species.

The mean unit weight of insect material

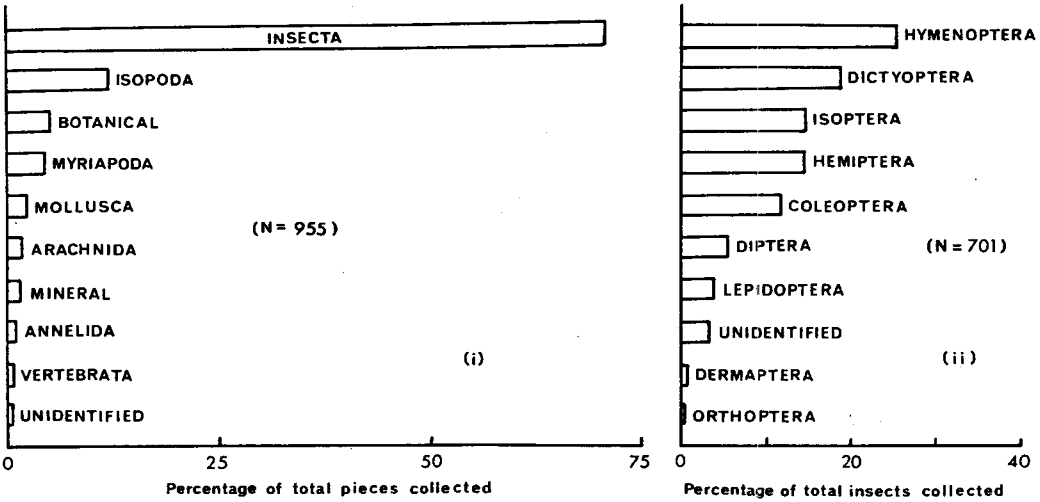

FIG. 3. Percentage composition of (i) solid material and (ii) insect material collected by foraging workers of *A.longipes*.

(prey or carrion) collected by foragers of *A.longipes* in the field was 23.5 SE ± 9.4 mg. Solitary foragers carried, on average, a load of 2.84 SE ± 0.24 mg but often loads were carried by more than one individual. In these instances the load per individual sometimes increased markedly (for example, a cockroach weighing 1.1 g was carried by thirty-one foragers, equivalent to a load of 36 mg per forager). The relationship between weight of a load and the number of ants carrying it was determined by regression, using the mean weight of the load carried by each given number of individuals (Fig. 4).

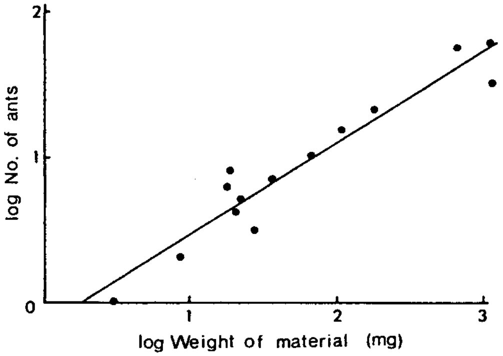

FIG. 4. Relationship between weight of material collected by foragers and the number of ants required to carry it. (Variance accounted for by regression = 91.6%; log no. ants = –0.16 + 0.629 log weight of material.)

Foraging activity

In cultures, foraging activity was monitored over a 2 week period using an electronic ant counter (Dibley & Lewis, 1972). Foraging ants reached feeding sites, via the gantry of the ant counter, along strings leading from the nest. Continuous monitoring over the whole period was not achieved because of failure in the counting device and loss of counting efficiency when ants remained in the light path, between light source and photoelectric cells. Foraging activity was well illustrated over the longest uninterrupted period (42 h), during which ants foraged throughout the day and night (Fig. 5), though not with the same intensity. Generally, foragers were most active in late afternoon and evening and there was some indication that activity was proportional to temperature (within the range observed) and decreased with increasing relative humidity (cf. Greenslade, 1972).

In the field, the ant counter was of less use because foragers did not follow a trail. Foraging activity was assessed by counting ants at sugared discs of filter paper and setting pitfall traps. Foraging occurred throughout the day and night, except during heavy rain and strong winds. No clear pattern of activity was observed, but foraging decreased often around mid-day in exposed areas. Some evidence suggests that cessation of foraging is related to substrate temperature, as the

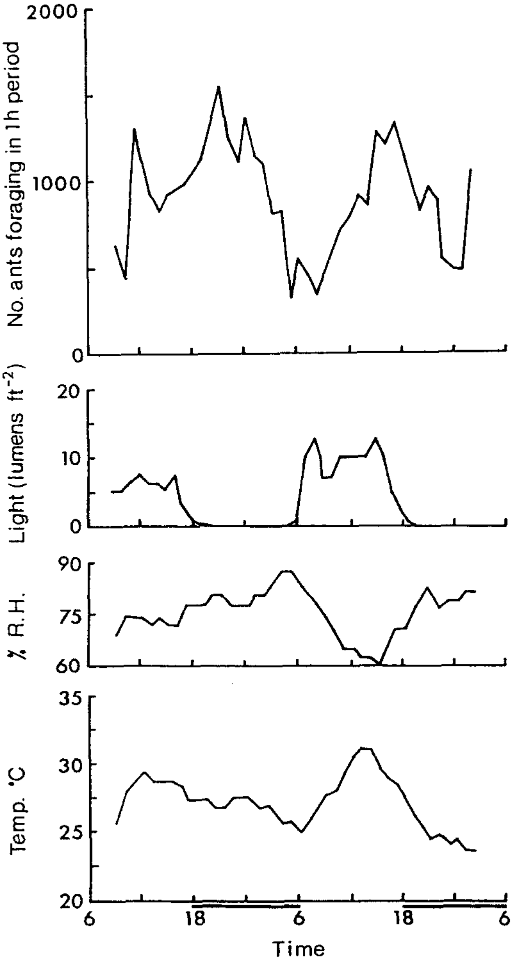

FIG. 5. Foraging activity of *A.longipes* in culture, with observations on light, temperature and relative humidity. (1 lumen ft^{-2} = 10.764 lux.) Time based on 24 h clock.

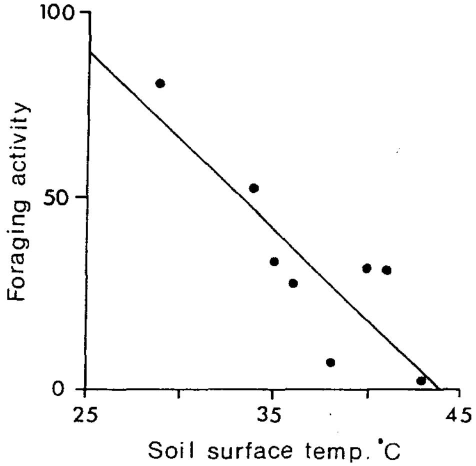

FIG. 6. Effect of high soil surface temperature on foraging activity. Activity was assessed as the mean number of ants in pitfalls in a 1 h period; mean temperatures for each period were used. (Variance accounted for by regression = 71.1%; $y = 208 - 4.7x$.)

regression of foraging activity (expressed as the number of ants in pitfalls h^{-1}) on mean soil surface temperature (measured using thermistors) accounted for 71% of the variance (Fig. 6), whereas only 28% of the variance was accounted for when air temperature was used. The regression, though based on a small sample, indicates that foraging ceases when ground temperatures reach 44°C. Pitfall catches and counts of ants at sugar bait indicate that maximum foraging activity occurred when surface temperatures were between 26 and 30°C (with the mode around 29°C) and was least at temperatures above 40°C (Table 4). Clearly, foraging activity increases with temperature only up to about 30°C; above this temperature activity decreases. This may explain why foraging is often at a minimum around noon, when ground temperatures are highest.

Discussion

From the literature it appears that *A.longipes* is predominantly ground-nesting (Greenslade, 1971a, 1972; Baker, 1976. Dammerman,

TABLE 4. The relationship between soil surface temperature and foraging activity (assessed using pitfalls and sugar baits)

	Soil surface temperature range (°C)				
	21–25	26–30	31–35	36–40	41–45
Per cent of total foraging activity	15.5	38	23	16.5	7

1929), but, as in Seychelles, arboreal nests may be common (Way, 1953).

Way (1953) in Zanzibar and Baker (1976) in Papua New Guinea observed large underground nest chambers, but these were not seen in Seychelles nor by Greenslade (1972) in the Solomon Islands. It may be that in Seychelles the granitic soils are too hard and the calcareous soils too unstable to allow extensive burrowing (Way's nests were in light, well-drained soils, heavier soils being avoided by the ant). Alternatively, suitable nesting sites under rocks, fallen vegetation and other debris may be so abundant on Mahé that underground nest-building is unnecessary. Fluker & Beardsley (1970) reported that the distribution of *A.longipes* in Hawaii was severely limited because of its habit of nesting under rocks or rock-lined irrigation ditches.

Temperature may also influence distribution locally. In Hawaii, *A.longipes* does not occur above 600 m, the restriction being attributed to the relatively low temperature above this altitude (Fluker & Beardsley, 1970); nor does it occur in Java above 100 m (Van der Goot, 1916). On Mahé, *A.longipes* has reached 450 m but, in view of its vertical distribution at other latitudes, it could probably survive at the highest altitude (900 m) found in Seychelles. Way (1953) indicated that *A.longipes* was inhibited by the relatively low temperature of soils shaded from sunlight by dense vegetation but in Seychelles it is abundant in dense cinnamon bush, where the ground layer is frequently in shade.

The distribution and persistence of *A. longipes* in Seychelles is possibly related to vegetation type. At Maldive, where trees were varied (coconut, breadfruit, mango, jackfruit and many others) and the undercover was mainly cinnamon bush with some citrus, a dense ant population has persisted for some years. At Union Vale, where the vegetation was more open (coconuts and cinnamon interspersed with grassland) the ants were less numerous and populations less persistent (paper in preparation). The vegetation in the Les Mamelles area was intermediate between that at Maldive and Union Vale and, in general, so was the density of *A.longipes*. It is thought that, at least in the Seychelles, vegetation type influences ant populations mainly through food supply by providing sugary substances which *A.longipes* feeds on directly, or by supporting populations of honeydew-producing insects. Observations in Seychelles did not confirm those of Way (1953) and Greenslade (1972) that *A.longipes* is restricted to the more open habitats.

In Seychelles, nest sites were generally aggregated but there was no obvious biological explanation for this. The majority of sites were provided by rocks and perhaps aggregation is related to fragmentation of rocks from larger granite boulders. In Zanzibar, underground nests of *A.longipes* were closely associated with the roots of palms and were also found grouped around isolated mango trees (Way, 1953).

Little information was obtained on duration of development of *A.longipes*, but observations of ants in culture indicate that eggs took about 20 days to develop and queen pupae about 30 days. These observations agree with those of Van der Goot (1916) who found that, in Java, eggs took 18–20 days, queen pupae 30–34 days, worker larvae 16–20 days and worker pupae about 20 days to develop. Fluker & Beardsley (1970) found that at 20–22°C *A.longipes* took 76–84 days to reach maturity. Worker longevity is about 6 months, and that of the queen probably several years, the queen laying about 700 eggs annually (Dammerman, 1929).

In Java, winged sexuals appeared only after prolonged drought (Van der Goot, 1916). This was not so in Seychelles, where alates occurred throughout the year, as in the Solomon Islands (Greenslade, 1971b), although peak production of males was generally at the end of the dry season.

The weights of stages of *A.longipes* were in accordance with those of Baker (1976). In May 1975, hundreds of alate and dealate queens of *A.longipes* were found (with several workers and worker pupae) amongst a pile of timber. Many of the queens were in a physogastric state, their mean weight being 42.58 SE ± 1.02 mg (cf. mean weight of queens from field nests, Table 2).

According to Greenslade (1971a) maximum foraging activity of *A.longipes* occurs at dusk, foraging being limited in the day by low humidities and at night by low temperature. In contrast, our observations of ants in culture indicated that foraging tended to increase as humidity decreased, but this was within limits less extreme than those found in the field. Under field conditions, activity decreased as ground temperatures exceeded 30°C and, presumably, ambient relative humidity decreased. Ground temperature (at least at higher temperatures) showed the closest relationship to foraging activity and we suggest that substrate temperature may be an important factor influencing foraging.

As Greenslade (1971b) has indicated, availability of food probably has a major effect on populations of *A.longipes*. In Seychelles, adults and brood are produced throughout the year, so one would expect there to be a constant demand for carbohydrate and protein. Consequently, seasonality in food requirements may be slight, though a change towards a greater proportion of proteinaceous material in the diet at times of maximum brood production would be expected. This aspect was not investigated in detail, but foraging activity of ants on the ground often increased after rainfall – a time when prey becomes more available to foragers (Greenslade, 1971b) – and maximum brood production was generally at the beginning or towards the end of the wet season. The success of *A.longipes* in Seychelles undoubtedly depends on its wide range of nesting habit, feeding behaviour and foraging activity.

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