COLONY DYNAMICS OF THE GREEN TREE ANT (*Oecophylla smaragdina* Fab.) IN A SEASONAL TROPICAL CLIMATE.

Thesis submitted by
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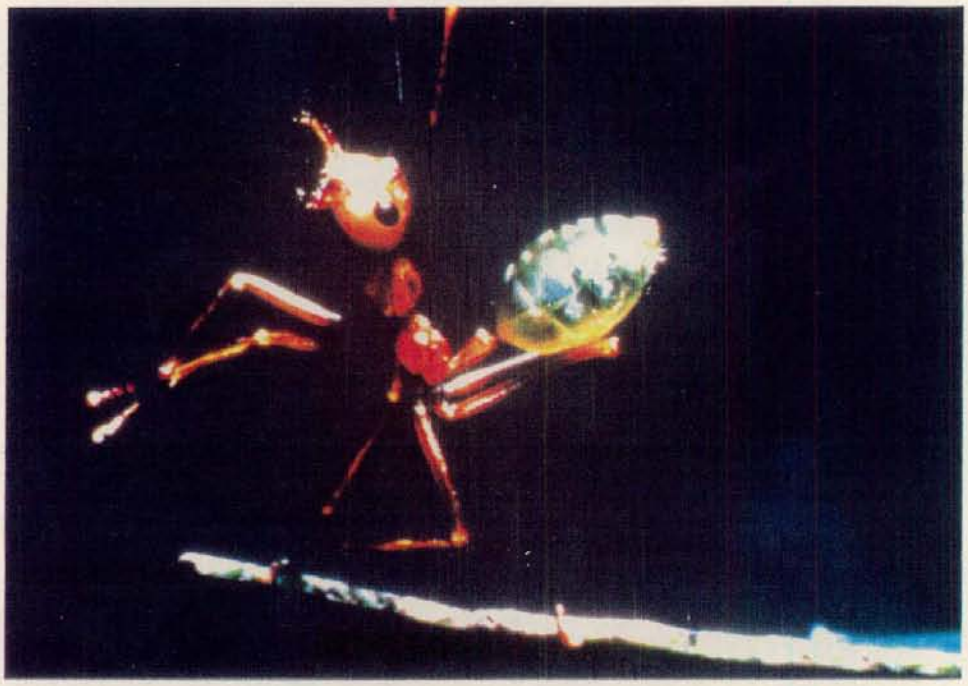
Frontispiece.

(a) Green tree ant major worker in alarm posture.

(b) Green tree ants capturing a wasp.



Abstract.

Most previous investigations of the weaver ant genus (*Oecophylla*) have been conducted in the relatively non-seasonal environment of the wet tropics (e.g. Greenslade, 1971a,b, 1972; Ledoux, 1950, 1954; Majer, 1976,a,b,c; Vanderplank, 1960; Way, 1954a,b). The present study documented substantial seasonal variation in colony structure and functioning of green tree ant *(O. smaragdina)* populations in the seasonally dry tropical climate which characterizes most of northern Australia.

The distribution of *O. smaragdina* within Australia was successfully defined by a combination of mean annual rainfall and average minimum temperature, with a curvilinear demarcation between sites with and without ants. Development and survival of ant brood was markedly reduced by low temperatures, especially the larval stage, which had a threshold temperature (when development theoretically stops) of about 17°C. In contrast, the thresholds for eggs and pupae were about 10°C and 7°C, respectively. At higher temperatures, the 2 physical variables probably indirectly limit ant distribution by controlling plant density; ants only inhabited sites with woodland or forest vegetation.

Colony extents (the numbers of trees occupied by colonies) were much larger in native vegetation than in a nearby mango plantation. This difference was probably due to the greater tree density in the native forest site. No canopy interconnections were available in the mango orchard to promote movements of ants between trees. Inter-tree migration is essential for weaver ant colonies, to disseminate brood

from the nest containing the colony's single egg-producing queen and possibly also to maintain a uniform colony recognition scent.

Levels of reproduction in green tree ant colonies were highest during the wet season and early dry season. Sexual forms were present in nests from November until March, and worker brood were most abundant from January until May. Larval and pupal brood levels rose with increasing precipitation up to monthly rainfall figures around 300 mm. Proportions of worker pupae were reduced during periods of higher rainfall, probably due to the production of sexuals at this time.

Colony extents, measured as the number of trees occupied, were smallest in native forest at the end of the dry season in November, and rose while colonies were reproducing. Most colonies reached peak extents in May, when the proportion of flowering trees was highest (and 2 months after the greatest levels of leaf flushing). After May, brood production generally decreased markedly, and colony extents in native vegetation slowly fell, with ants gradually evacuating from peripheral trees into smaller core areas of high tree density. Cycles of colony extent in the mango plantation lagged behind those in native vegetation by 2 to 4 months; maximum extents coincided with mango tree flowering from July to September. Tended homopteran levels in mango tree leaf samples were high during the flowering and fruiting period, suggesting that colony expansion may be facilitated by the increased availability of honeydew.

As colonies expanded, individual nests became smaller and the number of nests (per tree and per colony) increased. Ant distributions were thus dispersed more evenly throughout colonies during this period. This decentralization may improve foraging efficiencies, or may allow increased patrolling of territories when intrusions by other ant

colonies (both intra and inter-specific) are most likely. Highest levels of prey intake and ant movement from nests did coincide with periods of greatest reproduction and dispersion; however, the causal relations between these factors are unknown.

An electronic light beam counter was developed to monitor ant activity (measured as the number of ants leaving and returning from a nest, and standardized between different nests by dividing by the total population of each nest) in native forest over a two year period. Net daily activity was greatest during the wet season months from December to March, and lowest in the dry winter period. The magnitude of these seasonal differences was remarkably high; the largest mean activity of 8.83 ants/nest individual/day (in December) was over 10 times the smallest level of 0.501 (in August). Seasonal patterns of activity correlated well with patterns of total prey weight collected by ants. Liquid food intake, measured as the average weight difference of leaving and returning ants, showed a similar, but very erratic pattern; factors such as varying forager sizes, honeydew intake inside the nest, and differing physiological conditions of inhabited trees prevented successful quantification of this food source.

A consistent circadian pattern of ant activity was observed in autumn and winter (March, May, August): activity peaked around dusk, and dropped to a minimum in the early morning before dawn. This circadian pattern was less distinct or completely absent during the spring and summer months (October, December, January). Activity was generally correlated with temperature; the fitted parabolic relationship suggested that activity was markedly reduced by low temperatures, but was less affected by higher temperatures.

Circadian patterns of activity did not correlate to patterns of

food intake. Most prey was collected during the daylight hours, suggesting that *O. smaragdina* is primarily a visual predator. Honeydew intake also appeared to be greatest after dawn. Nocturnally active ants may be involved in other tasks, such as brood and young adult transport, colony scent dispersal, and territorial patrolling/guarding.

Mango trees with green tree ant populations had more tended homopterans and fewer numbers of most other arthropod groups than adjacent trees without ants. The proportions of leaves with chlorotic scars from homopterans (primarily *Phenacaspis dilata*) were greater in ant-occupied trees. The fractions of leaves with holes from chewing arthropods, and the average area of leaf missing were greater in ant-free trees.

Crop yields during the study were relatively low. However, ants appeared to augment fruit loss in trees with largest crops during the late stages of fruit development, probably by encouraging homopteran populations and so increasing sap loss. Green tree ants also appeared to reduce frugivory by fruit bats, the major predator of mango fruit.

TABLE OF CONTENTS:

LIST OF FIGURES.

LIST OF PLATES.

LIST OF TABLES.

1. General introduction.

The weaver ants of the genus *Oecophylla* are prominent members of forest insect communities throughout all of the tropical world except America. The two extant species are quite similar in morphology and behaviour, but display some colour variation. *O. smaragdina* (Fab.) ranges from tropical Asia to northern Australia, and onto some western Pacific islands (fig 3.1). The Australian subspecies, *virescens* (Fab.), has a pale green abdomen, hence the common name of green tree ant (Dodd, 1928), while mainland Asian populations have a uniform reddish brown colour (Wheeler, 1922). The African species, *O. longinoda* (Latr.), varies from reddish brown to dark brown.

1.1 Nest structure.

The weaver ants' most distinctive feature is their habit of using silk produced by their larvae to construct nests of living leaves. This process was described independently by Ridley (1890, in Wheeler, 1910) in India and Saville-Kent (1891, in Hemmingsen, 1973) in Australia. Further accounts have been given by Doflein (1905), Ledoux (1950), Hemmingsen (1973), and Hölldobler and Wilson (1983b). The following description is derived primarily from the 2 most recent sources.

When a new nest is required, individual workers scout for suitable clusters of leaves, which they grab with their mandibles and attempt to draw together. Other workers are attracted to the site, presumably by the success of the first workers, and join the effort. A large gap can be bridged by chains of ants, formed by each ant clasping the

petiole of the ant in front with her mandibles. Chains of at least 10 ants, spanning over 5 cm in length can be constructed; this chaining appears to be unique to the weaver ant genus.

Eventually, a number of leaves will have been stretched into position for binding, each held in place by rows of workers. Other workers carry late instar larvae in their mandibles to the binding sites. With a precise, coordinated set of movements, the ant uses the larva to lay a series of silken strands between the leaf margins, until a white sheet of silk joins the two. The larva moves very little during this "weaving" operation, acting as a passive shuttle.

Accounts of the variation in nest weaving with time of day, and with worker castes involved, have shown some discrepancies. Hemmingsen (1973) in Thailand observed nocturnal weaving with larvae by the larger major caste adults on the outside of the nest, while the smaller minor workers wove inside the nest during the day. Some earlier workers also suggested that little weaving occurred during the day, but Ledoux (1950) and Hölldobler and Wilson (1983b) both recorded daytime weaving on the outside of the nest. Diurnal weaving behaviour may vary among different populations, or possibly environmental factors such as temperature and relative humidity influence the times when larvae are used for weaving.

Less complex forms of nest weaving occur in 3 other genera of the subfamily Formicinae. Both species of the genus *Dendromyrmex* (Wilson, 1981) incorporate larval silk into their nests, which are also bound with fungus-impregnated vegetable fibre (or "carton"). Larvae perform all of the weaving movements to lay silk onto the nest, while being held passively in an appropriate site by adult worker ants, and will add silk to the nest even when unattended by workers. At least 2

species in the genus *Camponotus* (Schremmer, 1979), and a number of species of *Polyrhachis* (Hölldobler and Wilson, 1973b) also use larval silk in nest construction. In the few species observed to date, all larvae were held to stimulate silk production, but the larvae performed most of the weaving motions. Hölldobler and Wilson (1983b) have fitted these examples to an evolutionary gradient, from the primitive weaving of *Dendromyrmex* to the complex, highly coordinated nest construction in *Oecophylla*.

The nests of some Cuban species of *Leptothorax*, and *Technomyrmex bicolor textor*, from Java, also contain silk, but no evidence for larval production of this silk has been observed. As these species belong to the subfamilies Myrmicinae, and Dolichoderinae, respectively, which have no other weaving species, this silk is probably from other sources, such as spiders' webs.

The size of *Oecophylla* nests vary from a single folded leaf to many hundreds of leaves (plate 1.1). These size differences are controlled to some extent by the structure and density of foliage. A single palm frond, for example, can be utilized as a nest by joining the two sides of the frond with silk (Way, 1954a). Occasionally, ants construct nests in plants with very small leaves, such as *Leptospermum* species; such nests have walls composed almost entirely of silk (plate 1.1c). Nevertheless, some plants appear to be generally unsuitable for nest construction. The large leaves of plantain, the narrow leaves of oil palm, and the small leathery leaves of cashew, for example, were not utilized for nesting by the African weaver ant (Taylor, 1977).

Plate 1. Leaf nest of *O. smaragdina*.

(a) nest built from 1 leaf of *Elaeodendron melanocarpum*.
(b) Multiple leaf nest in *Drypetes lasiogyna*.
(c) Nest in *Leptospermum sp.*
(d) Nest in *Pongamia pinnata* (still occupied although all leaves were dead)

Plate 1.

1.2 Colony structure.

Weaver ants are predominantly arboreal (e.g. Hölldobler, 1980; Way, 1954a), but sometimes venture onto the ground to forage, or travel between trees when canopies do not interconnect (Jackson, 1988; Taylor and Adedoyin, 1978). Their colonies are among the largest in the ant family. Way (1954a) observed one colony inhabiting 151 nests, scattered throughout 8 coconut and 4 clove trees, and covering an area of 800 m^2. He estimated that this colony contained 480,000 worker ants, and 280,000 brood. Vanderplank (1960) and Hölldobler and Wilson (1978) also report populations of mature colonies in the range of 100,000 to 500,000, and Leston (in Majer, 1976a) estimated that colonies could number several million.

Most polydomous ant species (i.e. species whose colonies comprise more than one nest) have more than one reproductively active queen. However, a mature *Oecophylla* colony is strictly monogynous; the loss of the single gravid queen signals the demise of the entire colony (Crozier, 1970; Greenslade, 1971b; Hölldobler and Wilson, 1977b, 1983a; Way, 1954a). Greenslade (1971a) estimated from cyclical patterns of abundance in Solomon Island plantations that the average life span of colonies was 8 years. Vanderplank (1960) successfully reared colonies in potted clove plants for 5 years.

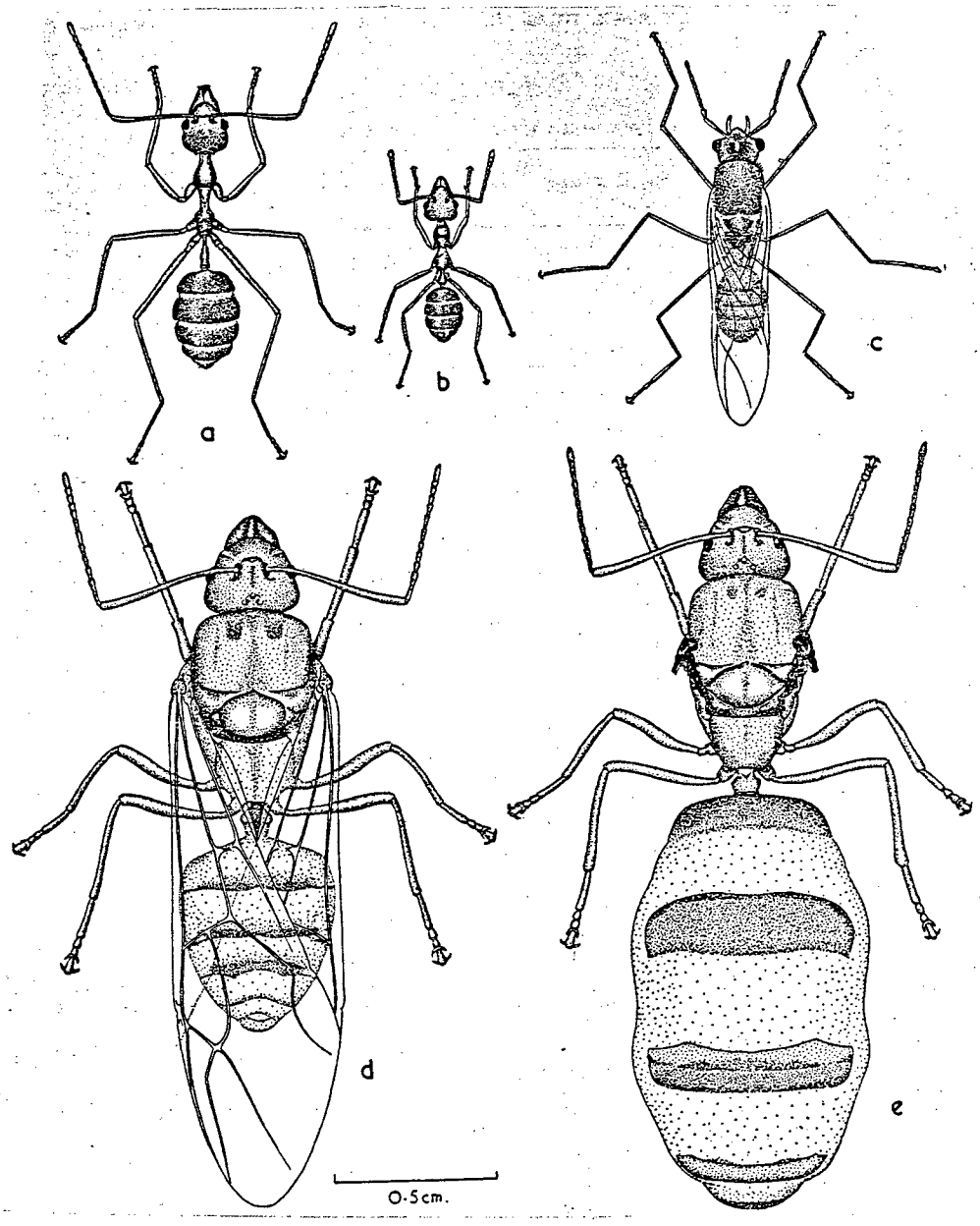
The various adult forms of weaver ant are shown in figure 1.1. The worker population is polymorphic (Cole and Jones, 1948; Weber, 1949). The smaller minor caste workers tend the brood, and rarely venture outside the nest. The larger major caste workers forage, and assist with care of the queen and larger brood. The major workers also defend the colony territory, although both castes will act in nest defence

Figure 1.1. Adult forms of *Oecophylla* (from Way, 1954a).

(a) major worker. (b) minor worker.

(c) male. (d) virgin female.

(e) gravid queen.



(Hölldobler and Wilson, 1977b). A feature unique to the weaver ant genus is that major workers outnumber minor workers (Wilson, 1953).

Winged male and female sexuals are produced during the wet season, and are released after rain (Bhattacharya, 1943; Gibbs and Leston, 1970; Greenslade, 1971b; Way, 1954b). Inseminated queens select a suitable site within a curled leaf or a cluster of leaves, and rear their first brood claustrally. Both haplometrotic colony founding (by a single queen - Dodd, 1902, 1928; Greenslade, 1972; Vanderplank, 1960) and pleometrotic colony founding (by a group of queens - Begg, 1977; Ledoux, 1950; Peeters and Anderson, 1989; Richards, 1969) have been recorded.

Weaver ants maintain their territory and coordinate their activities using a highly developed chemical communication system, in combination with visual and tactile cues. Ants are recruited to food, unexplored terrain, and territorial intruders using odour trails released from the sternal and rectal glands in the abdomen (Hölldobler and Wilson, 1978). Well established trails between nests are marked with rectal gland secretions, which remain effective for about three days (Jander and Jander, 1979). Localised alarm and attack responses are invoked by volatile chemicals from the mandibular gland in the head, and poison and Dufour's glands in the abdomen (Bradshaw, Baker, and Howse, 1975, 1979a,b,c). Drops of faecal material are deposited randomly throughout the colony territory; workers can distinguish alien from friendly terrain using these territorial marks (Hölldobler and Wilson, 1978, 1977a). This sophisticated chemical communication repertoire is among the most complex observed in the ant family.

The combination of well developed communication, aggressive territoriality, and decentralized multiple nests allows *Oecophylla* to

maintain absolute territories, which exclude most other ant species (Hölldobler and Lumsden, 1980). Similar absolute territories have been reported in a number of polydomous tropical ants with large populations (e.g. Greenslade, 1971b; Leston, 1970, 1973, 1978; Majer, 1972; Room, 1971). The patchwork distribution of the exclusive territories of weaver ant and other dominant arboreal ant colonies has been termed the ant mosaic by Leston (1973).

Interestingly, a few ant species can coexist with *Oecophylla*, without invoking a massive defence response (Hölldobler, 1980, 1983; Room, 1971). This selective enemy specification has also been observed in *Pheidole dentata*, and allows defensive responses to be directed towards the most serious competitors for essential resources, such as food and nest sites (Wilson, 1975, 1976c). In tropical arboreal mosaics, absolute territories appear to have evolved in response to competition for foraging space, rather than nest sites (Leston, 1973; Majer, 1976a,b; Room, 1971).

Oecophylla and other dominant ants act as keystone species (Paine, 1974, 1976), exerting a strong controlling influence on the other arboreal insect fauna through predation and competition for food resources (e.g. Bigger, 1981; Majer, 1976c; Risch and Carroll, 1982a,b; Way, 1954a). Before examining this aspect further, the diet of weaver ants will be described.

1.3 Diet.

The weaver ant, like many ant species, collects two food types: honeydew from various homopterans (and lycaenid caterpillars), and insect prey (Carroll and Janzen, 1973). Honeydew is collected from many

families of homoptera, including Coccidae, Stictococcidae, Pseudococcidae, Aphididae, Margarodidae, Membracidae, and Cicadellidae (Brown, 1959; Das, 1959; Vanderplank, 1960; Way, 1954a, 1963). Many ant-homopteran interactions are mutually beneficial; the ants obtain food rich in sugars and amino acids, and the bugs obtain some protection from predators and parasites (Way, 1963).

The coccid, *Saissetia zanzibarensis*, has developed a strongly mutualistic association with the African weaver ant (Way, 1954b). Without ant attendance, the coccids are virtually exterminated by contamination with mould, parasitism, and predation. *O. longinoda* workers also transport coccid nymphs to optimum feeding sites, and "cull" excess numbers by consuming them.

A number of lycaenid butterfly larvae (which produce sugary secretions from specialized dorsal glands) are also tended by ants, and are often kept within small leaf nests. Lycaenids tended by green tree ants in Australia include *Anthene seltuttus*, *Arhopala centaurus*, *Arhopala micale*, *Hypolycaena phorbas*, and *Theclinesthes miskini eucalypti* (Common and Waterhouse, 1981). However, this source of food is generally much less important than homopteran honeydew.

Weaver ants are generalist predators, attacking most arthropods that they encounter. The most abundant prey items recorded by Vanderplank (1960) were termites, ants, and honeybees. Other prey carried back to the nest include heteropterans, coleopterans, orthopterans, blattodeans, mantodeans, dipterans, and araneans (Majer, 1976c; Vanderplank, 1960; Way, 1954a). *Oecophylla* can reduce the levels of many untended insect groups substantially (Leston, 1973; Majer, 1976c; Room, 1973). For this reason, various studies have examined the potential of these ants to control certain insect pests of tree crops.

1.4 Impact of weaver ants on arboreal arthropod pests.

The earliest known example of biological control, recorded in the Nan Fang Ts'ao Mu Chuang (about 340 AD), described how *O. smaragdina* was used to control insect pests in Chinese orange orchards. Groff and Howard (1925) reported that citrus growers in the Saisha district import nests of weaver ants from southern China to protect their crops from the heteropteran, *Tesseratoma papillosa*, and some boring insects. However, weaver ants also increase the numbers of the harmful red scale, *Aonidiella aurantii*, in citrus trees, presumably by excluding its parasites (Flanders, 1958).

In Zanzibar, *O. longinoda* improves coconut crop yields by reducing the levels of the coreid bug, *Pseudotheraptus wayi*, which causes premature nutfall (Vanderplank, 1960; Way, 1953, 1954a). Similarly, *O. smaragdina* protects coconuts in the Solomon Islands from another coreid, *Amblypelta cocophaga* (Brown, 1959; Greenslade, 1971a; Stapley, 1971).

In cocoa trees, weaver ants reduce damage from the capsids, *Distantiella theobroma* and *Sahlbergella singularis* (Dun, 1954; Leston, 1970, 1973; Majer, 1976c). They also tend various stictococcids, but discourage the pseudococcid, *Pseudococcus njalensis*, which transmits swollen shoot virus (SSV). Ants of the genus *Crematogaster* tend *P. njalensis*, and thus aid the spread of the virus (Leston, 1970; Strickland, 1951). One pseudococcid tending species, *C. castanea*, can coexist with weaver ants, but the effect of this association on virus transmission has not been determined (Room, 1971; Taylor, 1977).

Other documented impacts of *Oecophylla* include protection of mango fruit from *Cryptorrhynchus* weevils (Friedrichs, 1920); reduction of

most insect pests in tea seed trees, but an increase in tended coccids (Das, 1959); and in arabica coffee, protection from the pentatomid, *Antestiopsis intricata*, but increased damage from homopterans (Das, 1959; Leston, 1973).

Leston (1973) and Room (1973) have outlined strategies for the development of insect pest control by manipulation of the ant fauna. Stapley (1971) successfully encouraged the spread of weaver ants in Solomon Island coconut plantations by exterminating the nests of its major competitor, *Pheidole megacephala*, with selective insecticide and herbicide treatments. Many ant manipulation trials have failed, however, due to lack of biological and ecological knowledge of the species concerned. Transplantation of weaver ant nests, for example, rarely leads to successful colony establishment because the reproductively active queen is not collected (e.g. Brown, 1959). A colony fragment also has little chance of surviving within the territories of other dominant ant species in the mosaic (Leston, 1973).

The usefulness of an ant species in crop protection may be nullified by detrimental interactions with other insect fauna. As already mentioned, ants can increase the levels of tended homopterans to harmful levels, and coexisting ant species may encourage detrimental insect species. By reducing predator populations, ants may allow some herbivores which are less vulnerable to ant predation, such as leaf-miners, to increase to harmful levels (Fowler and MacGarvin, 1985; Fritz, 1983).

The effectiveness of ant control may also vary temporally. For example, seasonal changes in the protein requirements of the colony, caused by seasonal patterns of reproduction (e.g. Brian *et al*, 1981; Sudd, 1987), can also alter the level of predation on insect pests

(e.g. Greenslade, 1971b; Robertson, 1988; Skinner, 1980b).

1.5 Aims of the present project.

Almost all previous work on the weaver ant genus has been conducted in the relatively non-seasonal environment of the wet tropics. The present study was undertaken to examine the distribution, colony structure, and activity of the green tree ant, *O. smaragdina*, and its impact on the arboreal arthropod fauna, in the highly seasonal, dry tropical environments which characterize most of northern Australia. The study aimed to answer the following questions:

1. What limits the distribution of green tree ants within Australia (chapter 3)?

2. Is there seasonal and geographic variation in the reproductive activity of colonies (chapter 5)? If so, are these related to physical environmental factors such as temperature and rainfall (chapter 4+5)?

3. Does the structure and extent of colonies change seasonally, in response to reproductive cycles and/or environmental factors (chapter 5)?

4. Does the behaviour and activity of ants vary seasonally and/or in response to environmental conditions (chapter 6)? More detailed analysis of activity dynamics (e.g. circadian task switching, length of foraging trips) was inhibited by the extreme aversion of these ants to any form of tag.

5. Do green tree ants have a significant impact on other arthropod populations, or on the condition of their host trees, in this environment (chapter 6+7)?

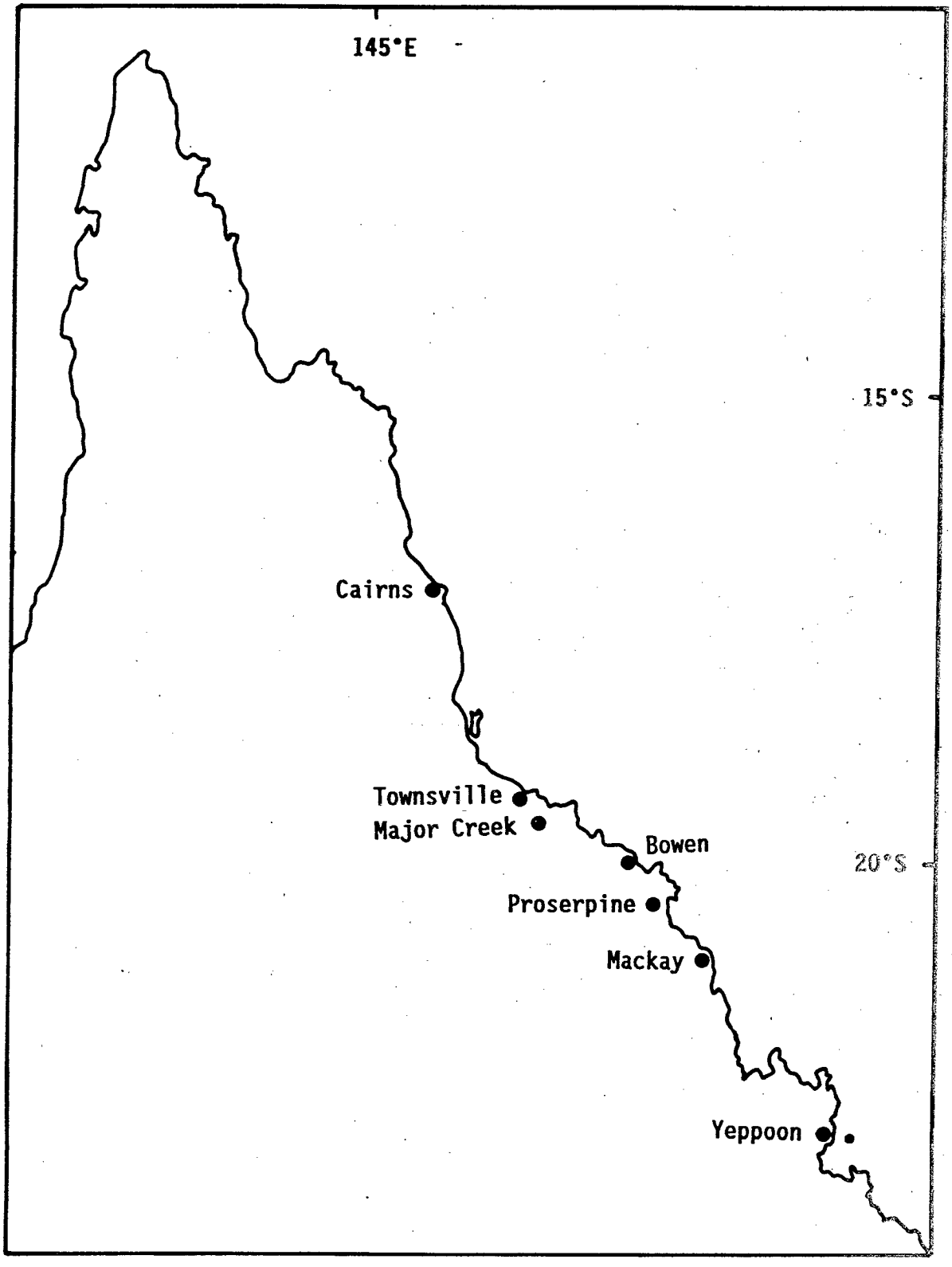
2. Description Of Study Sites.

2.1. Townsville.

Townsville (19°16'S, 146°48'E) lies on the edge of a narrow coastal plain in north-eastern Queensland (figure 2.1), bordered to the west by the Hervey's Range/Paluma Range escarpment, and to the east by the Coral Sea. Although this area originated as part of the Tasman geosyncline in the lower Paleozoic (500 - 600 million years ago), no rock formations from the early periods of this era occur on the land surface (Henderson, 1980). The earliest outcroppings in the region are the western escarpment, and residual mountains and hills, probably produced by granitic intrusions emplaced during the Devonian to Permian periods (280 to 400 million years ago), and raised into their present positions in the late Tertiary period to the early Quaternary period (10 to 30 million years; Hopley, 1978). This uplifting has produced the present system of relatively short streams (e.g. Ross River, Bohle River) flowing eastward from the escarpment and residuals into the sea, and streams to the west of the scarp (e.g. Keelbottom Creek, Star River) draining into the Burdekin River. Examples of the residual granitoid mountains in the Townsville region include Mount Stuart, Castle Hill, and the Mount Elliot Range.

The coastal lowland consists of alluvia eroded from the uplifted escarpment and residuals during the Quaternary period. Climatic fluctuations during glacial-interglacial cycles produced varying levels of deposition, and weathering of sediments. Recently, an increase in sea level has caused a small rise in rainfall, and thus deposition, although still high, has probably decreased slightly (Hopley, 1978).

Figure 2.1. Map of northern Queensland showing locations of study sites.



Most of these lowlands have mature, solodic, solodized soils, with well developed horizons (Murtha, 1978). The presence of a heavy clay horizon beneath shallow (15 - 25 cm) topsoil impedes drainage, and limits the agricultural potential of the area. The best soils in the region are associated with recent alluvial deposition, along flood plains, and old stream beds, and on the fringes of mountains and the coast.

Rainfall in the Townsville region is highly seasonal, with an average of 80% of the 1200 millimetre mean annual precipitation falling during the summer months from December to March (Bureau of Meteorology, 1975). These summer rains are occasionally generated by a widespread monsoonal trough, but more often by the irregular passage of upper atmospheric troughs or cyclones (Oliver, 1978). The time of onset, duration, and intensity of the wet season, and the annual precipitation level can thus fluctuate widely from year to year. Monthly rainfall figures recorded in Townsville from 1985 to 1989 (figure 2.2a) clearly demonstrate these trends. Wet season rainfall levels ranged from 257 mm (in 1984/85), to 1014 mm (1988/89), the commencement of the wet varied from October (1985/86) to February (1984/85), and the duration of the wet from 2 (1984/85) to 5 months (1988/89).

Temperature ranges from a mean maximum of 30.7°C in January, to 24.4°C in July, and mean minimum temperature from 24.5°C in January, to 15.4°C in July (Bureau of Meteorology, 1975). Frosts are very rarely experienced in this coastal region (Foley, 1945), with none recorded during the course of my project. Temperature undergoes much more consistent seasonal variation than rainfall, with mean monthly maximum and minimum temperatures during 1985 to 1989 differing by only 2.3°C and 5.7°C, respectively, from year to year (figure 2.2b).

Figure 2.2. Climatic patterns in Townsville from January 1985 to May 1989.

Figure 2.2a. Rainfall patterns

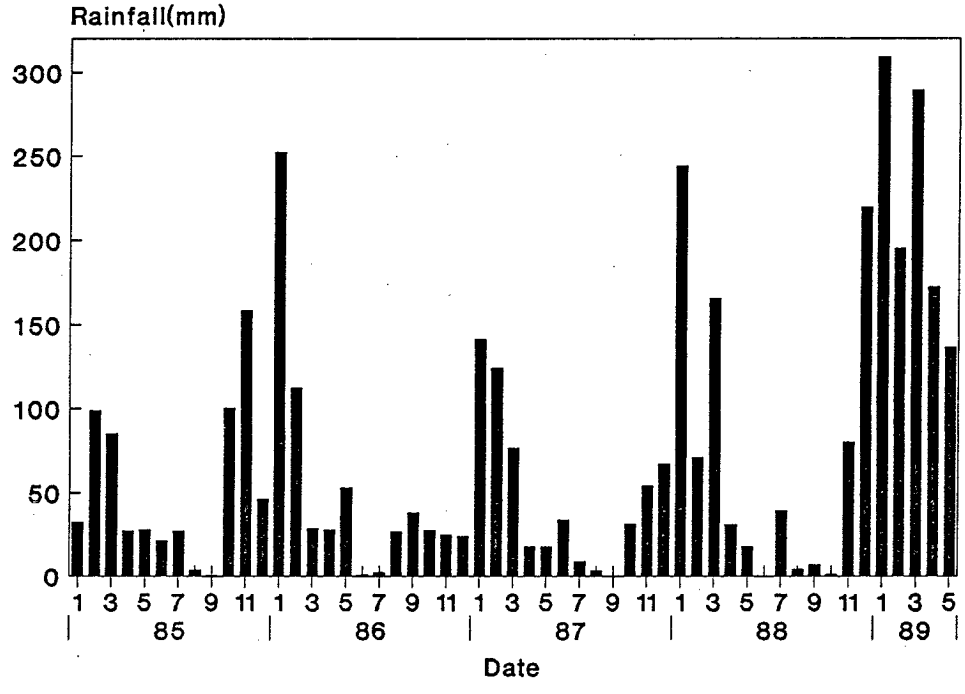
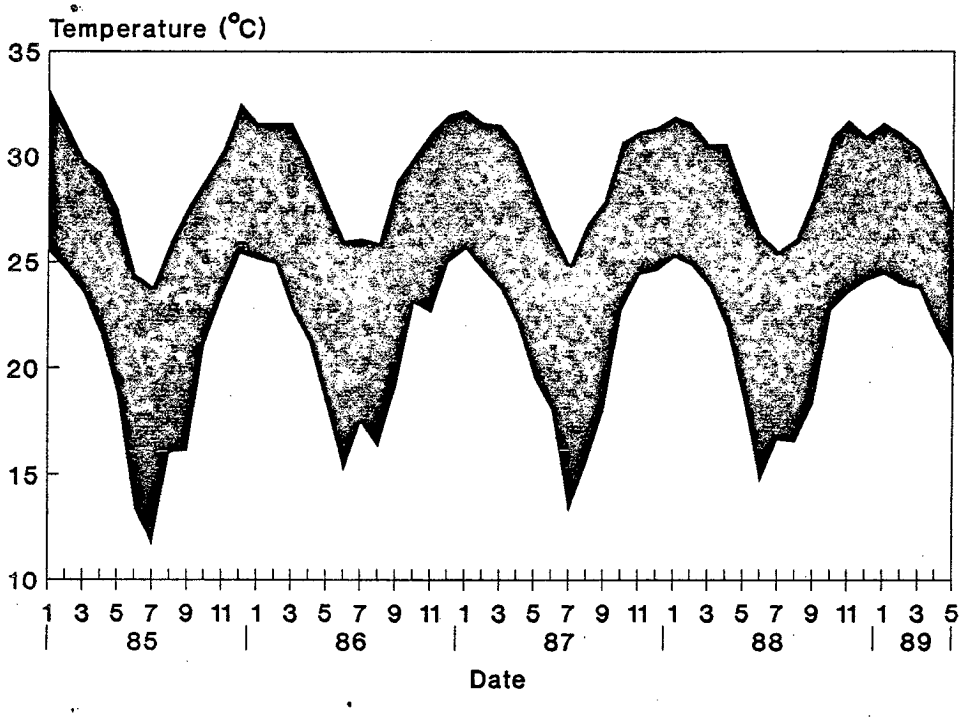


Figure 2.2b. Temperature patterns



Based on these climatic figures, the Holdridge (Holdridge *et al*, 1971) life zone classification system places Townsville within the cooler portion of the tropical dry forest zone.

The combination of poor soils and relatively dry, seasonal climate has constrained vegetation development in the region to open eucalypt woodland (plate 2.1), dominated by narrow-leaved ironbarks (*E. drepanophylla*), poplar gums (*E. platyphylla*), and the introduced chinese apple (*Zizyphus mauritiana*). Cockatoo apple (*Planchonia careya*) and broad-leaved paperbark (*Melaleuca viridiflora*) are common understorey trees, and spear grass (*Heteropogon spp.*), kangaroo grass (*Themeda australis*), and the naturalised red natal grass (*Rhynchelytrum repens*) the main grasses.

In regions of better soil quality, more complex and dense vegetation has developed, with occasional patches of quite dense closed forest. My Townsville study site was located within one such area, bordering Campus Creek, adjacent to the James Cook University campus (plate 2.2). All trees over 2 metres tall in the site were mapped using a bearing compass, tape measure, and an optical distance gauge, in 1985 (figure 2.3). This map was updated as trees grew, or died. The area to the east of the creek was open eucalypt woodland, which was uninhabited by green tree ants, and therefore unmapped. In May, 1988, 744 trees were found in the 14106 m^2 site, giving a density of 0.053 trees per m^2. The commonest tree species were chinese apple (*Zizyphus mauritiana*), northern swamp box (*Lophostemon grandiflorus*), *Pongamia pinnata*, and *Melaleuca spp.*, but many other species were also present (listed in figure 2.3). Vines were also abundant, including native jasmine (*Jasminium didymum* subsp. *racemosum*), stinking passion flower (*Passiflora foetida*), native grape (mainly *Cayratia trifolia*),

Plate 2.1. Open eucalypt woodland of the Townsville region.

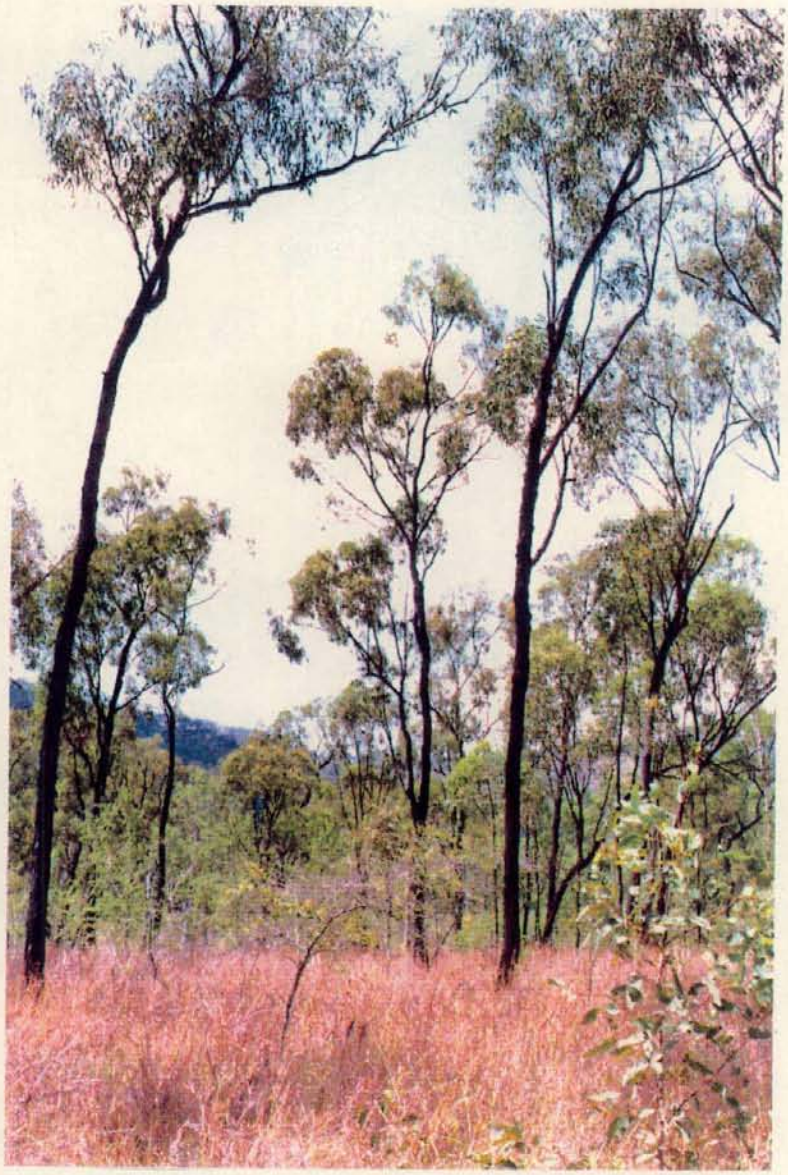
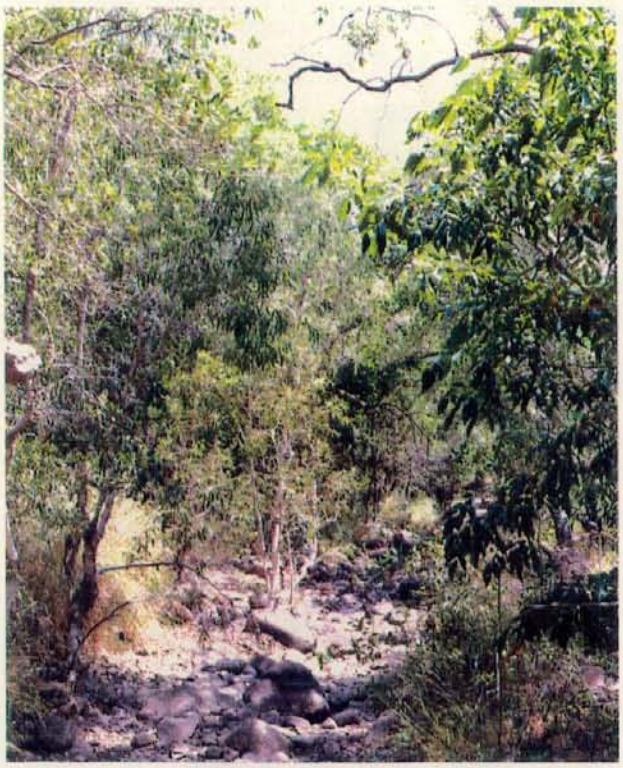


Plate 2.2. Vegetation of the Townsville study site.
(a) Campus Creek in January 1989. (b) Campus Creek in October 1987.
(c) Transitional zone from riparian forest to open woodland.



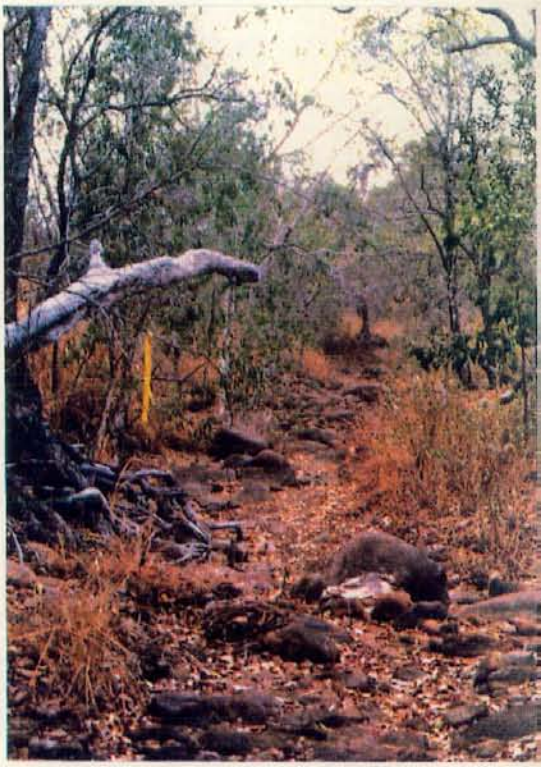


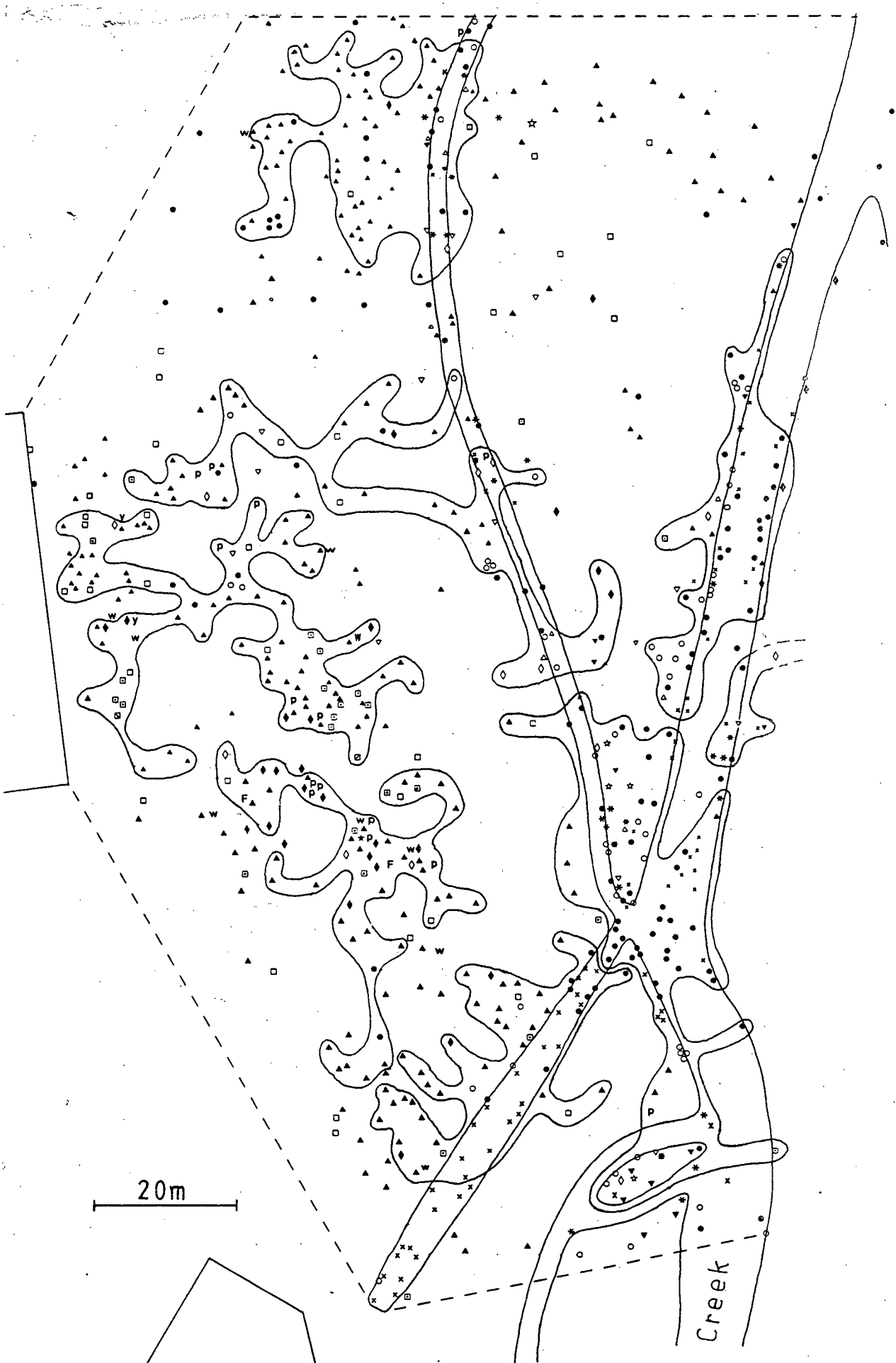
Plate 2.3. The Major Creek mango plantation.

Plate 2.4. Sampling the upper canopy of mango trees.

Legend for tree species found in Townsville study site.

▲	*Zizyphus mauritiana*
●	*Lophostemon grandiflorus*
○	*Pongamia pinnata*
□	*Eucalyptus platyphylla*
⊡	*Eucalyptus tessellaris*
▧	*Eucalyptus papuana*
♦	*Canarium australianum*
◊	*Pleiogynium timorense*
×	*Melaleuca spp.*
△	*Elaeodendron melanocarpum*
▽	*Drypetes lasiogyna*
▼	*Pouteria sericea*
*	*Exocarpos latifolius*
☆	*Acacia salicina*
✱	*Lysiphyllum hookeri*
p	*Planchonia careya*
w	*Alphitonia excelsa*
y	*Gardenia ochreata*
F	*Ficus opposita*
K	*Cochlospermum gillivraei*

Figure 2.3. Map of Townsville study site showing colony extents in May 1988.



and the introduced rubber vine (*Cryptostegia grandiflora*). Where tree cover was sparse enough to allow sufficient light through, an extensive ground cover was present, with herbs such as *Stachytarpheta jamaicensis*, the introduced *Lantana camara*, *Hyptis suaveolens*, *Crotalaria spp.*, and *Triumfetta rhomboidea*. These herbaceous shrubs were interspersed with clumps of grass, mainly spear grass, kangaroo grass, red natal grass, and guinea grass (*Panicum maximum*).

Plant species were identified by Dr. B.R. Jackes, Botany Department, James Cook University, or using the keys in her recent monograph, "Plants of Magnetic Island" (1987).

The vegetation of this site was markedly seasonal, due to the strong seasonality of rainfall. Some of the trees in the site, such as *Pongamia pinnata*, *Zizyphus mauritiana*, and *Eucalyptus platyphylla* were deciduous to varying degrees. This was particularly evident in late 1987 (plate 2.2b), after a very poor wet season (figure 2.2a). Most herbs and grasses also dwindled or disappeared during the dryer months, producing a much more open understorey later in the year. Insect numbers also varied seasonally, peaking in the wet season when foliage was abundant. Although not assessed in the present study, this trend has been well documented for tropical habitats in Costa Rica (Janzen and Schoener, 1968) and Ghana (Gibbs and Leston, 1970; Leston, 1970).

The most conspicuous arboreal ant species was the green tree ant, *Oecophylla smaragdina*. Other ants observed in trees included species of *Crematogaster*, *Iridomyrmex*, and *Polyrhachis*, *Opisthopsis haddoni*, *Paratrechina longicornis*, and *Tetramorium bicarinatum*. The commonest nocturnally active arboreal ants were *O. smaragdina* and several *Camponotus* species.

In more open areas, the meat ant, *Iridomyrmex purpureus sanguinea*

predominated. This dolichoderine ant was the only species which engaged in major conflicts with the green tree ant. Less conspicuous ground-dwelling ants included other species of *Iridomyrmex*, *Camponotus spp*, *Odontomachus sp*, and *Cerapachys sp*.

Ant species were identified by Dr. R.W. Taylor, Australian National Insect Collection, CSIRO Division of Entomology, Canberra. No voucher specimens have been lodged outside James Cook University to date.

2.2 Major Creek.

A second study site was established in 1986 on a plantation of mango trees (*Mangifera indica*) owned by the Wright family, about 1 km from Major Creek in the foothills of Mt. Elliot Range (plate 2.3). Mangos were the only fruit tree crop grown in this region of Queensland on a scale sufficient to support adequate populations of green tree ants for my research. The Major Creek farm was chosen because the owner was the sole person in the district who did not regularly use insecticidal sprays (which are very effective at destroying ants). Major Creek is approximately 50 km from my Townsville site, and experiences a relatively similar climate (K. Wright, pers. comm.; Oliver, 1978).

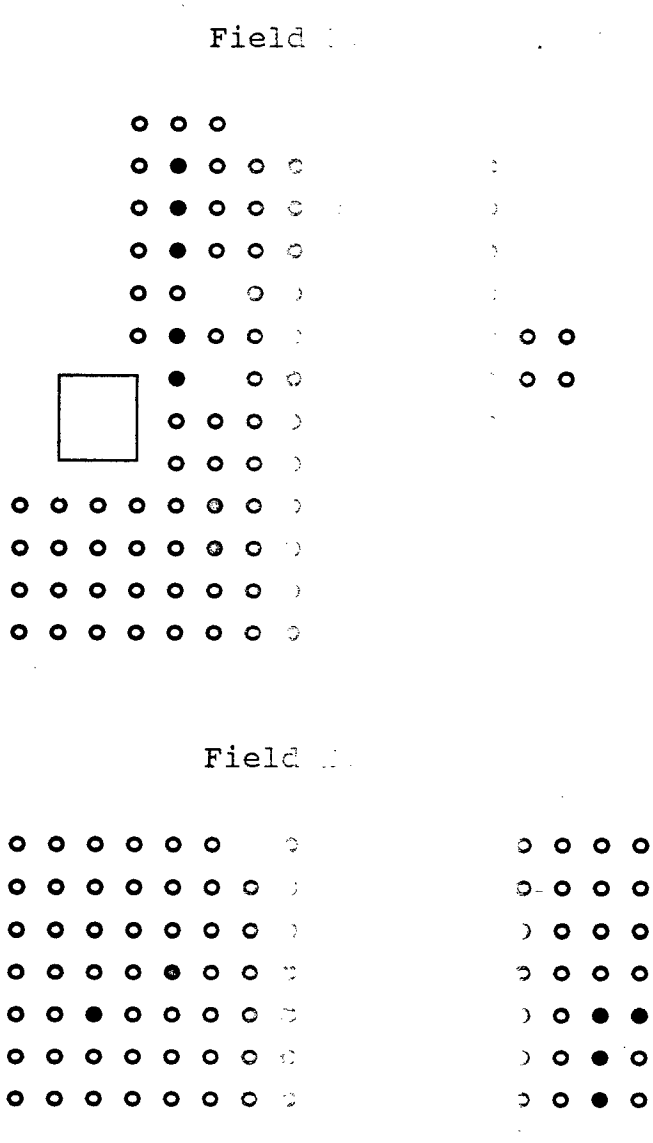
Two fields of trees were mapped, totalling 250 trees (figure 2.4). The 120 trees in field A were planted in 1974, and the 130 field B trees in 1976. As the average tree height was only 6.5 metres, access to all parts of the canopy was relatively easy, by ladder (plate 2.4), or by climbing. Trees were arranged in a square grid pattern, with an average spacing of 9 metres. No canopy interconnections between trees

had developed, due to the young ... low density of trees.

Regular slashing confined the ... vegetation to grasses, small herbs such as Stachytarpheta ..., and coppice regrowths of *Zizyphus mauritiana*. The ant fa... Major Creek plantation had a similar species composition to ...ille site. However, ground-dwelling ants were more abun... arboreal ants fewer, as vegetation levels were lower in ...abitat.

Figure 2.4. Map of Major Creek ... during May 1988.

o - Mango tree unoccupi... tree ants.
● - Mango tree occupied ... ee ants.



3. Distributional patterns.

3.1. Introduction.

The weaver ant genus, *Oecophylla*, occurs throughout much of the forests of the old world tropics (figure 3.1). The African weaver ant, *O. longinoda*, inhabits tropical Africa (Ledoux, 1950; Way, 1954a; Wheeler, 1922). The only other extant species, *O. smaragdina*, ranges from India, across most of tropical Asia to northern Australia, and onto many tropical western Pacific islands, as far east as Fiji (Cole and Jones, 1948; Dodd, 1928; Groff and Howard, 1925). The genus is absent from the tropical forests of America, which have an otherwise very diverse arboreal ant fauna (Wilson, 1959).

Wheeler (1922) further subdivided the 2 species into various subspecies and varieties, based on their considerable geographic variation. These morphological differences, and discrepancies in genetic studies by different workers (Bhattacharya, 1943; Ledoux, 1950; Vanderplank, 1960; Way, 1954a) have led Crozier (1970) to suggest that more than 2 species may exist. No-one has yet conducted a comprehensive genetic study to examine this possibility.

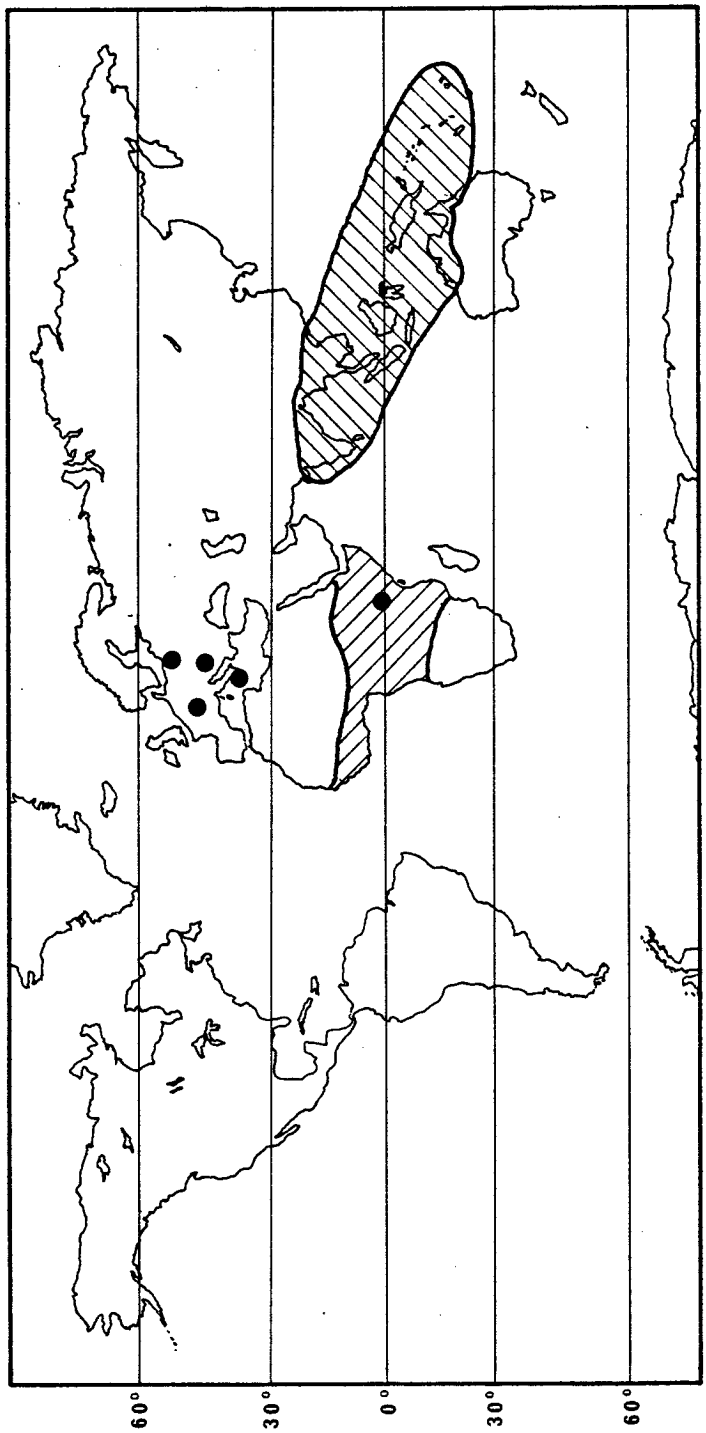
A number of extinct species have been identified from European tertiary fossil deposits (figure 3.1). Fifty specimens of *O. brischkei* Mayr, and one specimen of *O. brevinoda* Wheeler were found in Baltic amber from the early Oligocene epoch, 30 to 34 million years ago (Wheeler, 1914). These fossils are among the oldest records of ant genera still surviving today. Fossil remains of 24 extant genera have been identified from Oligocene sediments, and only one extant genus

Figure 3.1. World distribution of weaver ants.

▨ *Oecophylla smaragdina.*

▨ *Oecophylla longinoda.*

● Fossil records of *Oecophylla*



(*Iridomyrmex*) from an earlier Eocene deposit (Wilson, 1987). Another species, *O. sicula*, has been described from upper Miocene amber deposits in Sicily (12 to 15 million years ago). These species can be placed in a morphocline, consistent with the geological sequence, from *brevinoda* - *brischkei* - *sicula* - present species.

A lower Miocene deposit, recently discovered by L. Leaky, on Mfwangano Island, Kenya, contained over 300 specimens of *Oecophylla leakeyi* Wilson and Taylor, which most closely resembles *O. brischkei* in morphology. This unique fossil assemblage is probably the remains of an arboreal leaf nest, very similar to those constructed by present day weaver ants (Wilson and Taylor, 1964). Other common features include naked pupae (with no silk cocoon), and an adult size frequency distribution unique to this genus (with the larger major caste more numerous than the smaller minor caste). These findings suggest that the genus *Oecophylla* has remained remarkably stable in morphology and social structure for at least 20 million years.

Weaver ants disappeared from the Mediterranean area as it drifted out of the tropics with the northward migration of the Eurasian and African continental plates, producing a cooler climate (and associated vegetation changes). No *Oecophylla* fossil records have been discovered in the Australian region, so no information on the separation of the 2 present species and their biogeographical history is available. The spread of the ancestral *O. smaragdina* into Australia was unlikely to have occurred more than 15 to 20 million years ago, when this continent was significantly further south , and first collided with the Asian continental plate (Henderson, 1980).

In recent times, the distribution of the green tree ant in Australia has probably fluctuated, increasing during interglacials when

temperatures and rainfall were higher and lowland closed forests expanded, and shrinking during glacial periods (Kershaw, 1978). A major reduction in forests between 40000 and 30000 years ago, which Singh *et al* (1981) suggest was caused by a combination of decreased rainfall and aboriginal use of fire, reduced the available habitat for this ant species. A subsequent increase in rainfall and temperature after the end of the last glacial 10000 years ago has allowed the closed forests, and thus the range of the green tree ant, to re-expand.

The earliest European observation of the green tree ant was made by Joseph Banks, when James Cook first sailed along the east coast of Australia in 1778. He recorded this species as far south as Bustard Bay (24°S).

The present distributional limits of *Oecophylla* have not been examined in Australia, or elsewhere in the world. The large arboreal nests and aggressive nature of these ants make them highly conspicuous, and readily observed if present, so they make ideal subjects for distributional studies.

3.2. Methods.

Questionnaires were sent to all local government offices in Australia north of latitude 30°S, asking whether *O. smaragdina* was present in their shire. Because these ants are conspicuous, and are considered a nuisance by many householders (due to their bite), it is unlikely that people would be unaware of their presence if populations existed. Twenty of the 22 offices contacted answered the questionnaire.

This survey was supplemented by the direct inspection of 24

localities in coastal northern Queensland, between latitudes 15° and 30°S, during 1985. These sites were chosen primarily as accurate climatic data were available from the Bureau of Meteorology (1975, Foley, 1945), and also to cover the widest possible geographic range. The effectiveness of various weather parameters in predicting the distribution of *O. smaragdina* within Australia was tested using discriminant analyses.

Micro-distributional patterns were monitored in my Townsville study site, in conjunction with colony size observations (section 5.3.1). Each of the 750 trees in the site was surveyed for the presence of ants, in the following sequence. Firstly, the trunk and lower branches of the tree were examined for ant trails. If no ants were found, binoculars were used to scan the canopy for trails and nests. The presence of nests alone was never accepted as proof of ant presence, as nests were often abandoned in seemingly healthy condition during colony contraction periods. Some large trees had dense foliage that obstructed observation; for these, I climbed into the canopy to look for ants. Using this combination of techniques, quite small populations could be detected. Surveys were conducted twice yearly from 1986 to mid 1987, and every two months from July, 1987 till May, 1989.

The effect of tree density on distribution patterns was tested using a nearest neighbour technique (Greig-Smith, 1983). Trees were divided into three groups: trees which were occupied by ants on every survey, trees inhabited at least once during the study, and trees never occupied by ants. The distances from 60 randomly chosen trees within these categories to their nearest neighbours were measured, and compared using an analysis of variance. Preferences for particular tree species were examined by comparing the proportions of the total trees

of each species always, sometimes, and never occupied, for the most common species. The interactive effect of these two variables on nearest neighbour distances was examined using a 2 way analysis of variance.

3.3. Results

3.3.1. Distribution in Australia.

The presence and absence of *O. smaragdina* in 46 sites across northern Australia was mapped in figure 3.2. No colonies were recorded south of the tropics, with Broome, W.A. (17°57'S) the southern limit of distribution on the west coast, and Yeppoon, Qld (23°6'S) the southern limit on the east coast. Distribution in Queensland south of latitude 15°S was restricted to the coastal plain by the Great Dividing Range. The highest elevation where this ant was observed was 500 metres above sea level, west of Cairns (16°50'S).

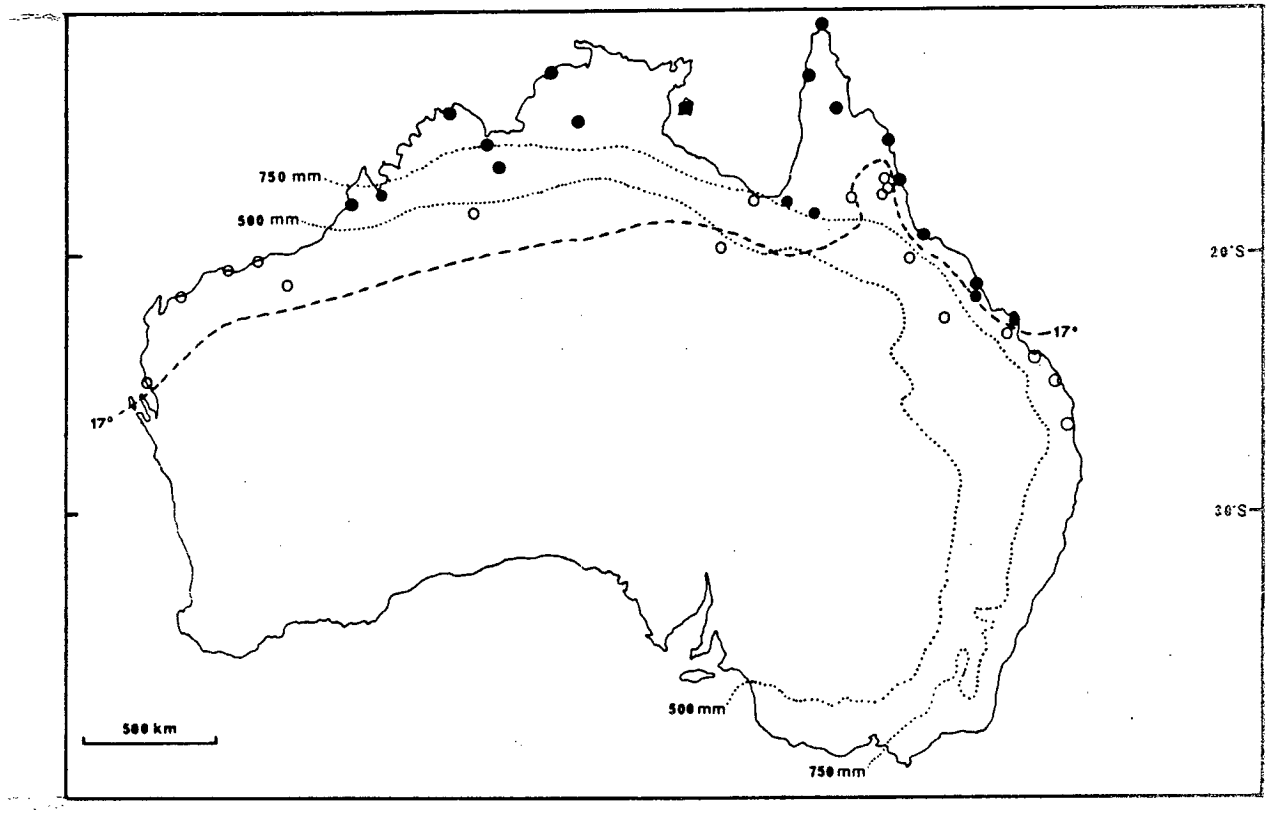
Isotherms and isohyets are shown on figure 3.2, but neither corresponds closely to the distribution of *Oecophylla*. The 17°C mean minimum temperature isotherm demarcated the distributional limits of this ant species reasonably well in eastern Australia, but extended too far south in western Australia. Similarly, the 500 mm average annual rainfall isohyet successfully separated sites with and without green tree ants in the west, but not in the east. Nor did any single temperature statistic (average, mean minimum, mean maximum annual temperature; number of frost days per annum) or rainfall variable (annual rainfall, number of rain days per year) appear to explain the

Figure 3.2. Australian distribution of *O. smaragdina*.

● Sites with *O. smaragdina*.

○ Sites without *O. smaragdina*.

500 and 750 mm mean annual rainfall isohyets and 17°C average minimum temperature isotherm are shown.



observed distribution pattern. When the data were plotted against rainfall and temperature in combination (figure 3.3a), much better separation between sites with and without ants was observed, with a curvilinear line of demarcation. To linearize this boundary, temperature and rainfall figures were converted to logarithms (figure 3.3b).

To determine which combination of climate parameters could best predict the observed distribution pattern, linear discriminant analyses were performed on various combinations of the transformed temperature and rainfall data. Mean minimum temperature (T_{min}) and average annual rainfall (R) were the most successful variables, correctly classifying 98% of the sites (Lokkers, 1986). The line of demarcation calculated by the discriminant analysis was:

$$4.26 \log(R) + 23.5 \log(T_{min}) - 42.4 = 0$$

This analysis demonstrates that a combination of high temperature and high rainfall was necessary to support populations of *O. smaragdina*. The curvilinearity of the boundary further suggests that either variable in isolation could limit distribution of this species at its lower extremes.

Some data published by Way (1954b) on the distribution of *O. longinoda* in eastern Africa was also entered onto the discriminant plot. All 6 sites (3 with and 3 without ants) were classified correctly by the discriminant function calculated for the Australian species.

Figure 3.3. Temperature and rainfall averages of sites with and without *O. smaragdina*. Townsille marked with asterisk.

Data for *O. longinoda* from African study by Way (1954b).

+ Sites with *O. smaragdina*. □ Sites without *O. smaragdina*.

△ Sites with *O. longinoda*. ▽ Sites without *O. longinoda*.

Figure 3.3a. Linear scales on axes

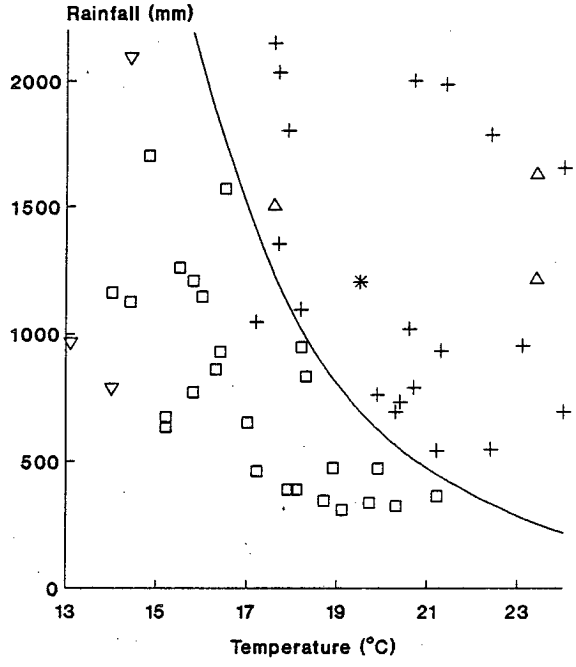


Figure 3.3b. Logarithmic scales on axes

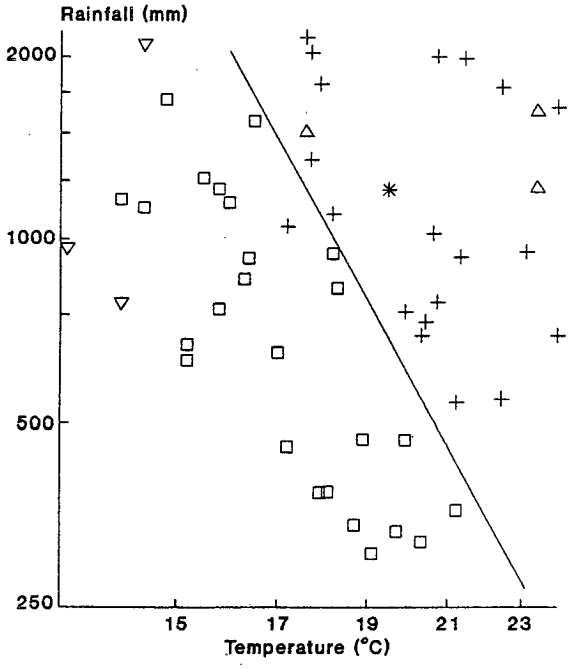
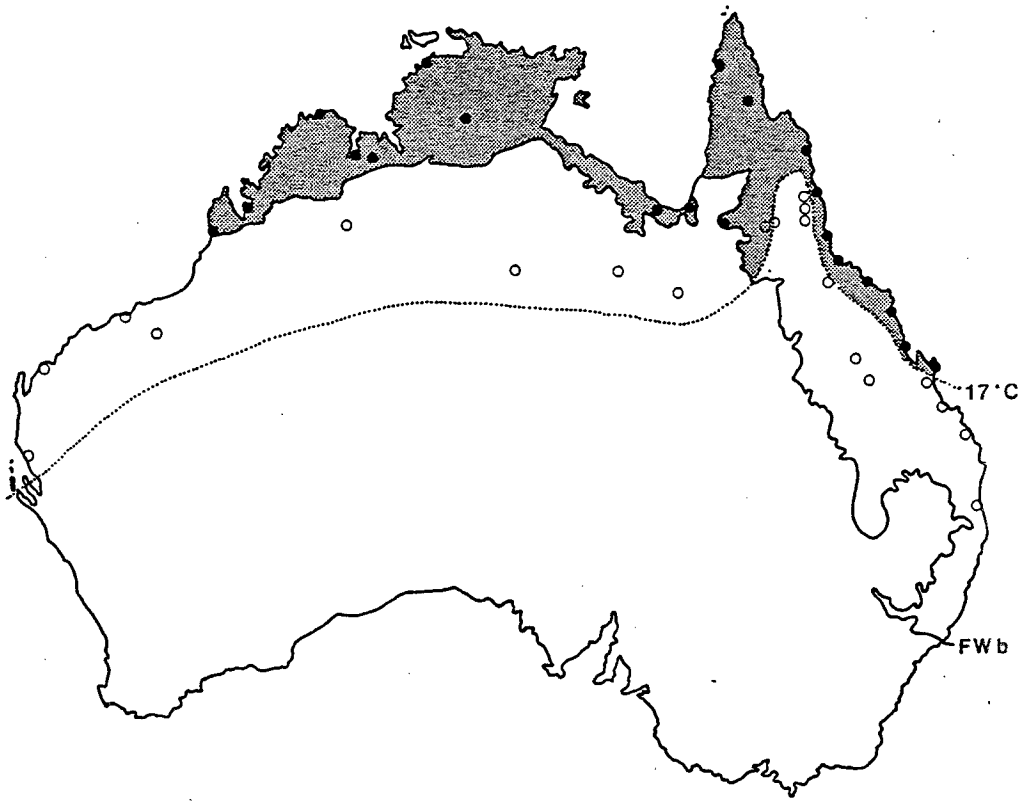


Figure 3.4. Australian distribution of *O. smaragdina* in relation to forest and woodland vegetation.

● Sites with *O. smaragdina*.

○ Sites without *O. smaragdina*.

Boundary of forest/woodland zone (FWb) and 17°C average minimum temperature isotherm marked. Stippled zones show areas with forest or woodland, and over 17°C average minimum temperature.



In section 4.3.2, the temperature threshold (i.e. the temperature at which the development of an ectothermic organism theoretically stops) of green tree ant larvae was calculated to be 16.8±0.7°C. This laboratory result is quite similar to the average minimum temperature of the coolest site where ants were observed (17.2°C at St. Lawrence). Analysis of distribution patterns in Townsville (section 3.3.2) demonstrated that tree density was a major limiting factor at this local scale. The occurrence of green tree ants was therefore compared to the distribution of forest and woodland vegetation, and the 17°C average minimum temperature isotherm (fig 3.4). Populations of *O. smaragdina* were present only in those areas with forest/woodland vegetation, and with an average minimum temperature exceeding 17°C.

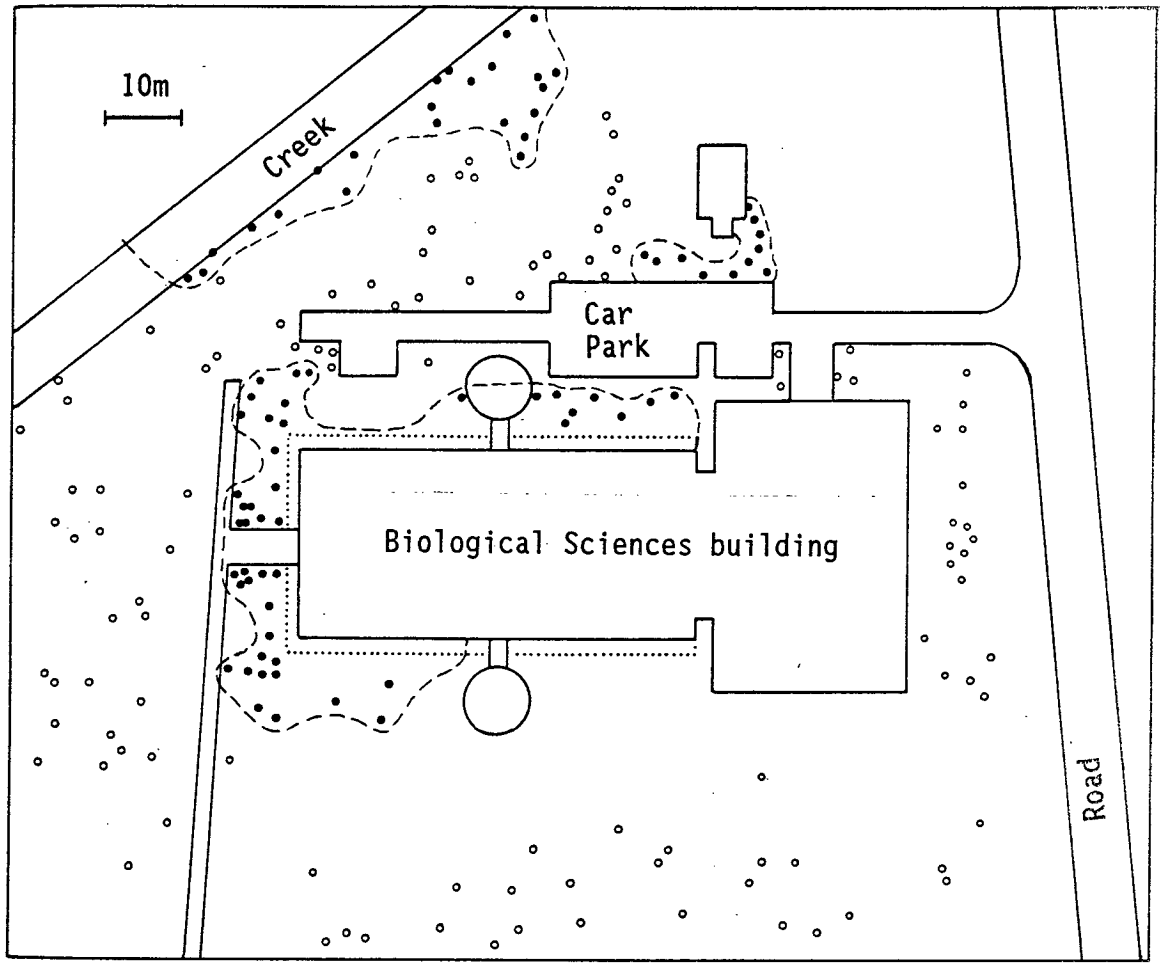
3.3.2. Distribution in Townsville.

In the Townsville district (marked on the discriminant plot with an asterisk), populations of the green tree ant were mainly restricted to the margins of watercourses and gullies, and swampy areas, where the thickest vegetation occurred. Colonies were also found in residential areas where people had grown large numbers of trees, such as mangos (*Mangifera indica*), poincianas (*Delonix regia*), and coconuts (*Cocos nucifera*). A striking example of this facultative usage of man-made habitat was observed around the biological sciences building at James Cook University. A map of the building and surrounding areas (figure 3.5) shows how colonies of *Oecophylla* have extended into the trees and gardens planted by the university groundspeople.

The distribution of ants in the trees of my Townsville study site (figure 3.6) was divided into 3 categories: core areas of trees

Figure 3.5. Distribution of ant colonies around biological sciences building, James Cook University.

- • Trees occupied by ants
- ◦ Trees not occupied by ants
- ⋯⋯ Garden bed surrounding building (used extensively by ants)
- - - - Colony boundaries



Legend for species found in Townsville study site.

Zizyphus mauritiana
Lophostemon grandiflorus
Pongamia pinnata
Eucalyptus platyphylla
Eucalyptus tessellaris
Eucalyptus papuana
Canarium australianum
Pleiogynium timorense
Melaleuca spp.
Elaeodendron melanocarpum
Drypetes lasiogyna
Pouteria sericea
Exocarpos latifolius
Acacia salicina
Lysiphyllum hookeri
Planchonia careya
Alphitonia excelsa
Gardenia ochreata
Ficus opposita
Cochlospermum gillivraei

Figure 3.6. Distributions of trees always, sometimes, and never occupied by ants in Townsville study site.

occupied every survey period, trees inhabited at least once during the study, and trees never occupied. Core areas occurred mainly along the creek, but some were also found in a band of high tree density in a low lying floodplain on the western side of the creek. No green tree ants were observed in the open eucalypt woodland to the east of the creek.

The mean nearest neighbour distances, with 95% confidence intervals, of trees in the three categories are given in figure 3.7. Statistics were calculated on square root transformed data, to normalise the Poisson distributed distance data typical of nearest neighbour analyses (Greig-Smith, 1983). An analysis of variance demonstrated a significant difference among the three categories ($F=46.4$, $df=2/177$, $P<0.0001$), with the smallest distance of 1.6 ± 0.18 metres between trees in core areas, and the largest of 3.37 ± 0.36 metres between trees never occupied by ants. Density is roughly inversely proportional to the square of nearest neighbour distance, so permanent ant occupancy was associated with areas of highest tree density, and ants were absent in areas of lowest vegetation density. This result is overly conservative, as the study site omitted the uninhabited, sparsely vegetated area to the east of the creek. Inclusion of this area would have increased the nearest neighbour distance (and thus decreased tree density) of the uninhabited tree category.

The proportions of trees in the three habitation categories also appeared to differ between tree species (figure 3.8). For tree species closely associated with the creek, such as *Pongamia pinnata*, *Lophostemon grandiflorus*, and *Melaleuca spp*, a large proportion (about 50%) were permanently occupied by ants. Trees which extended further from the creek, such as *Zizyphus mauritiana* and *Eucalyptus spp*, were less frequently occupied on a permanent basis.

Figure 3.7. Nearest neighbour distances of 3 tree categories

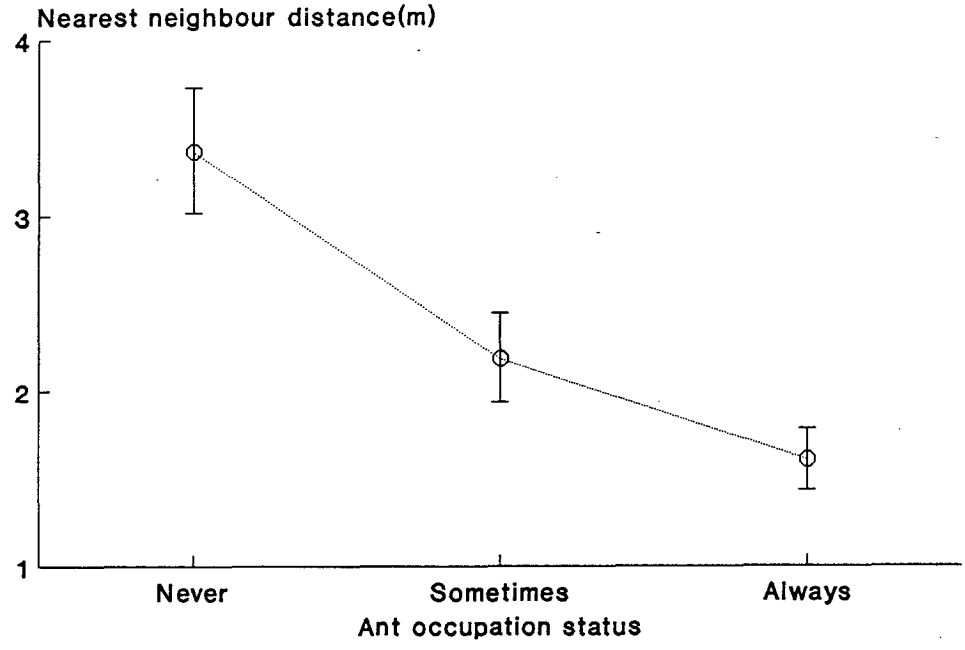
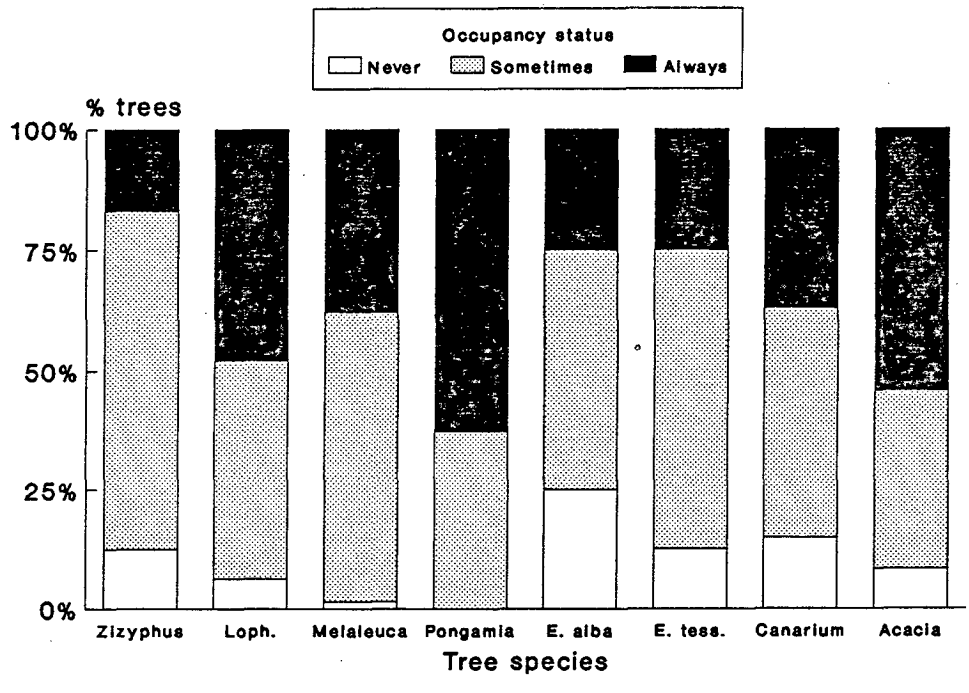


Figure 3.8. Tree species preferences



However, this apparent preference for species was probably an artifact of varying inter-tree distances between different species of trees. An analysis of variance demonstrated that the average distance to the nearest tree varied between the three most common tree groups, *Zizyphus mauritiana*, *Lophostemon grandiflorus*, and *Eucalypt spp* (F=5.3, df=2/171, P=0.006). In particular, *L. grandiflorus* individuals tended to be found in denser vegetation than did individuals of the other 2 species.

To test if tree groups influenced ant occupancy above and beyond the indirect effect of occurring in varying vegetation density, nearest neighbour distances of the different tree group and occupancy status categories were compared using a factorial analysis of variance. Distances varied only with respect to the level of occupation by ants (table 3.1). The non-significance of the interactive term (tree group by occupancy status) implied that these tree species were not influencing ant distribution independently of their varying nearest neighbour distances. In other words, the apparent preference of green tree ants for certain tree species could be explained solely by the fact that these species occurred in areas of different tree density.

Table 3.1: ANOVA table for nearest neighbour distances of trees.

Convention used in listing sources of variation:
A*B factors A and B crossed.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Species	2	0.3896	0.1948	0.83	0.4400
Occupancy status	2	15.852	7.9258	33.57	0.0001
Species*Occupancy	4	1.3051	0.3263	1.38	0.2424
Error	165	38.957	0.2361		
Total	173	60.298			

3.4. Discussion.

The distribution of *O. smaragdina* in Australia was successfully delimited by a curvilinear combination of temperature and rainfall. The importance of temperature in controlling the occurrence of ants has been well documented (e.g. Brian, 1965; Brown, 1973; Greenslade and Thompson, 1981). Brown reasoned that radiant heat, rather than temperature *per se*, was the limiting factor, as ants are absent above 2300 metres in closed canopy forests, but extend above 4000 metres on treeless slopes. Due to the attenuation of solar radiation in shady conditions, temperatures of ground-dwelling ants and their nests are reduced, impeding efficient foraging, and/or brood development. Some species which normally occur in forest habitats (such as *Iridomyrmex cordatus*) can extend their altitudinal limits by nesting in open, sunny sites (Greenslade, 1972).

Arboreal nesting ant species, such as *Oecophylla*, cannot utilize the warming effect of radiant heat on the surface soil. However, in closed forest, the upper canopies would receive much higher levels of insolation than the ground. Weaver ants generally construct their nests in sunny locations (Leston, 1973; Vanderplank, 1960; Way, 1954a; Weber, 1949). In Zanzibar cocoa trees, nests were concentrated in the southern side of the canopy in winter, and in the northern side in summer. Vanderplank (1960) correlated this migration to the position of the sun, maximizing insolation levels throughout the seasons. Way (1954a) suggested that nests were moved for shelter from the prevailing wind.

O. smaragdina workers showed wider tolerances to variation in temperature than the 3 other dominant ant species occurring in the Solomon Islands (Greenslade, 1972). Workers of this species were active

at temperatures as low as 12°C, although forager numbers were substantially reduced (chapter 6). However, the brood of weaver ants is much more vulnerable to cold temperatures. Data on the development of the first brood of colony founding queens of *O. longinoda* (Vanderplank, 1960; shown in fig 4.6) indicated a threshold temperature of about 20°C for larvae and pupae. In Townsville populations, thresholds varied between brood stages (chapter 4). The highest (and thus limiting) threshold temperature, of 16.8±0.7°C, was during larval development. These theoretical figures (calculated from the regression of temperature and developmental rate when rate = 0) must be extrapolated to field distributional observations cautiously (Messenger, 1959). The correspondence of the 2 measures was surprisingly good, however, with all recorded sites with weaver ants having an average minimum temperature over 17°C.

The distributions of many animal and plant species can be best explained by a combination of temperature and moisture (e.g. Messenger, 1959; Odum, 1982; Swincer, 1986). Most studies of climatic limitations of ant distribution have considered only temperature (and the related factor, radiant heat). The importance of the rainfall regime on the occurrence of ants can be inferred from the distinctly different faunas of mesic and xeric tropical environments (Brown, 1973). Moisture probably mainly influences ant distributions indirectly through vegetation changes, although direct effects undoubtedly occur (e.g. through flooding of nest sites). As mentioned earlier, the dense canopies of moist forests can limit ground dwelling ants by reducing insolation levels. The distributions of ant species which tend homopterans for part of their food intake are dependent on vegetation which will support homopteran populations. Various arboreal ants, such

as *Oecophylla* and some *Crematogaster* species, construct nests only in trees, and forage primarily in the canopy. Some ant species have become totally dependent on particular plant species, in obligate mutualisms. Colonies of the acacia-ant, *Pseudomyrmex spp*, for example, occur only on swollen-thorn acacias, which provide nest sites, and specialized food bodies for the ants.

A plethora of models relating vegetation distribution patterns to temperature and moisture indices have been developed over the past 50 years. One of the most comprehensive of these is the Holdridge life zone system, which uses biotemperature and precipitation climatic data to divide the world into over 100 vegetation types, or "life zones" (Holdridge *et al*, 1971). Unfortunately, biotemperature values cannot be exactly calculated from average temperature data, but the sites inhabited by green tree ants could be approximately assigned to the tropical and subtropical life zones of rain forest, wet forest, moist forest, and dry forest.

Townsville, with an average temperature of 24.1°C and mean annual rainfall of 1200 mm, lies towards the cooler boundary of the tropical dry forest zone. The occurrence of *O. smaragdina* in this region was limited to areas of higher tree density, where interconnecting tree canopies facilitated movement of workers throughout the colony (which may extend over 100 trees). Taylor and Adedoyin (1978) observed that *O. longinoda* also prefers an interlocking canopy.

In tropical tree crops, such as cocoa and coconuts, the distribution of weaver ant colonies was not affected by tree or canopy density, but was limited by the occurrence of a number of other arboreal ants (e.g Brown, 1959; Greenslade, 1971a; Majer 1976a,b,c; Room, 1971). These species, termed dominants by Leston (1973), could

exclude other dominant ants from their territories, producing a mosaic pattern of ant colonies throughout the plantation. The mosaic distribution of dominants is regulated by intra-specific and inter-specific competition between dominants, habitat preferences, and climate (Majer, 1976a,b,c). In some studies, *Oecophylla* colonies appeared to be competitively inferior to the other dominants (e.g. Brown, 1959; Greenslade, 1971a). The competitive abilities of each dominant probably vary substantially with changes in factors such as vegetational succession, canopy condition, and seasonal weather patterns. For example, Majer (1976a) found the territories of *Crematogaster depressa*, which builds carton nests, increased at the expense of the leaf nesting species, *O. longinoda* and *Macromischoides aculeatus*, during the dry sunny season. The original pattern of territories was restored following rainy weather. Majer correlated these fluctuations to a reduction in cocoa canopy density during the dry period. Seasonality in colony structure of *O. smaragdina* will be considered in more detail in later chapters.

Ant mosaics have been observed in the arboreal ant faunas of cocoa plantations in Ghana, Cameroon, Nigeria, Zanzibar, New Guinea, and Brazil, and coconut plantations in Zanzibar and the Solomon Islands. These areas lie in the tropical wet forest and rainforest life zones, with more moist, equatorial climates than Townsville. Greenslade (1972) found that the temperature and moisture tolerances of *O. smaragdina* were greater than those of the other 3 dominant ants in the Solomon Islands (which is geographically quite close to north Queensland). The absence of a mosaic pattern of ants in the present study site was thus probably due to the inability of other potentially dominant ant species to cope with the Townsville climate.

Green tree ants showed no preferences between the 3 commonest tree groups in the study site, *Zizyphus mauritiana*, *Lophostemon grandiflorus*, and *Eucalyptus spp.* Way (1954a) observed that *O. longinoda* seldom nested in trees with leaves too inflexible to bend together, or very small leaves. The large leaves of plantains, the narrow leaves of oil palms, and the small leathery leaves of cashews are also not utilized for nest construction (Taylor, 1977). In Townsville, nests were rarely seen in *Lysiphyllum hookeri* (round bipinnate leaves 1-2 cm in diameter), *Leptospermum spp.* (thin 0.5 cm by 5 cm leaves; plate 1), and *Casuarina spp.* (minute leaves in whorls around branchlets). However, ants regularly foraged within these trees, and used them as pathways between trees with nests, when they occurred within the territory of a colony. The possibility that these trees were occupied less frequently by ants was untested, as insufficient numbers occurred in the study site to allow statistical analysis. The 3 tree species which were tested all had suitable leaves for nest construction, but the numbers of leaves available for nest building varied markedly throughout the year. Seasonal changes in the numbers of nests in *Z. mauritiana* trees are examined in chapter 5.

4. EARLY COLONY DEVELOPMENT.

4.1 Introduction.

Two principal methods of reproduction have developed in the family Formicidae (Brian, 1965). Colonies of most species periodically produce sexual forms that mate, disperse, and begin new colonies. In some species, colonies may divide into two parts, each with workers, brood, and at least one queen.

Colony budding is a gradual process of colony division seen in ant species whose colonies have many queens (i.e. are polygynous), such as *Monomorium pharaonis* (Peacock and Baxter, 1950), and *Iridomyrmex purpureus* (Duncan-Weatherley, 1953). As the colony grows, new nests "bud" out from the parent nest, with nests often retaining close links. Some monogynous species, such as *Eciton spp.* (Schneirla and Brown, 1952), undergo periodic colony fission, a much more dramatic splitting of the parent colony into two distinct colonies, each with one queen. Ledoux (1950) and Bhattacharya (1943) observed colony fission in colonies of *Oecophylla longinoda*, and *O. smaragdina*, respectively, and stated that queenless colony fragments would adopt new queens. All other workers, however (Way,1954a; Vanderplank, 1960; Crozier, 1970; Greenslade, 1971b; Hölldobler and Wilson, 1977b; my own observations), have found no evidence of fission in this monogynous genus, with queenless fragments producing only male sexuals, before dying out.

In most species which release sexuals, both males and females are winged, and thus have potentially much higher dispersal capabilities (Wheeler, 1910; Brown, 1973). Production and release of sexuals by conspecific colonies is usually closely synchronized, using either

environmental cues such as temperature and moisture (Brian, 1977; Gibbs and Leston, 1970; Wheeler, 1910; Wilson, 1963), or endogenous rhythms (McCluskey, 1958), or both. This synchronization of release allows genetic mixing between colonies (Wheeler, 1910; Wilson, 1963), and may act to swamp the capacity of predators, thus ensuring the survival of some founding queens. The release of sexuals is also presumably timed to coincide with environmental conditions most conducive to survival of the queens and their brood (Greenslade, 1971b, 1972).

After mating, dispersal, and location of a suitable nest site, a queen rears her first brood, either using food collected by herself (in Myrmeciines and most Ponerines: Wilson, 1971), or using food reserves stored in the fat body and wing musculature of the queen's body (claustral foundation). The initial brood may be produced by one queen (haplometrosis) or by a group of cooperating queens (pleometrosis). In many pleometrotic species, group founding is facultative, not obligatory. The number of queens in founding colonies of *Myrmecocystus mimicus* range from 1 to 9 (Bartz and Hölldobler, 1982), and from 1 to 7 in *Iridomyrmex purpureus* (Hölldobler and Carlin, 1985). Suggested advantages of group founding in pleometrotic species include: allowing a bigger and better nest to be constructed (Peeters and Anderson, 1989); improved egg production and survival (Bartz and Hölldobler, 1982; Markin *et al*, 1972); and faster brood development (Ledoux, 1950; Rissing and Pollock, 1988; Wilson, 1963).

Ant development, from egg to adult, is easiest to observe at the founding stage, when brood numbers are low, and no adult worker ants are present. A number of researchers have examined developmental rates and/or survival of the founding brood (e.g. Brian, 1951; Ito *et al*, 1988; Ledoux, 1950; Vanderplank, 1960), but little is known about the

effects of environmental factors, such as temperature and moisture.

Temperature has a major effect on the development of ectothermic organisms (Uvarov, 1931). The developmental rate (=1/developmental time) of an insect is typically proportional to temperature over a certain range. As temperatures fall below this range, the rate asymptotically approaches zero. Rising above this range, developmental rate reaches an optimum, and then falls off sharply. The two extremes usually also cause high mortality levels. A plethora of models relating developmental rate to temperature have been devised (reviewed by Wagner *et al*, 1984), but linear modelling using the proportional range of the curve is the simplest, and most widely used approach (e.g. Campbell *et al*, 1974; Jones *et al*, 1987; Messenger, 1959).

In this study, the development of the first brood of founding queens of *O. smaragdina* was examined. The effects of temperature on developmental rate of brood (using a linear model), and the success of founding queens in rearing brood were recorded. Some data on pleometrotic colony foundation were also collected.

4.1. Methods.

Alate queens of *O. smaragdina* are produced during the wet season months from November to February, and are released from nests after rainy periods (Greenslade, 1971b; Vanderplank, 1960; Way, 1954a). Within a few days, the newly released queens seek out a protected site in a tree canopy, usually a leaf rolled into a partial tube, or a group of tightly clustered leaves. By searching through such patches of foliage after rain, I collected varying numbers of alate, or recently dealated queens before they had laid any eggs. Occasionally, large

swarms of queens were released (e.g. in Tippett Street, Townsville, thousands of queens were released after rain in February, 1985), and a large number of queens could be obtained. Some queens were also brought to me by other students and staff of James Cook University.

To observe the development of the first brood produced by these colony-founding queens, they were placed in artificial nest sites of two designs. The first artificial nests were 50 ml glass vials with lids vented by fine gauze. Humidity was maintained by moistening a small piece of cotton wool in the lid every day. Later nests incorporated a permanent water supply, which was sealed into the end of longer 100 ml vials with a cotton plug. This reduced disturbance to the queens by eliminating the need for daily moistening.

The queens in their nest vials were reared in constant temperature cabinets (20, 22, 27,and 30°C) or constant temperature rooms (24 and 30°C) with a photoperiod of 12 hours light, 12 hours dark. The nests were shaded to resemble the light levels found in their natural leaf nest sites. The numbers of queens reared at various temperatures are shown in table 4.1. In the 1985 trials, numbers of eggs, larvae, and pupae were recorded until the first adult workers eclosed. In later years, only presence of each stage was recorded.

Table 4.1: Numbers of colony founding queens used in constant temperature development trials during 1985 to 1988.

Year	Number of queens reared at given temperatures (°C)					
	20	22	24	27	30	35
1985	13	0	12	13	12	12
1987	9	9	0	0	0	0
1988	0	0	8	11	8	8

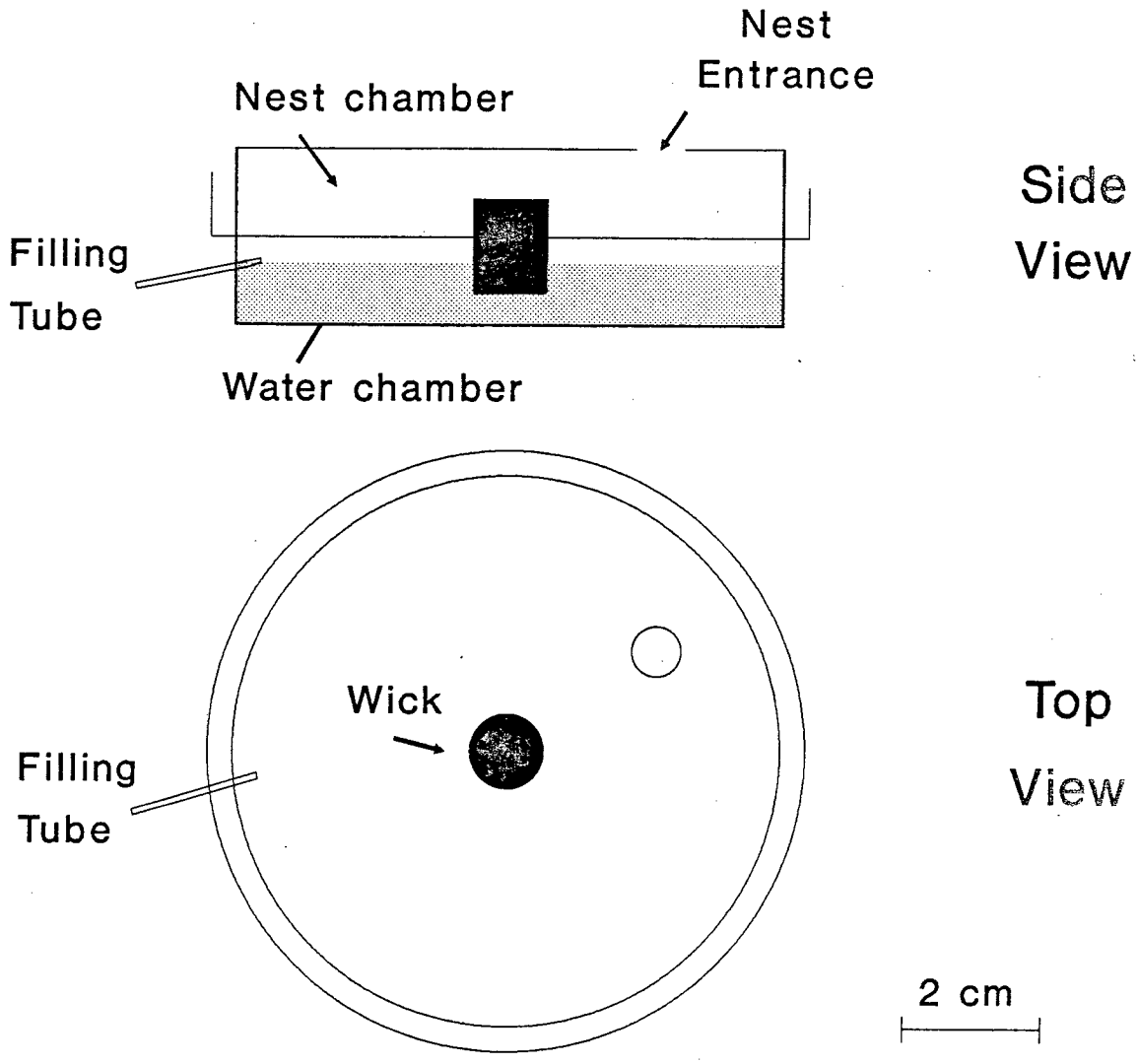
The rate of development from egg to larva was calculated for each queen as the inverse of the number of days taken from oviposition of the first egg to hatching of the first larva. Rates were similarly determined for first larva to first pupa, and first pupa to first adult. These values were plotted against incubation temperature for each stage, and regressions calculated for the linear portions of the curves. Confidence intervals of the threshold temperatures (the X-axis intercept, where development theoretically reaches 0) were calculated as described by Campbell *et al* (1974).

Twenty nests were established with multiple queens, ranging in number from 2 to 5. Unfortunately, these and all the other queens which were incubated in the 27°C cabinet in 1985 were killed by an unidentified pathogen before their brood had developed to the pupal stage. Insufficient queens were collected in subsequent years to repeat this trial, but at least one nest of 2 queens was raised at each of the temperatures used in 1987.

Three to five days after the first adult workers emerged, the nests were transferred to various further trials. Thirty fledgling colonies were placed in tree canopies from which they were originally collected. Another 30 were established outdoors in potted plants of 2 species, *Cassia mimosoides*, and *Mangifera indica*. These young colonies were (supposedly) protected from ants and other terrestrial predators by moats of water. The remainder were maintained in constant temperature rooms at 24°C or in the laboratory. The colonies were fed on the artificial ant diet devised by Bhatkar and Whitcomb (1970), 10% honey solution and freshly killed insects.

When colonies outgrew their original nests, larger artificial nests were provided. These nests, shown in figure 4.1, were built using

Figure 4.1. Design of artificial ant nest.



plastic petri dishes of 9 cm diameter. The lower chamber was a water reservoir, with a tube attached for refilling. A cotton wick from the water reservoir maintained humidity and provided water for the upper nest chamber. Ant access into the nest was provided by a 7 mm hole drilled in the roof. A removable dark green cover simulated the natural light intensity and colour of a leaf nest, while allowing the nest interior to be observed when necessary.

Aggression between queens was examined using alate queens which were mature (as gauged by the development of the abdomen colour from an initial brown to a pea-green colour), but had not been released from the parent colony. Queens from the same nest, different nests from the same colony, and different colonies, were collected. Twenty-five queens were paired with queens from the same nest, 25 with queens from the conspecific nest, and 25 with queens from the alien nest. Each pair was housed in a 100 ml vial nest, which had been thoroughly cleaned to remove the odours of any previous inhabitants. Nests were observed twice daily for signs of antagonism. Occasionally, fighting between queens was directly observed, but more commonly, evidence of aggression was inferred from damage to one or both queens, such as severed limbs, and torn abdominal segments.

4.3. Results.

4.3.1. Phenology of 1st brood production.

Queens which successfully reared brood through to adult workers showed consistent phenological patterns of brood development at each

temperature. Even queens reared at 20°C, and which developed brood only to the larval stage, displayed a uniform developmental history. These patterns were examined by plotting the average numbers of eggs, larvae, pupae, and adults produced by successful queens at the temperatures, 20, 24, 30, and 35°C, over time (figures 4.2-4.5a). Data with 95% confidence intervals were also plotted (figures 4.2-4.5b).

Within 5 to 10 days after dealation, all queens had produced a relatively uniform egg batch of 25 to 40 eggs. However, further development varied greatly at different temperatures.

At 24°C (figure 4.2), brood numbers showed a rapid initial climb in the first 10 days, when the queens laid an average batch of 31.5±3.6 eggs. After this period of high production, numbers rose much more slowly, with only about 12 brood added over the following 25 days. Although the queen certainly reduced her egg output over this period, this low rate of increase may also be due in part to cannibalism by the larvae, or the queen. Larvae began hatching within 11 days, and larval numbers peaked after 23 days with an average of 28.7±4.1 larvae. Egg levels simultaneously dwindled to only 6.6±1.3, and remained low until emergence of the first adult worker, on day 39. The first pupae appeared after 23 days, and steadily rose in numbers up to an average of 18.5±1.5, after 38 days.

Advanced larvae were used by the queen to produce silk for an enclosed brood chamber inside the nest vial. Silk production began 11.4±3.1 days after the first larva hatched, when maximum larval length was 54.7±6.5 mm.

At 30°C (figure 4.3), much faster development was observed (see section 4.3.2), with an egg batch of 36.1±4.6 laid after 5 days, first larvae hatching within 8 days, first pupae after 17 days, and first

Figure 4.2. Phenology of first broods of queens at 24°C.

Figure 4.2a. Phenology of 1st broods of 10 queens at 24°C

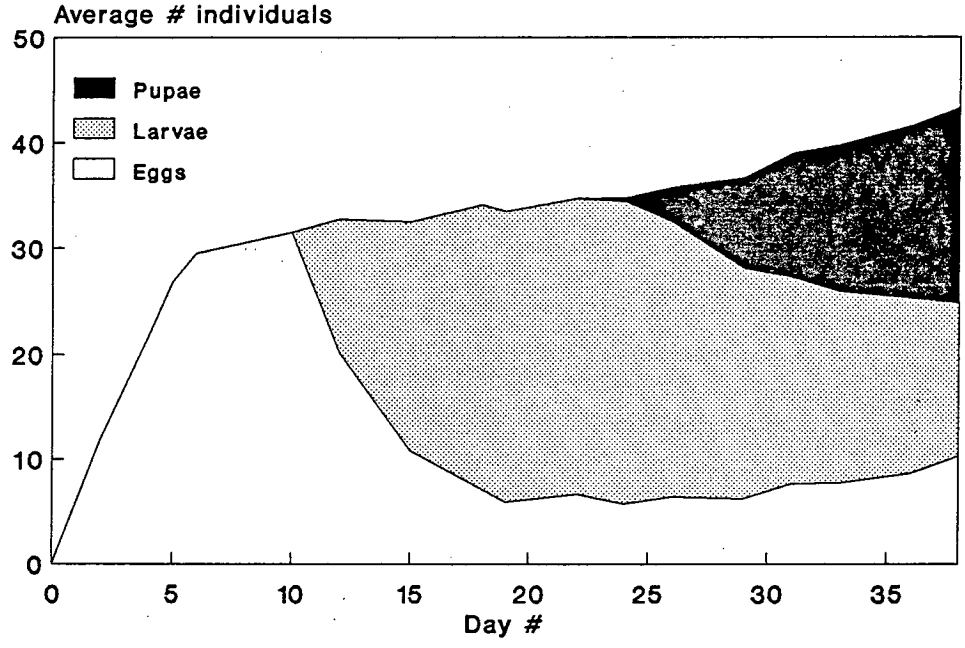


Figure 4.2b. Phenology of 1st broods at 24°C (with 95% confidence limits)

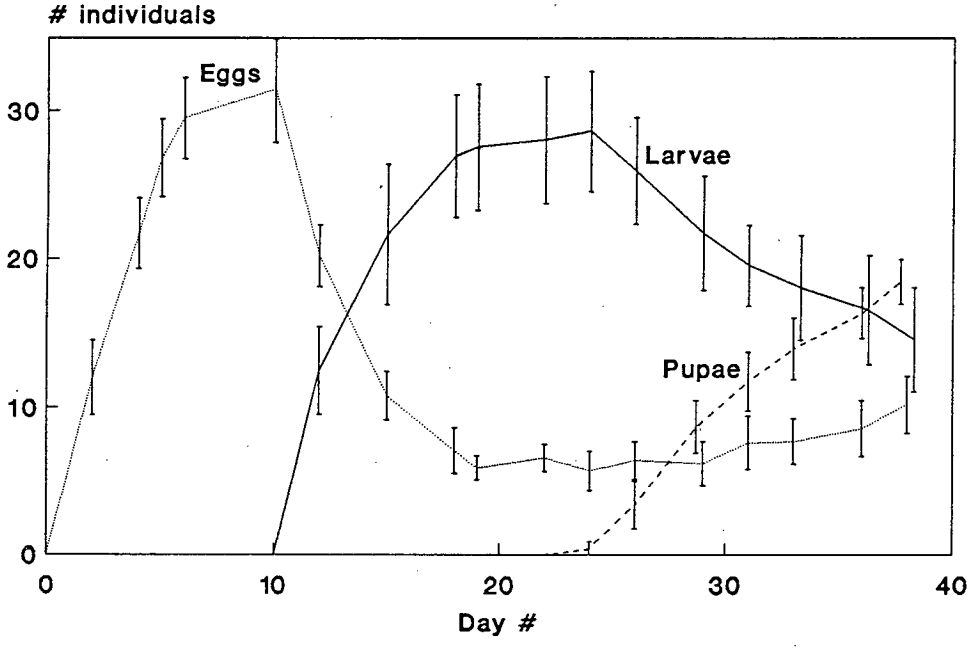


Figure 4.3. Phenology of first broods of queens at 30°C.

Figure 4.3a. Phenology of 1st broods of 7 queens at 30°C

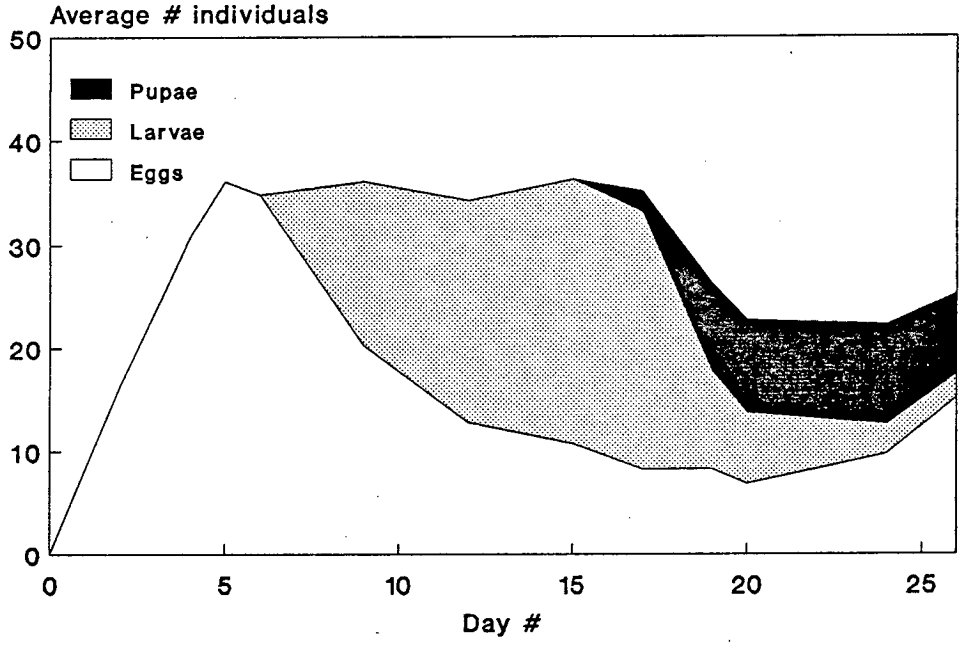


Figure 4.3b. Phenology of 1st brood at 30°C (with 95% confidence limits)

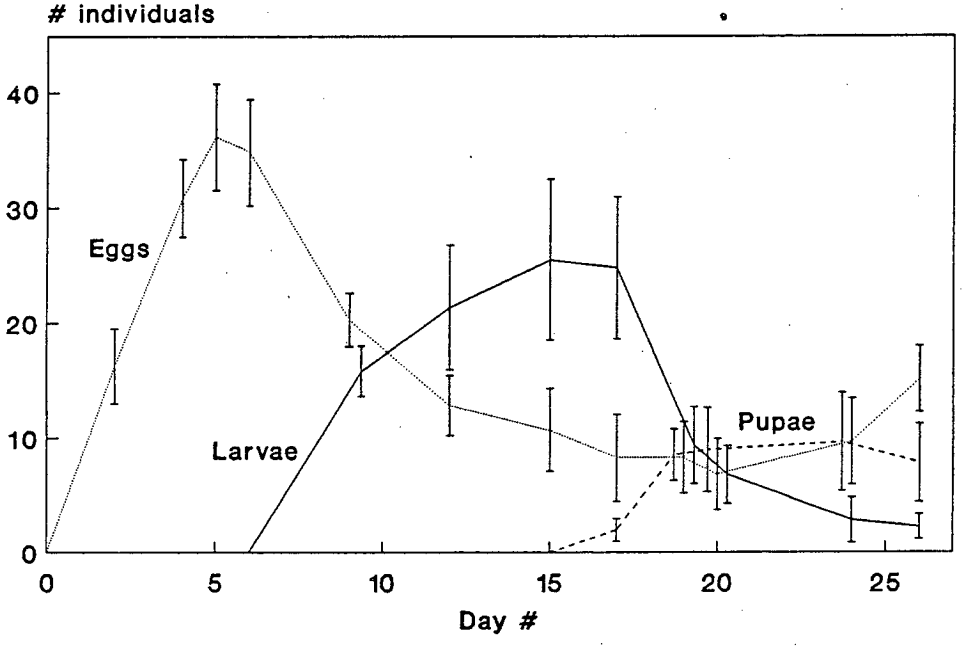


Figure 4.4. Phenology of first broods of queens at 35°C.

Figure 4.4a. Phenology of 1st broods of 7 queens at 35°C

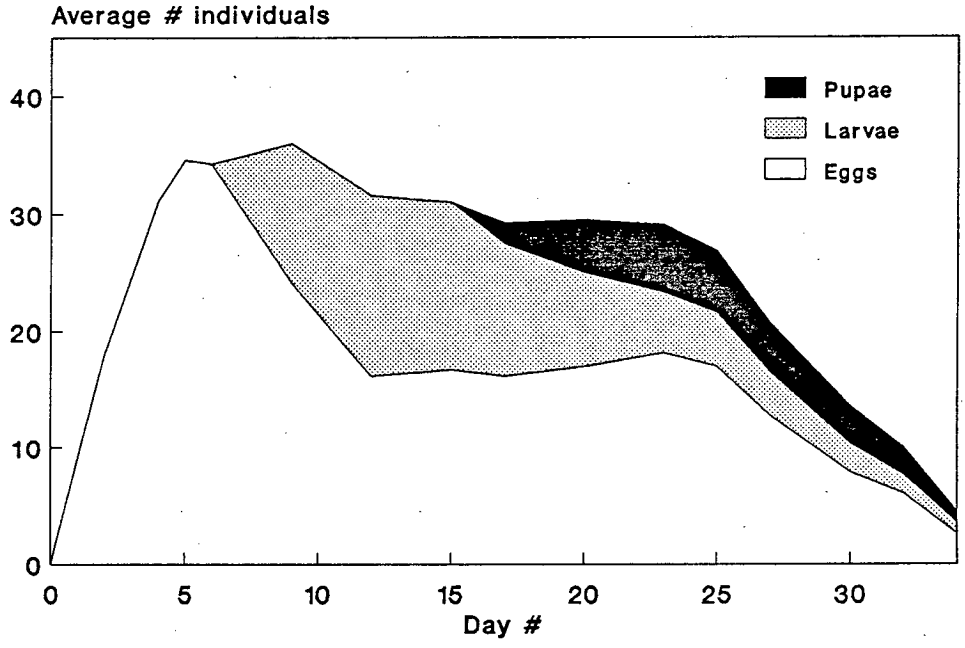


Figure 4.4b. Phenology of 1st broods at 35°C (with 95% confidence limits)

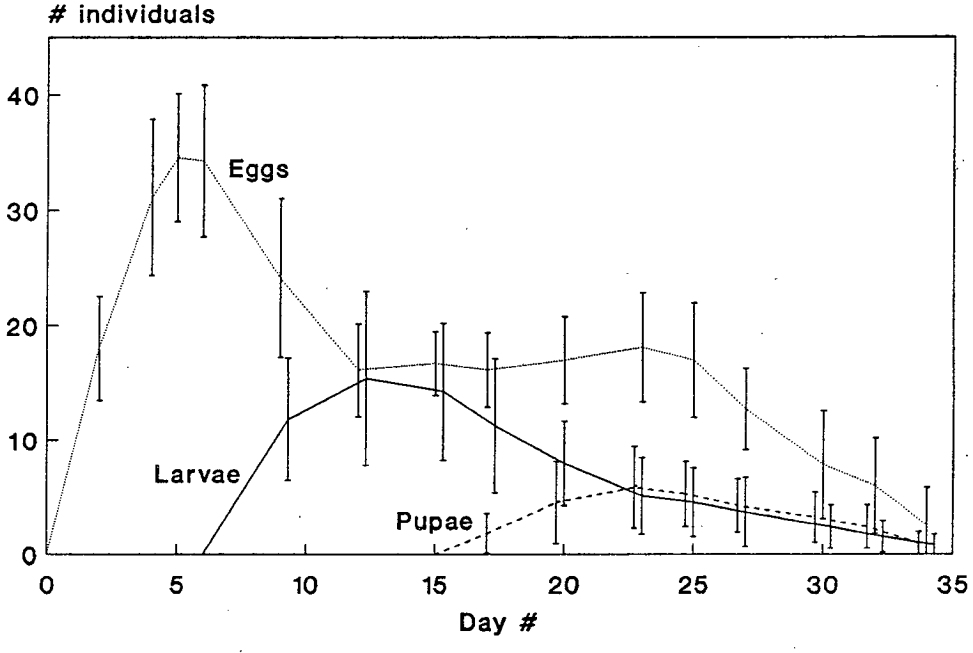


Figure 4.5. Phenology of first broods of queens at 20°C.

Figure 4.5a. Phenology of 1st broods of 6 queens at 20°C

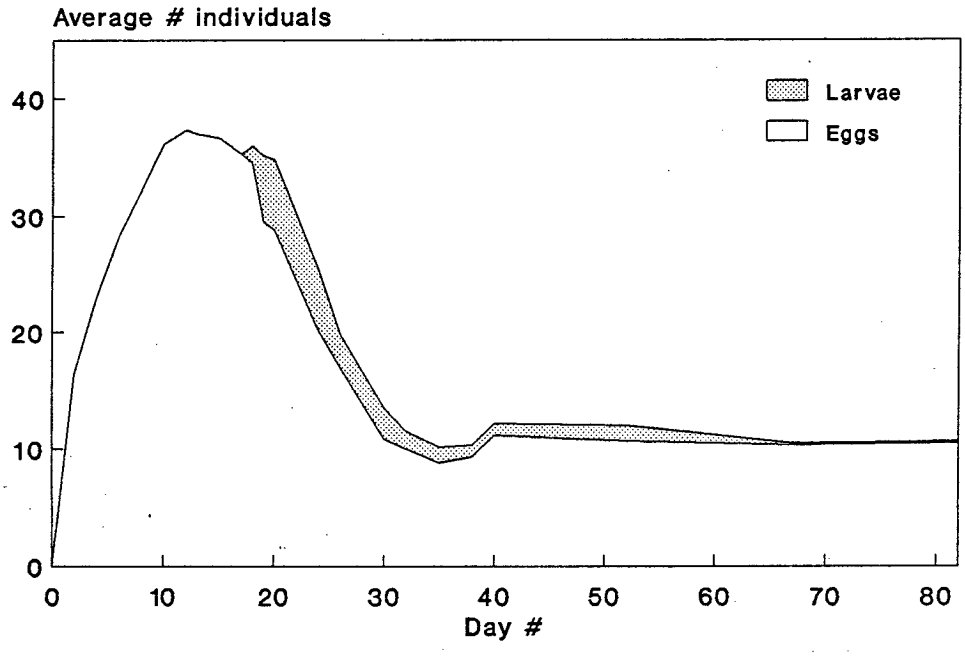
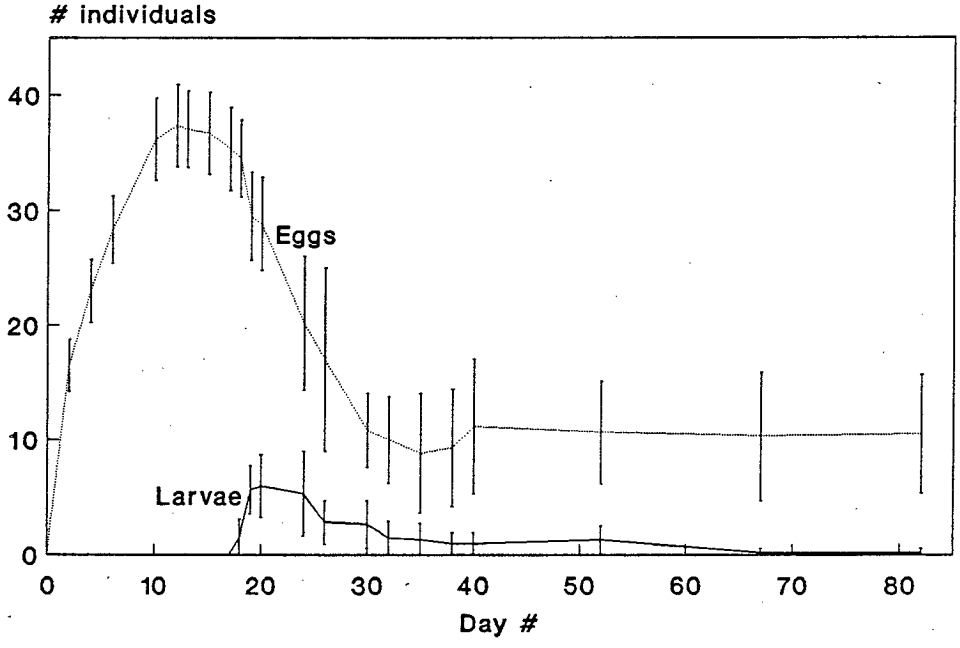


Figure 4.5b. Phenology of 1st broods at 20°C (with 95% confidence limits)



adults within 28 days. The mean maximum larval number of 25.6±7 occurred on day 15, and greatest pupal number of 9.7±4.3 after 24 days. Brood levels resembled those seen at 24°C, until day 18. With the appearance of pupae at this time, a significant drop in average brood numbers was observed, from 35.1±5.2 on day 17, to 22.7±6.0 on day 20 ($t=7.91$, 6df, $P=0.0002$). This marked drop was due largely to a crash in larval numbers, from 24.9±6.2 to 9.4±3.4 larvae, which was only partially offset by a corresponding gain of 9.7±2.5 pupae. Total brood numbers remained at this reduced level until the emergence of first adults. An increase in egg numbers by some, but not all, queens was observed at this stage.

Early development of brood at 35°C resembled that at 30°C, with 34.3±6.5 eggs after 5 days, and first larvae hatching within 8 days (figure 4.4). Fewer larvae hatched, however, with a maximum of 15.4±7.6 larvae, on day 12. Fewer pupae were also produced, with a peak of 5.9±3.6 after 23 days, while egg numbers remained higher than at lower temperatures, with 18.1±4.8 eggs on day 23. Total brood numbers slowly declined from a maximum of 36±10.7 on day 10 to 29.1±9.3 on day 23, then dropped more quickly to only 4.4±5 after 34 days. Only half of the queens at 35°C successfully produced adults, and these only produced a few which died within 5 days. After 37 days, no queens had surviving brood, and all were dead by day 40.

No queens at 20°C successfully reared adult workers, and few produced pupae (figure 4.5). An egg batch averaging 37.3±3.6 eggs was laid within 12 days, and the first larvae hatched after 16 days. Larval numbers remained very low throughout, with a maximum of 6±2.7 on day 20. A few queens produced a solitary pupa which died soon afterwards. Many brood died, with total numbers dwindling from a peak of 37.3±3.6

on day 10 to only 13.5±3.4 on day 30. Brood numbers were not regularly recorded past 40 days, but remained very low until day 85, when 10.5±5.2 brood remained. The surviving queens were then moved to 30°C, where some successfully produced adults.

4.3.2 Developmental rates.

The rates of offspring development for each queen from first egg to hatching of the first larva, first larva to first pupa, and first pupa to first adult were plotted against incubation temperature in figure 4.6.

The relationship between temperature and developmental rate of the egg stage was linear from 20°C to 30°C, but levelled out to an maximum value of about 0.14 at 35°C (fig 4.6a). A regression analysis was performed on the 36 data values in the temperature range 20-30°C; a linear relationship with temperature explained 91% of the variation in developmental rate. The derived equation was:

$$DR = -0.0677 + 0.00608\ T$$

where DR was developmental rate (/day)

and T was temperature (°C).

This equation gave a threshold temperature (when developmental rate theoretically reaches 0) of 10.3°C, with 95% confidence limits of ±1.4°C.

Developmental rate of the larval stage showed a similar linear relationship with temperature from 20°C to 30°C, and dropped slightly from 30°C to 35°C (fig 4.6b). 89% of the variation in developmental

Figure 4.6a. Developmental rates from egg to larva

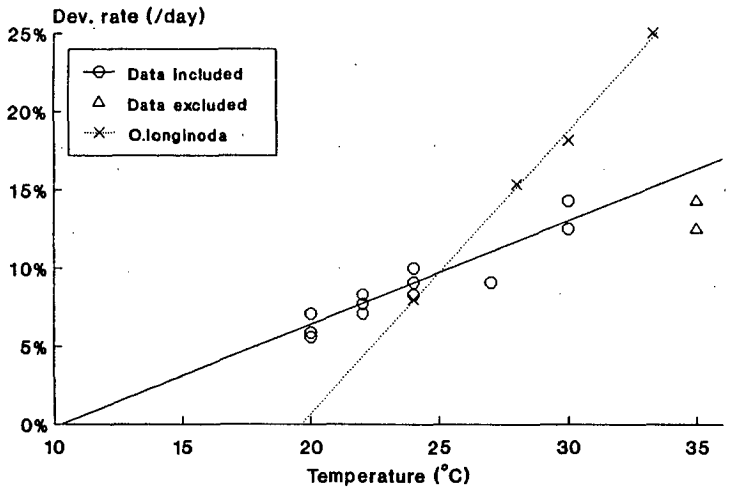


Figure 4.6b. Developmental rates from larva to pupa

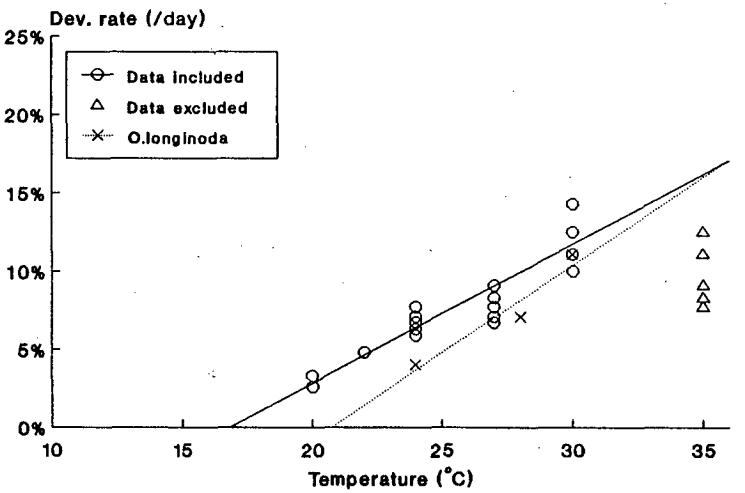


Figure 4.6c. Developmental rates from pupa to adult

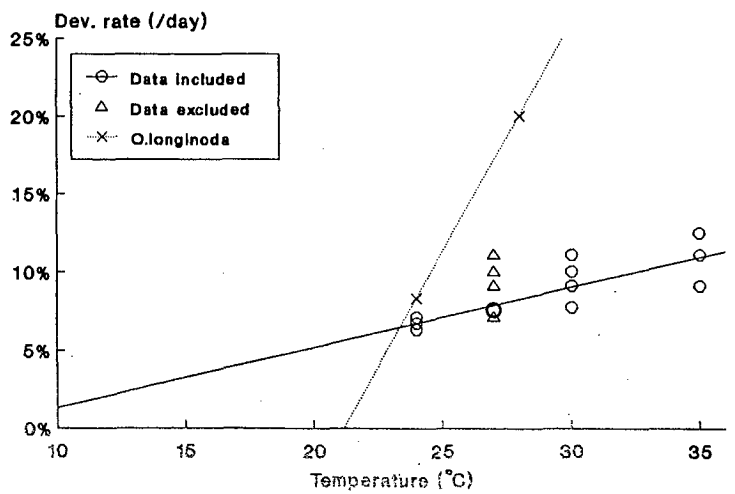


Figure 4.6d. Developmental rates from egg to adult

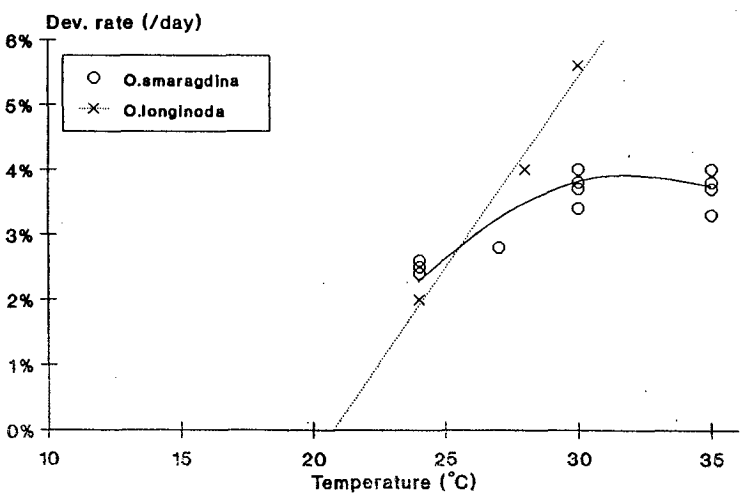
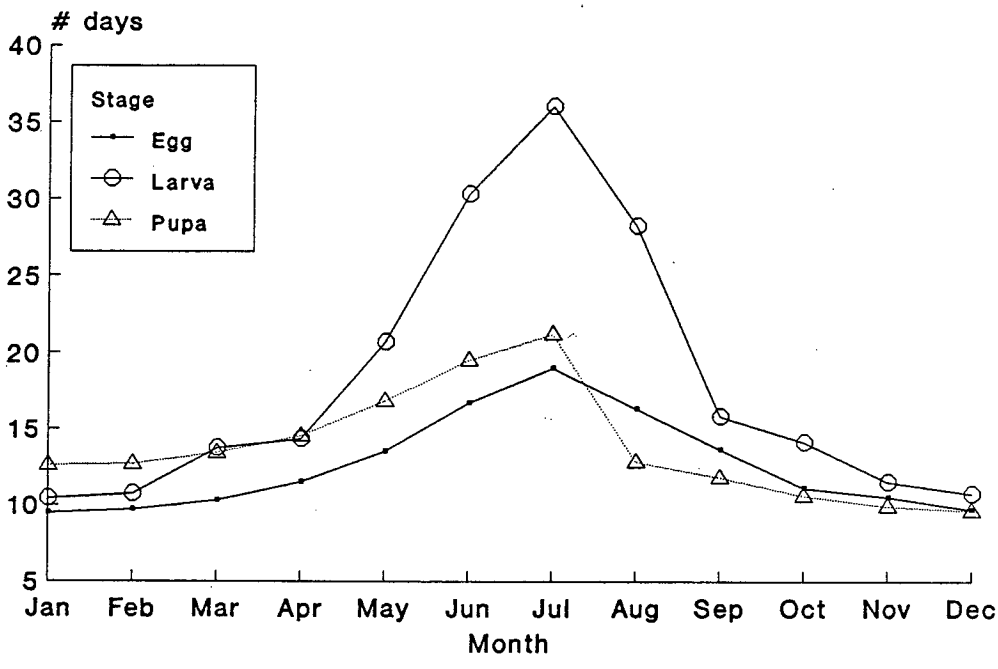


Figure 4.6a-d. Developmental rates of immature stages in first broods.

Data for *Oecophylla longinoda* from African study by Vanderplank (1960).

Figure 4.6e. Monthly variation in times taken to complete development of each immature stage.



rate was explained by a regression with temperature in the range of 20°C to 30°C (with 34 data values), and was described by the equation:

$$DR = -0.15 + 0.00892\ T$$

The slope of this relationship was much steeper than those of the other two developmental stages, and yielded a very high threshold temperature of 16.8±0.7°C.

The relationship between developmental rate from pupa to adult and temperature was less well documented than those for the other two stages (fig 4.6d). No pupae at 20°C or 22°C developed into adults, reducing the range of data considerably. A problem in the cooling system of the 27°C cabinet in 1985 resulted in the loss of data at this temperature. The remaining data at 24°C, 27°C, 30°C, and 35°C showed a linear increase in developmental rate with rising temperatures, so these 29 data values were used in the regression analysis. 82% of the variation in developmental rate was accounted for by the equation:

$$DR = -0.025 + 0.0038\ T$$

This equation gave a 6.6±8.3°C threshold. The very high confidence interval reflects the lack of data, especially at low temperatures, and means that the estimate of 6.6°C is unlikely to be accurate. Development of pupae was certainly disrupted at much higher temperatures than this.

The rate of development of the 29 broods for which I had complete unbiased data from egg to adult was also calculated (fig 4.6d). Developmental rate peaked at 30 and 35°C, and was effectively 0 at

20°C. Insufficient data was available to calculate a regression of brood development from egg to adult.

Using these developmental rate regressions, the time taken for each immature stage to complete development can be calculated for a specified temperature regime, either constant or fluctuating. A computer program was used to calculate the accumulation of development during sinusoidal temperature cycles (which approximate daily temperature patterns relatively well). The time taken for development of each stage in Townsville was estimated for each month by using the average minimum and maximum temperatures recorded by the Bureau of Meteorology for that month (figure 4.6e). Both eggs and pupae show only a small rise in developmental times during the winter months. Larvae, however, display a three-fold increase in the length of development from summer to winter.

4.3.3. Success rates.

The proportions of queens which successfully reared at least one larva, pupa, and adult were plotted for each incubation temperature in figure 4.7a. At a temperature of 24°C, all queens produced adults. Queens at 27°C and 30°C showed some failures in development of pupae and adults, with 55% and 64% of queens, respectively, successfully rearing adults. At 35°C, 42% of queens produced an adult worker ant. However, all of these queens and their brood died soon afterwards, due to unknown, possibly humidity related, causes. Queens kept at 20°C had least success in rearing brood, with 80% producing larvae, only 25% developing pupae, and none rearing brood through to adult workers.

Figure 4.7. Success rates of first broods at different temperatures.

Figure 4.7a. Success rates of 1st broods at different temperatures

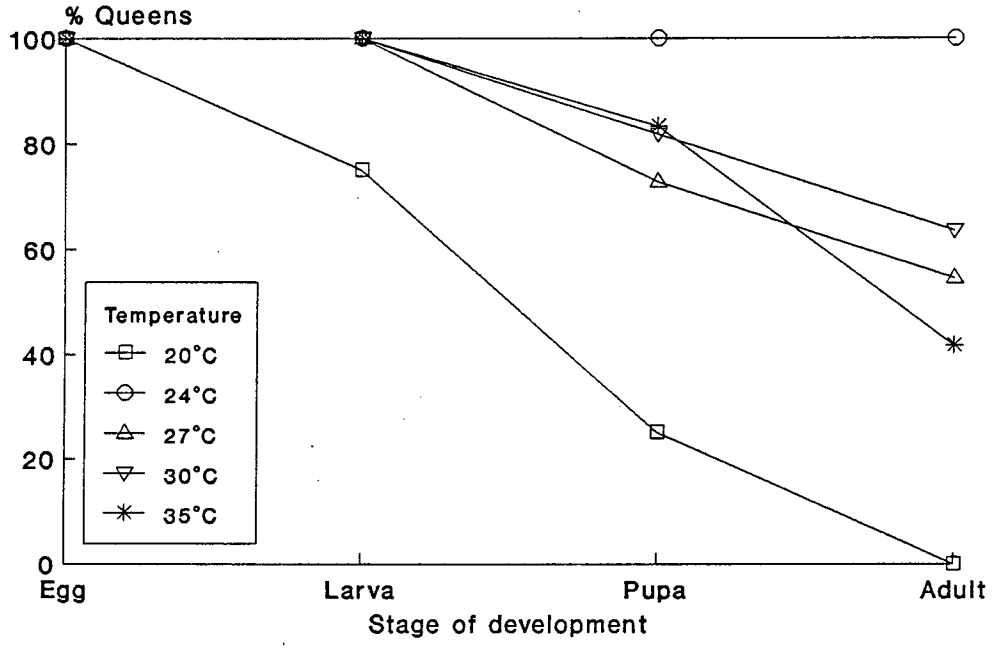
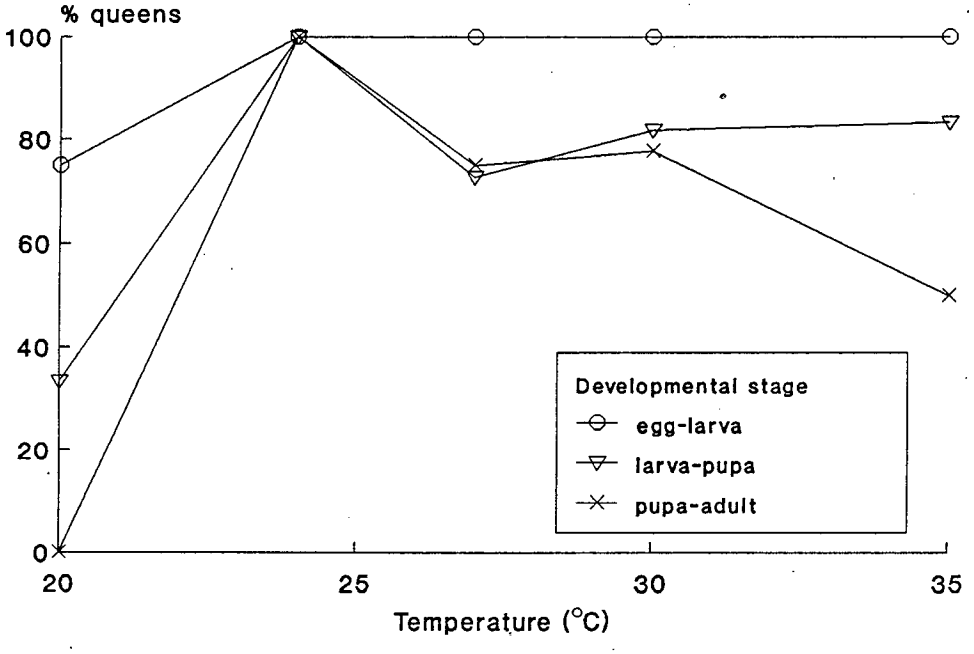


Figure 4.7b. Success rates of 1st broods at each developmental stage



To determine which stages of development were most affected by temperature extremes, success rates of egg to larva, larva to pupa, and pupa to adult were plotted against incubation temperature (fig 4.7b). Success rate was calculated as:

$$\frac{\text{(Number of queens with brood at initial stage)} \times 100\%}{\text{(Number of queens with at least one brood at next stage)}}$$

Egg to larval development was least affected by temperature, with 100% success at all temperatures except 20°C. Development of brood from larva to pupa was more sensitive, with about 80% success at higher temperatures (27, 30 and 35°C), and only 25% at 20°C. The most susceptible period was the final developmental stage from pupa to adult, with 0% success at 20°C, about 75% success at 27 and 30°C, and 50% surviving at 35°C.

4.3.4 Pleometrotic colony founding.

Only 15 multiple queen groups were found in the 197 fledgling colonies collected in the field from 1985 to 1989. The breakdown of numbers of queens per founding colony are given in table 4.2.

Table 4.2: Distribution of queen numbers found within fledgling colonies collected from 1985 to 1988.

Number of queens	Year			
	1985	1986	1987	1988
1	80	49	23	45
2	7	2	-	1
3	2	-	-	-
4	1	-	1	-
>4	1	-	-	-

Queens of *O. smaragdina* artificially combined in the laboratory often attacked each other in a similar fashion to worker ants from different colonies (see section 5.2.1). By collecting unreleased alate queens from various nests of the same and different colonies, inter-colony queen aggression was found to be much higher than intra-colony aggression. In 11 of 25 cases of inter-colony queen combinations, aggression causing some damage to one or both queens was seen within 1 day, whereas no cases were observed between queens of the same colony. This suggests that most of the colony founding queens I collected were from different colonies. Queens which were collected from a mass swarm in Tippett Street, Townsville, in February, 1985, however, were combined in groups of up to 10 without any signs of aggression. This large swarm was thus probably the product of a mass release from one colony.

Unfortunately, most of the multiple queen groups from the 1985 swarm were killed by an unknown pathogen infecting the 27°C constant temperature cabinet. Several groups of 2 queens were later successfully reared at temperatures of 24 and 30°C, and 1 group at 27°C. These broods developed at similar rates to those of solitary queens (figure 4.8). Numbers of eggs and larvae produced were approximately twice the levels produced by single queens. At 24°C, egg numbers peaked at 69±8.2 and larvae at 49±21.7 in the 2 queen nests, compared to 31.5±3.6 eggs and 28.7±4.1 larvae in 1 queen nests. At 30°C, peak levels produced by 2 queen groups were 57.5±13.6 eggs (cf. 36.1±4.6) and 51.±22.6 larvae (cf. 25.6±7). Egg production and larval rearing ability per queen were thus similar in 1 and 2 queen groups.

Figure 4.8. Phenology of first broods of pleometrotic queen groups (2 queens per group)

Figure 4.8a. Phenology of 1st broods of 2 queen groups at 24°C

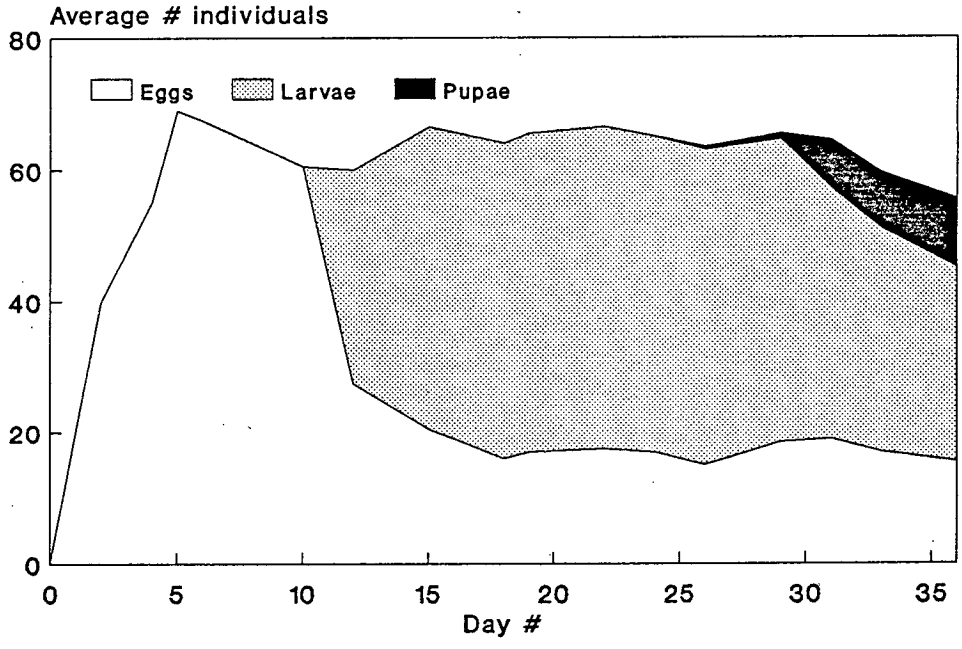
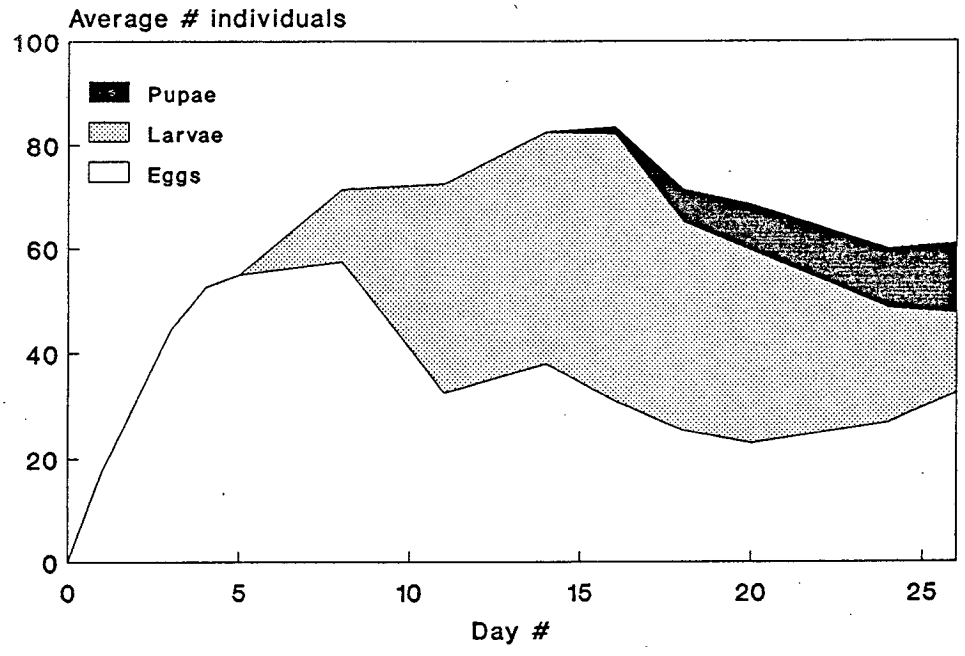


Figure 4.8b. Phenology of 1st broods of 2 queen groups at 30°C



However, pupal production per queen appeared to be lower in the pleometrotic nests. Maximum pupal levels in 2 queen groups were 10.5±12.3 (cf. 18.5±1.5 for 1 queen) at 24°C, and 13.5±10.6 (cf. 9.7±4.3) at 30°C. Much of this reduction was caused by trampling and crushing of the developing pupae by queens in the confined nests. More pupae may have survived if nest size was increased, or if less slippery nest surfaces were used (as queens sometimes fell down, crushing brood). On one occasion, a queen was observed to maim a previously healthy looking pupa, biting almost through its abdomen. This behaviour may represent incipient aggression between the 2 queens, and their respective offspring.

4.3.5 Colony development after first adult emergence.

The first adult workers produced were intermediate in size between the minor and major worker castes of a mature colony. They remained within the silken chamber constructed by the queen for 1 to 3 days, before tearing a small access hole through one wall. In the laboratory, the young workers then fed on a liquid diet, such as honey solution, or a diluted mix of ant diet. No insect prey were accepted until the third to fifth week after first adult emergence, when 10 to 20 workers were active. Both liquid food and insect prey were consumed from this stage onwards.

In 4 of the 5 pleometrotic fledgling colonies (2 queens each) which successfully produced workers, rejection of one of the queens was observed within 2 weeks of worker emergence. Workers were occasionally observed grasping a queen and pulling her away from the brood area. The rejected queens had missing appendages in two cases, and all died

within 5 days of expulsion from the nest.

The survival abilities of the young colonies in field and lab conditions were minimal. All of the 30 returned to trees from which they were originally collected were killed, mainly by other ant species. At least one of the 30 colonies placed in potted plants was consumed by an unidentified bird. Another four disappeared, possibly also attacked by birds, or some other winged predator. In seven colonies, the queen died. The remaining colonies were destroyed by *Iridomyrmex purpureus* ants, when a tree branch fell across the water moats protecting the colonies from such attacks.

Many of the queens kept in constant temperature rooms and the laboratory were destroyed by *Monomorium pharaonis* ants. This Houdini of the ant family also attacked a number of queens which were inside supposedly sealed vials! Some queens also died from unknown causes, presumably disease or malnutrition, and any surviving workers usually succumbed within another 2 weeks.

4.4. Discussion.

These results clearly demonstrate the importance of temperature in the phenology, rate of development, and survival of brood produced by founding queens of *O. smaragdina*. At 20°C, no brood successfully developed beyond the pupal stage, and at 35°C, the few adult worker ants which eclosed died within a week. In similar trials, Vanderplank (1960) found a temperature of 33.3°C to be lethal to the brood of founding *O. longinoda* queens in Zanzibar. Viable worker populations in both species were only produced from 24 to 30°C. The highest mortalities during my trials were usually observed during the pupal

stage, possibly due to the constant very high humidity maintained in the nest vials.

Queens at all temperatures produced an initial egg batch of 25 to 40 eggs within 5 to 10 days. Ledoux (1950) recorded an average batch size of 25 eggs for the African species, and Vanderplank (1960) a somewhat larger number of 65. This latter figure may have included total egg production until first adult emergence. Vanderplank also measured developmental times of the first brood of *O. longinoda* queens at 4 temperatures - 24, 28, 30, and 33.3°C (see figures 4.6a-d). Developmental rate of the brood of the African species appears to rise much more steeply with temperature, and the threshold temperatures of all stages are uniformly high, at about 20°C. This may be due to interspecific differences, or to latitudinal changes in thresholds of development, as Vanderplank was working on populations in Zanzibar (6°S), much closer to the equator than Townsville (19°S). It would be interesting to compare the rates of development of more equatorial *O. smaragdina* populations with the Townsville data.

The threshold temperatures for brood development of Townsville queens were found to vary markedly, from 10.3±1.4°C for egg development, to 16.8±0.7°C for larval development. Such a high larval threshold would slow larval growth in cooler weather, and thus maintain a population of larvae, when brood production was low (see section 5.3.5). This may ensure a continuous supply of larvae, which produce silk for nest construction and repair. The brood of queens in Zanzibar, however, had similar thresholds for all developmental stages (Vanderplank, 1960). In more equatorial regions, such as the Solomon Islands (9°S) and Zanzibar (6°S), *Oecophylla* colonies produce brood throughout the year (Greenslade, 1971b; Way, 1954a), so a higher larval

threshold is probably not necessary. Colonies of the weaver ant, *Polyrhachis dives*, also maintain larvae throughout the year (Yamauchi *et al*, 1987), presumably for nest maintenance, while eggs and pupae are absent in winter; it would be interesting to determine whether a similar pattern of variable development occurs in this species. Larval dormancy, as recorded by Brian (various references, listed in Brian, 1965) in several temperate ant species, was not observed in these trials, but may occur in mature colonies.

The very low survival of founding queens that I observed in the field has been noted in previous work on *O. smaragdina* (Greenslade, 1971b; Bhattacharya, 1943), and *O. longinoda* (Leston, 1973; Vanderplank, 1960). Vanderplank recorded 12 species of ants which preyed on queens in Zanzibar, and I have observed 4 ant and 2 bird predators in Townsville. High mortality of queens is common for ant species which practise founding flights. For example, Autuori (1950, in Weber, 1967) observed a 99.95% mortality in young nests of a tropical leaf-cutter ant, *Atta sexdens*. With such low survival rates, founding queens must be produced in very large numbers for a colony to succeed in reproducing (see section 5.3.5).

Examination of the scanty literature on colony founding success suggests that survival may be greatly enhanced in certain situations. Various workers (e.g. Jackson, 1984; Leston, 1973; Way, 1954a) have observed the presence of gaps, or "no-ant's lands", between neighbouring ant colonies in tropical tree crops, and speculated that queens may successfully colonize these patches in the ant mosaic. Seasonal and yearly fluctuations in colony boundaries, however (Greenslade, 1971a; Vanderplank, 1960; section 5.3.1), would probably engulf such fledgling colonies in most cases.

A senescing *Oecophylla* colony may produce pockets of vegetation protected from other ant species within its territory. Most studies show that when the queen of a colony dies, the unfertililized workers produce only males (Crozier, 1970; Hölldobler and Wilson, 1983a), and will not accept a new queen, slowly dwindling away over a period of about 1 year (Vanderplank, 1960; Way, 1954a). Protected gaps, where alate queens could settle, may appear in the canopy for considerable lengths of time.

Circumstantial evidence for this mode of colony foundation was gleaned from long term sampling data (collected, and collated from earlier work, by Greenslade (1971a), for coconut farms in the Solomon Islands) which suggested an approximately 8 year cycle in *O. smaragdina* abundance. He interpreted this 8 year trend as the average lifespan of tree ant colonies, but this pattern further suggests the synchronised founding of new colonies, at approximately the time of the death of the old colony. Majer (1976a) produced artificial ant-free gaps in cocoa canopy, and found that numbers of founding queens of *O.longinoda* were much higher in trees where populations of this species, or another dominant ant, *Crematogaster depressa*, were removed. Successful production of workers by founding queens was recorded only in these artificial gaps.

Suitable areas for colony foundation may also be caused by heavy storms, such as cyclones. Ant species nesting in the canopy (such as *Oecophylla*, and various *Crematogaster* spp.) are particularly adversely affected by strong winds (Greenslade, 1971b; Leston, 1973; Taylor and Adedoyin, 1978), with nests torn apart, and trees occasionally blown over. Begg (1977) observed decreased numbers of *O. smaragdina* nests, and fewer ants per nest, in areas most affected by

Cyclone "Tracy", in Darwin, Australia. In these cyclone damaged sites, he also recorded some successfully established fledgling colonies, with adult workers and up to 3 queens per nest. "Tracy", and other major natural disturbances, probably reduce predator and competitor populations sufficiently to allow survival of some founding queens.

Pleometrosis improves survival of founding colonies in *Myrmecosystus mimicus* (Bartz and Hölldobler, 1982), *Solenopsis invicta* (Markin *et al*, 1972), and various other ant species (Rissing and Pollock, 1988). Peeters and Anderson (1989) list some possible benefits of group founding for *Oecophylla*, including faster increase in the number of workers in the colony, and a leaf nest that can be built larger and faster than by a single queen. In my laboratory trials, 2 queen groups produced more larvae, which could thus produce more silk for nest construction. However, pupal and adult worker numbers were similar to those in haplometrotic founding nests. This increased mortality may be due to overcrowding effects in the small nest vials, such as trampling, and humidity-related fungal attack. It may also be caused by incipient aggression between the 2 queens and their partner's offspring; insufficient queens were available to properly examine this aspect.

Both single queen founding (Dodd, 1902, 1928; Greenslade, 1972; Vanderplank, 1960), and multiple queen founding (Begg, 1977; Ledoux, 1950; Peeters and Anderson, 1989; Richards, 1969) have been recorded in *Oecophylla*, but survival of the 2 types in the field has not been compared. The present study found 100% mortality in fledgling colonies of both types.

Limited indirect evidence suggests that pleometrosis in *O. smaragdina* is possible only between queens of the same colony.

If true, this raises some interesting questions:

(1) Do queens from one nest remain together after being released from the nest? (2) If not, can they detect other queens, for example, by smell, when searching for a nest site?

The first scenario requires queens to be mated before release. No queens that I collected before their release from their parent nest produced viable eggs, but Vanderplank (1960) found queens just emerging from the nest were fertilized, and observed males entering nests, presumably to mate with queens. Hölldobler and Wilson (1977b) state that mating occurs outside the nest, but offer no details of the mating flight. I never witnessed the release of queens from a nest, and it probably occurs under cover of darkness.

In the second scenario, the probability of queens locating a con-colonial partner would be related to the density of released queens in the area. Most queen groups I collected were in areas of high queen density, with the largest aggregations found in a huge swarm of thousands of queens, in a suburban garden in Tippett Street, Townsville. My observations thus tenuously support the second method.

As mature *Oecophylla* colonies are monogynous, all but one queen in pleometrotic founding colonies must be ejected or killed at some stage. This process occurs in other ant species, either by fighting among queens, or by workers eliminating queens (Bartz and Hölldobler, 1982). Peeters and Anderson (1989) never observed direct aggression among the 10 queens, or between queens and workers, in a laboratory reared fledgling colony of *O. smaragdina* from Kakadu national park, Australia (approximately 2000 km from my Townsville study site). Begg also found young colonies of this species with workers and up to 3 queens in a nearby locality, suggesting low levels of aggression up to

this stage. In my laboratory nests housing 2 queens, one queen was always rejected within 2 weeks of emergence of workers. Workers were occasionally observed grasping a queeen's appendages and pulling her from the nest. The rejected queen was abandoned outside the nest, where she usually died within a few days. On one occasion, a queen was even observed to bite a healthy pupa before the emergence of any adults. This geographical variation in persistence of pleometrosis is most interesting, in relation to the similar discrepancies in reports of acceptance of new queens by queenless weaver ant colony fragments. Ledoux (1950) and Bhattacharya (1943) found adoption of new queens possible, in Ivory coast and Calcutta populations, while Vanderplank (1960), Crozier (1970), and Hölldobler and Wilson (1977) found colonies were strictly monogynous in Zanzibar, Malaysia, and Kenya. If these differences are real, the capacity of ants to distinguish kin from non-kin (i.e. kin recognition) must vary substantially between populations within the genus *Oecophylla*.

A number of sources of chemical recognition cues have been reported in hymenopterans. Genetically determined cues, or "discriminators", and environmental cues (from food, nest materials, or micro-organisms) have been reported in species such as *Camponotus spp.* (Carlin and Hölldobler, 1986, 1988), *Solenopsis invicta* (Obin and Vander Meer, 1988), and *Rhytidoponera confusa* (Crosland, 1989). Although the relative importance of genetic and environmental cues varies from species to species, both systems are probably present in many social insects to some degree (e.g. Crosland, 1989). Most populations of *Oecophylla* possess a very active recognition system, as demonstrated by the immediate aggressive response of workers to alien ants (used for colony boundary mapping in this study, and by

Hölldobler, 1980, 1983). Also, when queenless colony fragments were separated for more than 1 month, their odour cue had changed enough to be rejected (i.e. produced an attack response similar to that caused by alien ants) by the parent colony and other conspecific fragments.

Inter-population variation in the aggression of pleometrotic queens after worker emergence, and in adoption of foreign queens, could be explained by 3 possible causes. Aggression may be lowered by increased similarity of diets. In *Solenopsis invicta*, the formation of polygynous colonies (with lower kin recognition capabilities than monogynous colonies) has been linked to trophallactic "appeasement" between foreign workers, which slowly integrates the environmental odour of the 2 colonies (Obin and Vander Meer, 1988). The genetic recognition system may also have changed, either through reduction of its capacity to discriminate between different odours, or by high homozygosity of recognition alleles producing unusually similar odour templates. Our understanding of the mechanisms of kin recognition could benefit greatly from the study of different populations with varying kin-recognition abilities.

5. COLONY STRUCTURE.

5.1. Introduction.

A mature ant colony is composed of a population of mostly or wholly sterile female workers, produced by one or more fertile, egg-laying queens. The worker caste performs most of the colony labour, including brood care, nest construction and maintenance, colony defence, and foraging. Winged male and female forms are produced at intervals to reproduce new colonies. The colony lives in a nest, which provides shelter from inclement weather and a suitable stable microclimate for brood development, and can supposedly be more readily defended against attack from other ants or predators (Sudd and Franks, 1987).

Within these broad criteria, ant colonies vary widely in structure. Population sizes of colonies range from less than 100 in many rainforest species (Wilson, 1959), to over 1 million, for example in army ants (Schneirla and Piel, 1948), weaver ants (Leston, in Majer, 1976a; Yamauchi *et al*, 1987), and some *Formica* species (Rosengren *et al*, 1985, 1987). Colonies of most species possess only one functional reproductive queen (monogynous), but a substantial minority are polygynous, with varying levels of acceptance and dominance between the different queens. The worker population in some species varies widely in size and/or morphology, with up to 3 distinct castes. Such polymorphic workers occur in 44 of the 263 extant ant genera (Oster and Wilson, 1978), and have allowed the development of a division of labour based on size differences (size polyethism, discussed in section 6.1.1).

A staggering diversity of nesting sites are utilized and constructed by ants. "Typical" ant nests excavated into the soil can differ in the depth and size of chambers, so regulating temperature and humidity levels. Many species (e.g *Formica spp, Lasius spp, Myrmecia spp*) also build distinctive mounds for thermoregulation, using excavated soil material. In cool temperate areas, ants such as *Myrmica scabrinodis* and *Lasius flavus* nest under stones, which absorb more radiant heat than the surrounding soil (Brian and Brian, 1951). Decomposing logs and twigs are utilized as nest sites by many forest dwelling ants. Wilson (1959) found the majority of species in lowland rainforest of New Guinea nesting in rotting wood, and few in the soil or under rocks.

Some arboreal ants nest in pre-existing cavities or excavate cavities in living or dead wood. Other species construct nests on tree trunks or branches, or inside cavities, using carton. Maschwitz and Hölldobler (1970, in Sudd and Franks, 1987) found the carton of *Lasius fuliginosus* nests was a composite material made of wood (or sometimes soil) and honeydew, infiltrated with fungus. The genus *Oecophylla* and some species of *Polyrhachis*, *Dendromyrmex*, and *Camponotus*, construct nests of living leaves bound together with larval silk (described in section 1.1).

A number of tropical plants have specialized hollow structures which are inhabited by ants. The bull's horn acacias of the American tropics have hollow thorns that are occupied by ants of the genus *Pseudomyrmex* (Janzen, 1966). *Iridomyrmex myrmecodiae* nests in the hollow bases of *Myrmecodia sp*, an Australian epiphyte (Brown, 1959), and species of *Pachysima* inhabit hollow branches of the African tree,

Barteria fistulosa (Janzen, 1972). The associations between these ants and their myrmecophytic plants are often obligate, with the plants providing nest sites and food, and the ants providing protection from predators and other competing plants.

In many ant species, an ant colony may occupy more than one nest. This polydomous habit is especially common amongst arboreal ants, such as the weaver and carton nesting ants (Leston, 1973), but also occurs in some ground nesting ants such as *Iridomyrmex purpureus* (Greenslade, 1975), and some *Formica* species (Rosengren *et al*, 1985). Decentralizing the colony population with multiple nests allows the foraging territory to be more effectively protected from neighbouring colonies (Leston, 1973), and may enable a larger territory to be maintained (Hölldobler and Lumsden, 1980).

The extent of the area foraged by colonies is related to the population size, and the quality and quantity of the food supply. Bernstein and Gobbel (1979) found that the average area foraged by colonies of ants in western North America decreased with increasing food density. Colony area may also be regulated by inter-specific and intra-specific competition (Elmes, 1987). This is especially evident in the mosaic distribution patterns of the highly aggressive ant species in tropical tree crops (see section 3.4). Colonies in this habitat are under compression, and artificial gaps produced by ant removal are rapidly occupied by adjacent colonies (Majer, 1976a; Vanderplank, 1960). Competition appears to be less intense in most terrestrial ant communities, where species are generally less territorial, and mosaics of mutually exclusive ant distributions have not been observed (Jackson, 1984).

The production of brood in many ants is associated with seasonal

climatic patterns. Most temperate species rear brood during the warmer months, and are reproductively inactive during winter. The most comprehensive study of temperate ant reproduction is that of Brian (1957, 1965, 1973, 1977, 1981) for the genus *Myrmica*. Queens produce 2 egg batches, the larger first one in early summer, and the second in late summer. Most develop into workers during the same year, but some hibernate as larvae until the next spring. These overwintered larvae develop into either sexual or worker adults, depending on the levels of food supplied. The colony and climatic cycles appear to be synchronized by short day lengths and dropping temperatures during winter, and maintained by endogenous rhythms for the remainder of the year. Cool temperate species of *Leptothorax* and *Tetramorium* show a similar pattern of brood seasonality (Brian, 1977). Colonies of other temperate ants, including species of *Formica* and *Lasius* hibernate without brood during winter (Schmidt, 1974); queens and adult workers remain inactive deep in the nest interior, until triggered by spring warmth into returning to the surface. All brood production in these species occurs during the warm summer months.

Many tropical rainforest ants do not show clear seasonal patterns of reproduction, and have adult and brood stages present continuously (Wilson, 1959). Greenslade observed similar aperiodicity in the worker brood of 4 species (including *O. smaragdina*) inhabiting coconut plantations in the Solomon Islands. However, the young stages of sexual forms were most abundant in the wet season. Way (1954a) also observed most sexual brood in Zanzibar populations of the African weaver ant during the wet months.

Brood production in some species of army ants is synchronous, but is regulated endogenously by the queen, rather than by external factors

(Schneirla and Piel, 1948). During the stationary phase of the colony (when the colony remains in one bivouac site, and the previous brood are all at the pupal stage), the queen lays a single large batch of eggs. Shortly after these eggs hatch, the pupae of the previous brood emerge, triggering the colony into the nomadic phase. The colony emigrates regularly during this period, until the larvae pupate, and the colony then returns to the stationary phase. Totally endogenous control of brood production has also been observed in the tropical pest species, *Monomorium pharaonis* (Petersen-Braun, 1977).

The dynamics of the various aspects of colony structure are best known for temperate ant genera, such as *Myrmica* (e.g. Brian *et al*, 1981), and *Formica* (e.g. Rosengren *et al*, 1985, 1986; Schmidt, 1974; Skinner, 1980a). Tropical studies are more fragmentary, generally focusing on specific attributes of agriculturally important ant communities (e.g. mosaic ant literature) or tropicopolitan pest species (e.g. pharaoh's ant, fire ant). The majority of this work has been conducted in the wet tropics, where seasonality is minimal.

The present study examined the colony structure dynamics of *O. smaragdina* in Townsville, a dry tropical forest habitat (Holdridge *et al*, 1979). Seasonality in colony extent and reproductive activity was monitored, and compared to other studies of tropical ant colony structure.

5.2. Methods:

The structure of *O. smaragdina* colonies was explored at three scales: colony, tree, and nest. At the colony level, the number of trees and total area occupied by colonies of the green tree ant were

examined. Longevity and density of ant nests within colonies were measured in two tree species. Age structure (proportions of larvae, pupae, worker castes, and sexual forms) and fluctuations in worker size were explored at the nest level.

5.2.1. Colony extent: Tree number and area occupied.

The extent of populations of the green tree ant was monitored in the Townsville and Major Creek study sites. Trees at each site were surveyed for the presence of ants, as described in section 3.2. Using these survey techniques, quite small populations could be detected. These populations were differentiated into separate colonies, by utilizing the strong inter-colony aggression displayed by this species. Hölldobler (1980) demonstrated that a group of weaver ants transferred to a tree occupied by a foreign colony quickly elicited a group attack response, and were rapidly pinned down and killed. After some experimentation, I found that even a few alien workers would produce an unambiguous attack response from the resident workers. The precise mechanism used by ants in determining whether another ant is alien is uncertain, but probably involves varying mixtures of volatile chemicals which are continuously distributed among the colony's workers, and are detected by chemoreceptors on the antennae (reviews in Fletcher and Michener, 1987; Waldman, 1988). The transferred ant also behaved quite differently when placed in foreign territory, often dropping off the tree before encountering another ant. This behaviour was observed in the laboratory trials of Hölldobler and Wilson (1977a, 1978), and was found to be caused by a colony-specific territorial pheromone which was laid randomly in spots of faecal material

throughout the colony area.

Ants were captured and transferred inside small vials to avoid possible scent contamination from my hands. A group of five workers was usually sufficient for each trial, but more groups were used if less than 25 ant interactions were observed (e.g. as occurred when all ants leapt off the tree). Continuity of each colony was checked by transferring ants over the full length of the colony.

The number of trees of various species found within the boundaries of each colony, and which were inhabited by ants, was used to estimate colony extent. Unfortunately, a tree is not a uniform unit, in time or space. At any one time, this measure of colony size was biased by size differences between tree species, and trees within each species. Larger trees potentially provide more food resources (both insect prey and homopteran populations), and support more leaves for nest construction. Large trees may exclude other trees through shading effects, thus influencing tree densities. Each tree also varied in size during the study period due to growth and senescence.

The mango trees at the Major Creek site were of similar size (most being planted in 1976), and spaced regularly (with a 9 metre inter-tree distance), minimizing these biases. In the Townsville site, trees at all stages of development (from 0.5 to 20 metres tall) were present, but only individuals over 2 metres tall were recorded. A second measure of colony extent was derived for this site by measuring the area of ground occupied by each colony. This colony area measure reduced the bias due to varying tree size. However, tree counts have the undeniable superiority of directly estimating the primary habitat of the tree ant, whereas colony area measures ground area, which is a much less utilized resource. A more useful estimate of colony extent would be the three

dimensional volume of tree canopy occupied, but would require regular aerial photography of the site, and extensive stereoscopic work. This was not feasible in the present study, but recent developments in computer image analysis could make such measures a realistic proposition in the future.

Colonies in the Townsville site were mapped twice yearly during 1986 and 1987. From 1988 onwards, colonies were monitored every 2 months. Data for the Major Creek site was collected every 2 to 3 months, from December, 1986 till February, 1989. Observations during 1986 suggested that colony size was related to the physiological condition of the inhabited trees. The changing vegetative and reproductive status of the 11 most common tree species in Townsville, and of the mango trees at Major Creek, was quantified by examining 10 randomly chosen specimens of each species for young leaf flush, mature leaves, flowers, and young and mature fruit. These proportional occurrence data were collected along with colony extent information from 1987 onwards.

5.2.2. Nest density and longevity.

Nest density was measured as the number of large (>125 cm^3) and small (<125 cm^3) nests per tree, for 10 trees chosen randomly from within ant colonies. In the Townsville site, *Zizyphus mauritiana* and *Pongamia pinnata* were monitored; they were the first and third most common species in the study site, respectively, and also small enough (<10 metres tall) to inspect thoroughly for nests. Similar counts for mango trees at Major Creek were abandoned because many nests were hidden by the dense foliage of these trees. Density data was collected

in conjunction with colony size studies, from March, 1988 onwards.

Nest longevities were examined on a relatively opportunistic basis whenever a nest observed in the density trial was known to be constructed very recently. Signs of recent construction included chains of ants still holding leaves of the nest together, very small amounts of silk binding the nest, and groups of workers using larvae to complete the continuous silk leaf bindings seen in a finished nest. These nests were marked on my site map, and inspected every week until abandoned. Seventeen nests were monitored in *Zizyphus mauritiana* and 20 nests in *Pongamia pinnata*.

5.2.3. Nest composition.

Age structure was examined in conjunction with distributional field work, from March, 1984 to January, 1985. Five nests were randomly selected from trees at eight sites along the Queensland coast, every 2 months. The sites chosen, from south to north, were Yeppoon (the southernmost limit of this ant species, 23°8′S), St. Lawrence (22°21′S), Mackay (21°9′S), Bowen (20°S), Ayr (19°34′S), Townsville (19°16′S), Ingham (18°39′S), and Cairns (16°55′S). Choice of nests was usually constrained by the length of my ladder to a maximum height of 6 metres, although some trees were climbed for nests up to 10 metres in height. Previous work (Lokkers, 1982) suggested that small nests were often "bivouac" nests for foragers, with no reproductive function, so only nests of at least 1 litre volume were collected. Each nest was pruned off the tree as quickly as possible, and sealed into a plastic bag containing ethyl acetate. The ants were removed from the nest by washing with water into a fine mesh filter. As these samples were often

very large, they were divided using a rotary plankton splitter into a countable portion of about 2000 individuals. The different forms of ant recorded were larvae, pupal and adult workers of both castes, pupal and adult queens, and adult males.

This sampling technique underestimates the number of major workers, as unknown numbers are outside the nest foraging at any one time (Greenslade, 1971). I had hoped to quantify this factor through mark/recapture trials, but no successful marking technique was found (see section 6.2.3). Nests were always sampled as close as practicable to midday to minimize circadian variation in forager numbers.

The numbers of each form were converted to proportions to allow direct comparisons between nests of unequal total populations. The effects of different sites and months, and physical parameters, such as temperature and rainfall, on patterns of nest composition were examined using analyses of covariance. Proportions were converted using the arcsine square-root transformation to reduce the heterogeneity of variances occurring in fractional data which approaches 0 or 1 (Zar, 1984).

Further nest composition data were collected during nest activity trials (chapter 6), with 2 nests per month inspected for 18 months from December, 1986 to March, 1989. These data were used to test the accuracy of the predictive model developed from the 1984/1985 results. A less restrictive minimum nest size criterion of 250 ml was used in these later trials, as nests over 1 litre became quite scarce in January of the previous investigation. Total population sizes in these nests varied widely, so absolute counts were examined for seasonal patterns.

Seasonal variation in size of adult ants was assessed using 40

adult major caste workers from each of these nests. As ants had been stored in alcohol, total body lengths were distorted, so scape (1st antennal segment) lengths were measured, using a binocular microscope with a graduated eyepiece. This measurement has been previously used by Wilson (1953). The relationship of scape length to length of thorax (actual measurement included alitrunk plus petiole) was examined in 125 major and 49 minor workers freshly collected in March, 1989.

5.3. Results.

5.3.1. Colony extent: Tree number and area occupied.

The total number of trees in the Townsville study site occupied by *O. smaragdina* varied from a minimum of 373 trees in November, 1988, to a maximum of 571 in May, 1989 (figure 5.1). The percentage of trees inhabited in the site ranged from 50.1% to 76.7%. A distinctly seasonal pattern was observed, with peak numbers of occupied trees in May, and lowest levels in November. Unfortunately, the sampling periods of January and August chosen in the first 2 years fall between these extremes, and so were less than useful in interpreting seasonal patterns. Subsequent figures are thus presented without these sample dates.

The green tree ant population in the study site was found to consist of 8 separate colonies, in February, 1986. The queen was accidentally killed in one of these colonies in January, 1987. No further worker or female sexual brood were subsequently found in this queenless colony, and all individuals had disappeared by January, 1988. Some male sexuals were produced, presumably by unfertilized worker

Figure 5.1 - 5.2. Colony variation in Townsville study site.

Figure 5.1. Temporal variation in total trees occupied

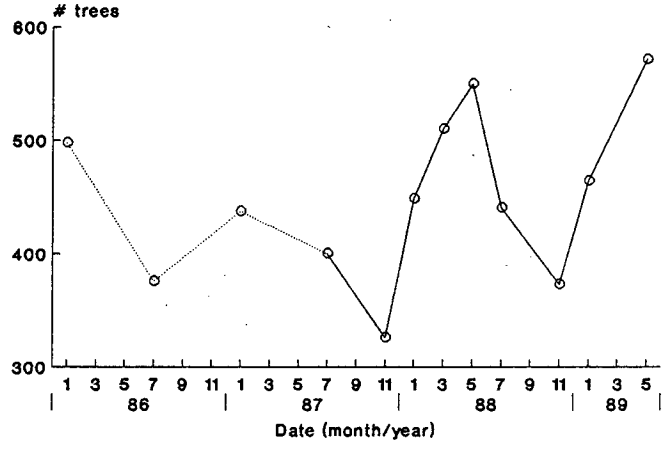


Figure 5.2a. Temporal variation in trees occupied per colony

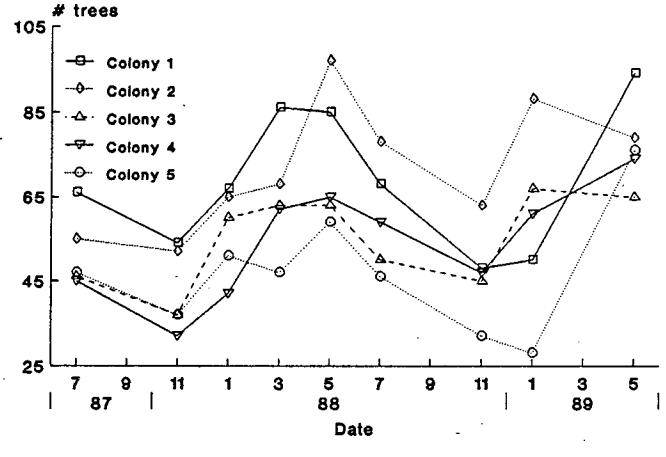
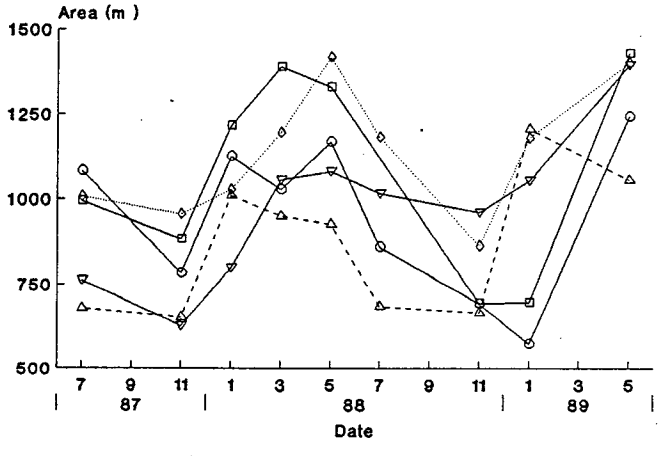


Figure 5.2b. Temporal variation in area occupied per colony



ants. Another two colonies engaged in a major territorial dispute during 1988, which resulted in a large increase in one colony, at the expense of the other (see section 5.3.2). The extents of these two colonies, encoded 6a and 6b, were displayed on the site map in figure 2.3, during the period of strongest conflict, in May, 1988.

The remaining 5 colonies displayed similar patterns of variation, in both numbers of trees occupied (figure 5.2a) and total ground covered (figure 5.2b). The size of most colonies peaked in March to May, with an average of 75.7±9.4 trees/colony, covering 517.6±53.2 m^2 of ground area. Minimum colony size, of 44.7±9.4 trees, and colony area of 323.4±38.5 m^2, occurred in November. As these 2 measures were so similar, with no indication of any consistent biases, only tree numbers will be considered from this point.

A very different pattern of variation was observed in populations of *O. smaragdina* at the Major Creek mango tree plantation. Tree occupation levels were much lower, with only 12% to 25.2% of the 250 trees on the farm inhabited during the study period (figure 5.3a). This low level of occupancy could be due to the large distance of about 9 metres between trees, and the lack of any interconnections between adjoining canopies of the relatively young trees. Distributional analysis (section 3.3.2) gave a mean nearest neighbour distance of trees never occupied by ants in the Townsville site of only 3.4±0.4 metres.

Average colony sizes were much smaller, ranging from 1.5±0.5 trees to 3.2±1.2 trees (figure 5.3b). The cycle of colony variation was also displaced in comparison to the Townsville site, by 2 to 4 months, with maximum colony sizes in July to September, and minimum in December to January. As the two sites are only 50 kilometres apart, climatic

Figure 5.3. Colony variation in Major Creek study site.

Figure 5.3a. Temporal variation in total trees occupied

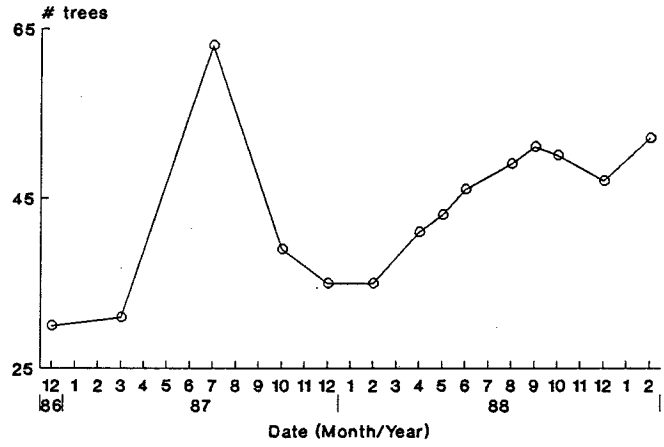


Figure 5.3b. Temporal variation in trees occupied per colony

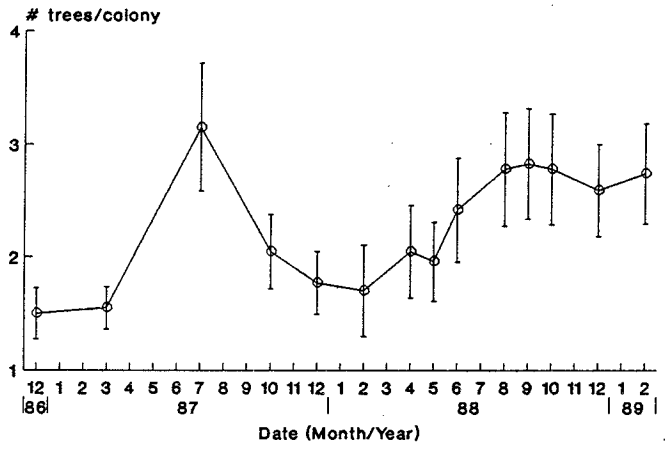
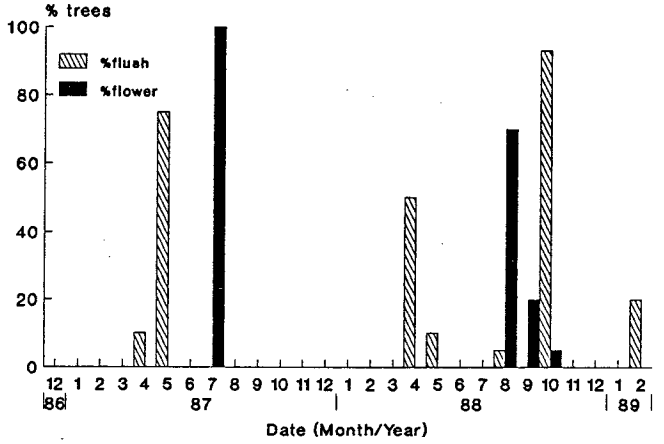


Figure 5.3c. Temporal variation in mango tree status



conditions at both are very similar, and cannot explain these discrepancies in colony size variation.

Increases in total trees occupied and trees per colony at Major Creek appeared to occur during periods of tree leaf flushing and flowering (figure 5.3c). The maximum in number of trees occupied by ants seen in July, 1987, coincided with a period of intense flowering, when all trees in the plantation flowered. A lower peak in tree occupation in September, 1988, occurred one month after a smaller burst of flowering, when 20% of trees still had flowers. The numbers of inhabited trees were lowest when trees were neither flowering nor producing new leaf flushes. Increasing tree occupation by ants was recorded in early 1988 and 1989, when new leaf flushes were observed on some trees.

Similar relationships were seen between the physiological status of most of the common tree species in the Townsville site, and the numbers of each occupied by ants (figure 5.4). The maximum number of inhabited trees of *Zizyphus mauritiana* occurred in May, when levels of flowering were highest (figure 5.4a). Similarly the peak number of *Lophostemon grandiflorus* trees occupied in March occurred one month after maximum flowering (figure 5.4b), and peak habitation and flowering of *Melaleuca* trees coincided in March (figure 5.4c). Occupancy levels of *Pongamia pinnata*, however, were low when they flowered from September to November, because these deciduous trees were bare of leaves during this period (figure 5.4d). The number of occupied trees of this species peaked in May, just before leaf drop commenced.

As each colony in the Townsville site was composed of different proportions of various tree species, composite measures of reproductive and vegetative status were derived for each colony, on each survey

Figure 5.4. Temporal variation in number of trees occupied and tree condition for 4 tree species in Townsville study site.

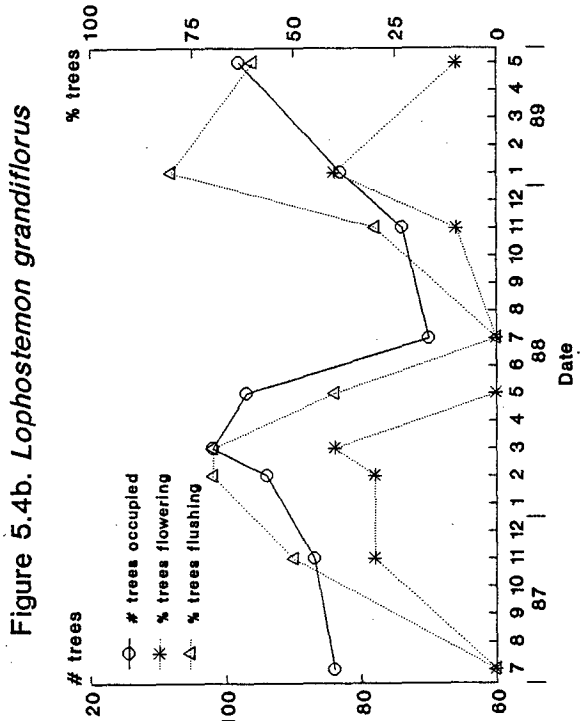


Figure 5.4b. *Lophostemon grandiflorus*

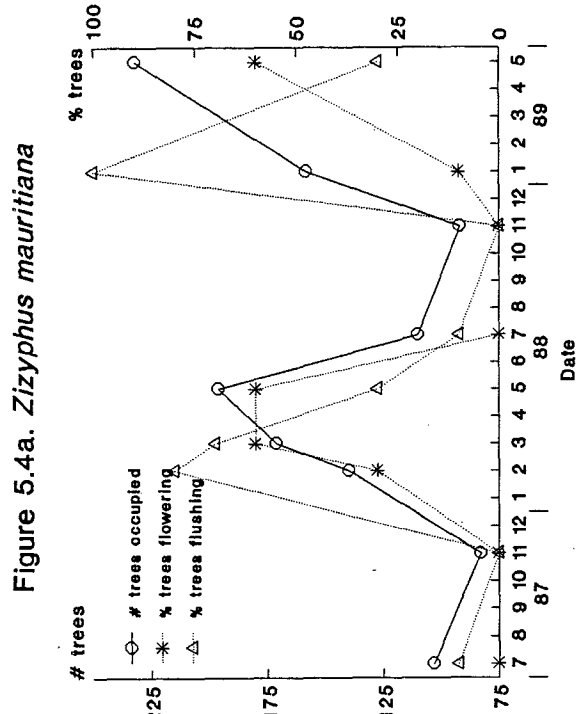


Figure 5.4a. *Zizyphus mauritiana*

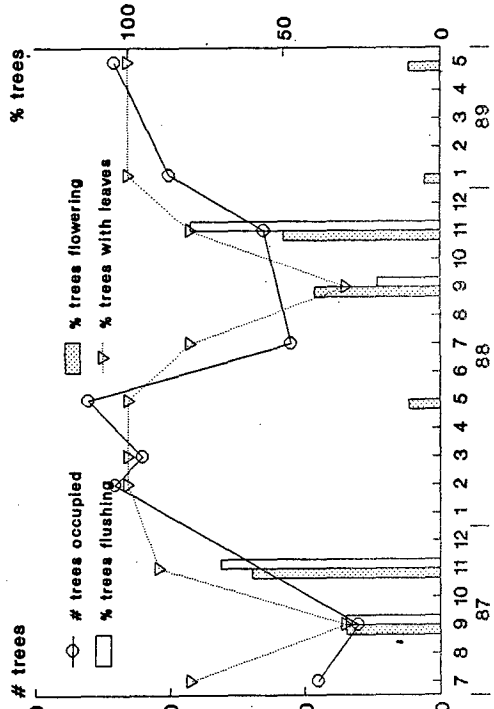


Figure 5.4d. *Pongamia pinnata*

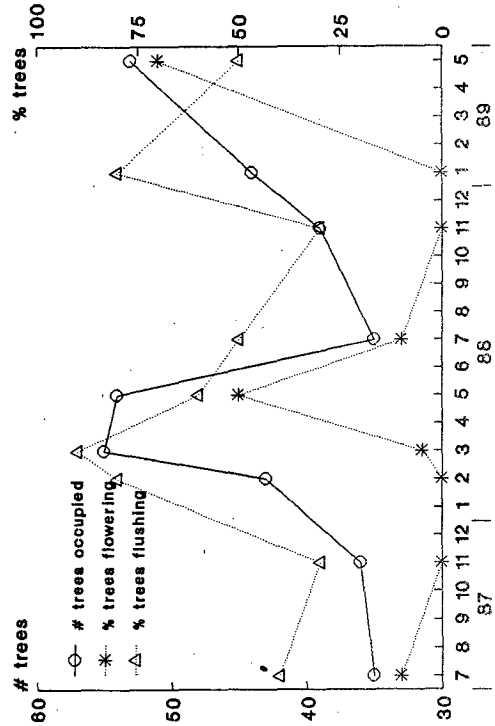


Figure 5.4c. *Melaleuca spp.*

date. Overall measures for the total site were also determined. Only the 5 most common tree groups were used (*Zizyphus mauritiana*, *Lophostemon grandiflorus*, *Pongamia pinnata*, *Melaleuca spp*, and *Canarium australianum*),as these comprised over 80% of the total trees in the study site. Each composite flowering measure, for example, gave the proportion of trees in this group of species that were flowering during the survey period, and was calculated using the formula:

$$R_{tot} = \Sigma_{i=1,5}(P_i R_i)/\Sigma_{i=1,5} P_i$$

where P_i = proportion of species "i" in colony (or total site)

R_i = proportion of flowering trees in species "i"

R_{tot} = composite measure of flowering status.

This statistic ranged from 0, when no trees were flowering, to a maximum of 1, when all were flowering.

The total number of trees occupied by green tree ants was closely correlated with the composite flowering proportion (figure 5.5). The cycle of composite leaf flushing levels appeared to precede the flowering and tree occupancy cycles by approximately 2 months. Composite measures of young and mature fruit did not appear to correlate with occupancy levels.

To standardize occupancy levels between colonies with varying total tree numbers, the number of trees inhabited by one colony at one time was divided by the maximum number ever occupied by that colony. A significant positive correlation ($R=0.66$, 37df, $P<0.0001$) between this proportional occupancy figure and composite flowering level was found (figure 5.6a). A similar analysis was performed for composite leaf flushing data which was lagged by 2 months (figure 5.6b), and gave a less precise, but still significant result ($R=0.56$, 37df, $P=0.0001$).

Figure 5.5. Temporal variation in trees occupied and composite tree status

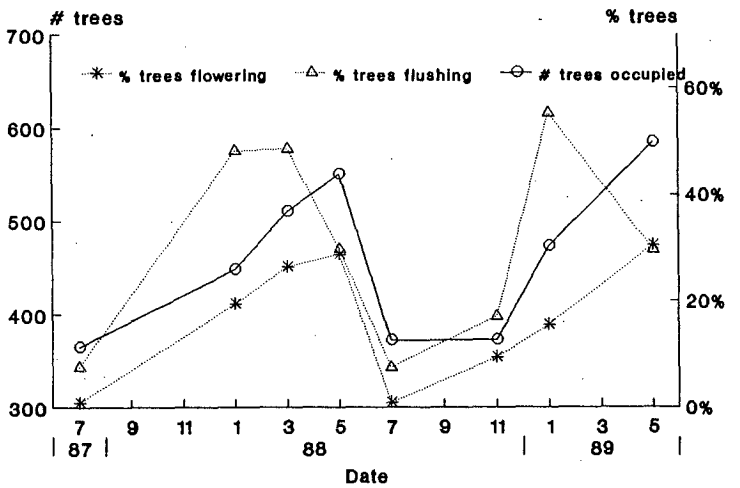


Figure 5.6a. Regression of % trees occupied on composite flowering status

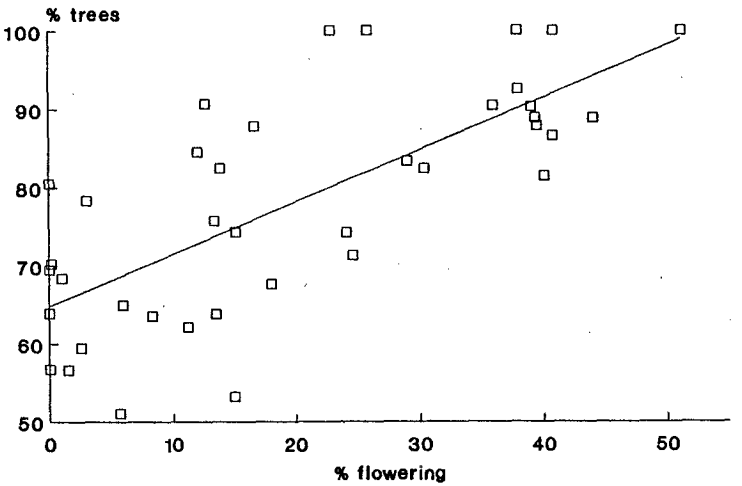


Figure 5.7. Temporal variation in trees occupied by conflicting colonies

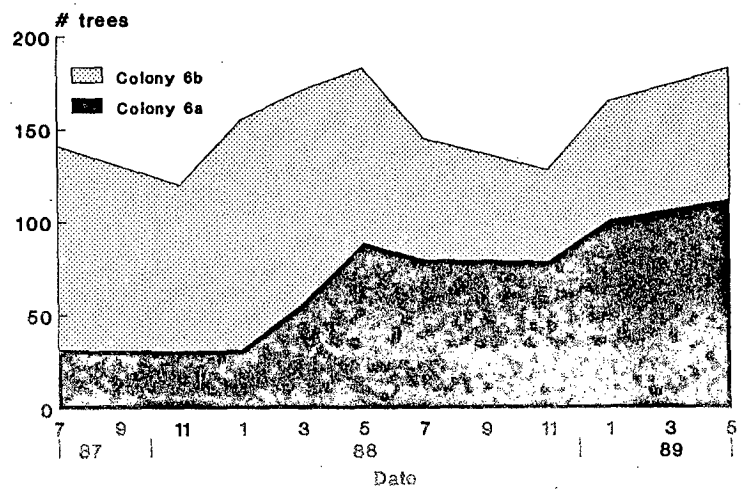
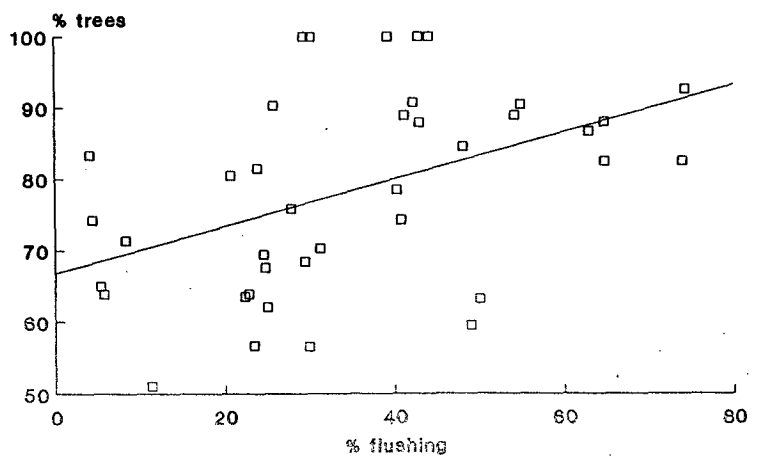


Figure 5.6b. Regression of % trees occupied on composite flushing status (lagged by 2 months)



5.3.2. Inter-colony aggression and colony size.

Aggressive encounters between ants of neighbouring colonies were most prevalent during periods of colony expansion, from January to May. Most conflicts led to the formation of "no-ant's lands" (Hölldobler and Wilson, 1977), which were patrolled on either side by groups of worker ants. Occasionally, major conflicts occurred, involving hundreds, or thousands of ants, and could lead to the takeover of a tree by the invading colony. A few trees regularly underwent changes in ownership by two competing colonies, once or twice per year.

These conflicts appeared to have little significant impact on the colonies involved, with one notable exception. Large scale conflicts between 2 colonies, code-named 6a and 6b, during mid 1988, produced a major increase in the size of colony 6a, at the expense of colony 6b (figure 5.7). Over 50 trees changed possession over a period of 6 months, for unknown causes. The most obvious explanation, that the queen of colony 6b had died in 1988, was made doubtful by this colony's subsequent increase in size during 1989.

5.3.3. Nest density.

Numbers of nests within trees varied greatly, both spatially and temporally. Nest size was also very variable, ranging from a single leaf folded over to form a chamber of a few cm^3, to huge nests containing hundreds of leaves, with volumes approaching 0.5 m^3. The average numbers of small (< 125 cm^3) and large (> 125 cm^3) nests, with standard errors, in 10 trees of *Zizyphus mauritiana*, were plotted in figure 5.8a. Variation in nest numbers, even between trees of the same

Figure 5.8a. Temporal variation in nest densities in *Zizyphus mauritiana*

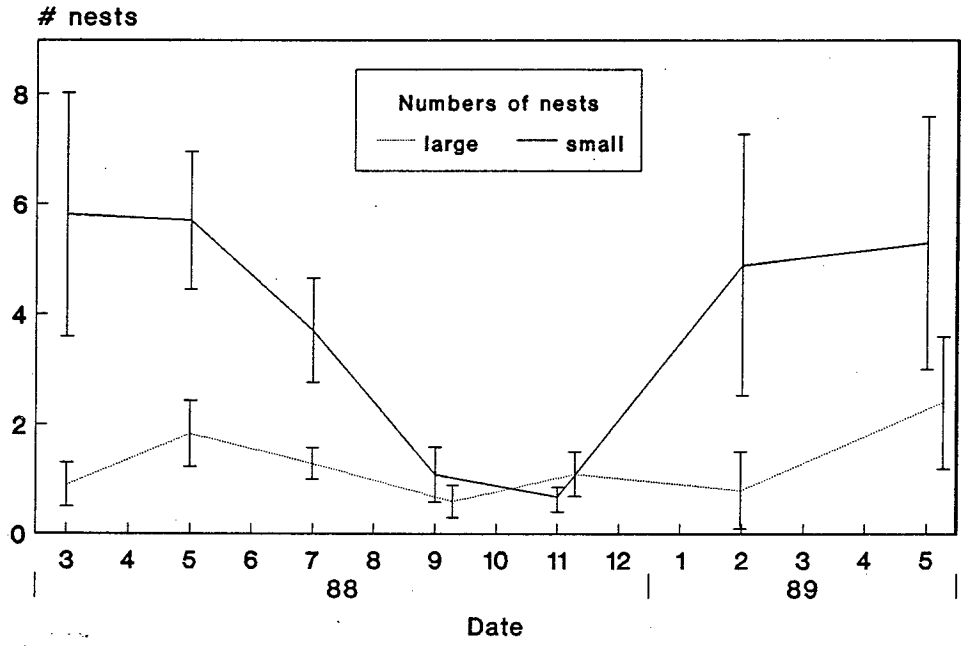
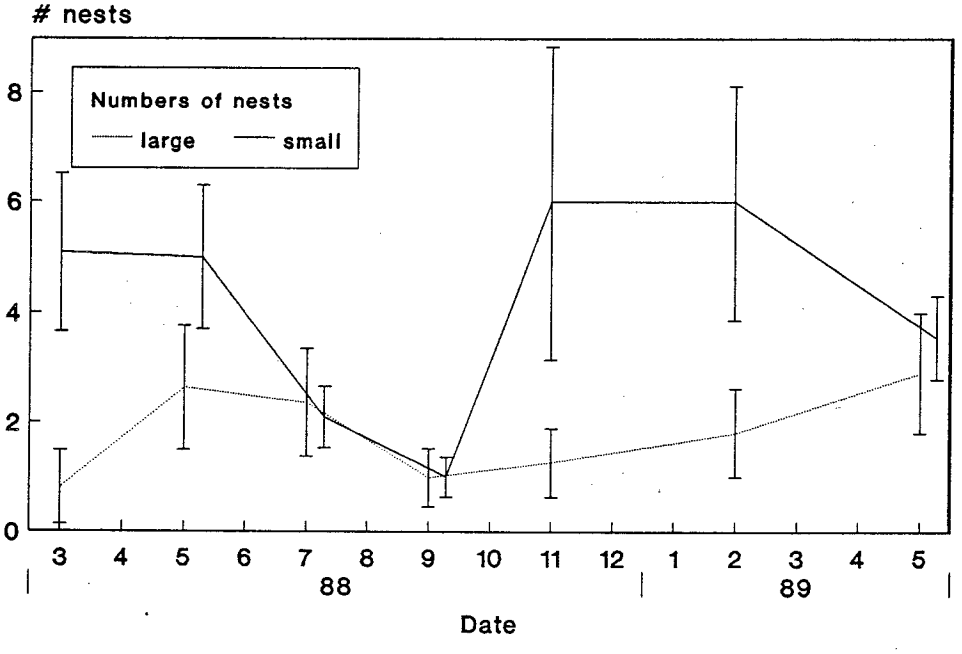


Figure 5.8b. Temporal variation in nest densities in *Pongamia pinnata*



species, was high, as demonstrated by the large standard errors observed. Densities of small nests peaked during the colony expansion period, from January to May. This is also the season of maximum physiological activity for this tree species, with both new leaf growth and flowering (figure 5.4a). The number of small nests dropped after May, and very few were found from September to November, when tree occupancy of colonies was dropping, and *Z. mauritiana* trees were physiologically inactive, with sparse leaf cover. The densities of large nests were generally lower than those of small nests, and showed much less seasonal variation. There was a slight increase in large nest number during May, but the high levels of variability between trees make this trend uncertain.

The densities of large nests in *Pongamia pinnata* trees (figure 5.8b) showed a similar, but slightly more pronounced seasonal trend, with a maximum of 2.6±1.1 nests per tree in May, and a minimum of 1.0±0.5 in September. A distinct seasonal pattern of variation in small nest densities was also observed, but the cycle in this tree species appeared to precede that seen in *Z. mauritiana* by about 2 months. A similar anomaly was detected in the seasonal occupation rates of *P. pinnata* (section 5.3.1), and was probably caused by this deciduous tree's lack of leaves for nest construction from July to September (figure 5.4d). A large rise in numbers of small nests, from 1.0±0.4 to 6.0±2.9 nests per tree, was observed from September, when only 30% of trees had leaves (which were mostly old and yellowing), to November, when all trees had young, healthy canopies.

5.3.4. Nest longevity.

Nests were inhabited by ants for widely varying periods. Lifespans ranging from 3 to 18 weeks were recorded for the 56 nests that were successfully monitored from their date of construction till they were abandoned. The average occupation time for 17 nests in trees of *Z. mauritiana* was 10.8 weeks, ± 95% confidence interval of 1.5 weeks. Way (1954a) obtained a similar figure, of 12 weeks, for nests of the African weaver ant, *O. longinoda*, in clove trees.

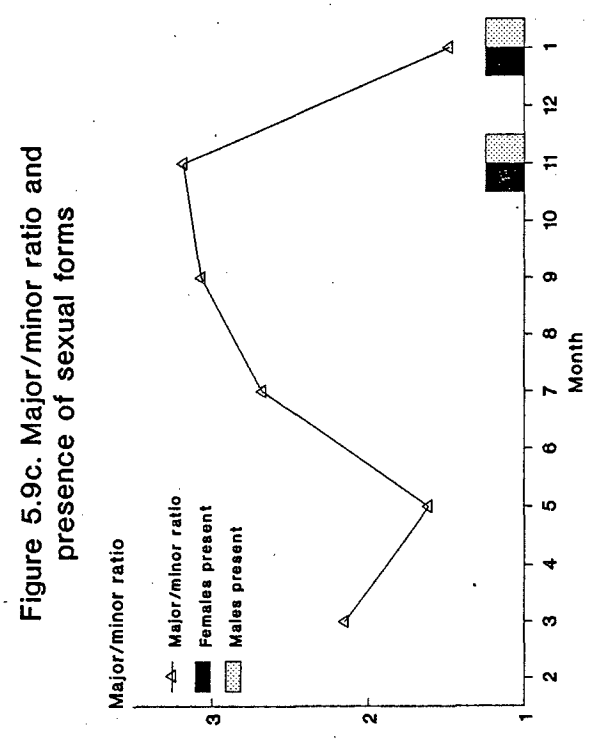
The mean period of habitation of 20 nests observed in *P. pinnata* trees was 7.0±1.6 weeks. This slightly smaller lifespan was probably due to the strongly deciduous habit of this tree species. Occasionally, ants would maintain a large nest, composed entirely of dead leaves, in a tree with no other foliage (plate 1.1d). Such nests were only found in large *P. pinnata* trees which were utilized as major pathways within a colony. Nests also appeared to be occupied for shorter periods during the middle of the year, when leaves were senescing and dropping off, but too few nests were successfully monitored to test this observation.

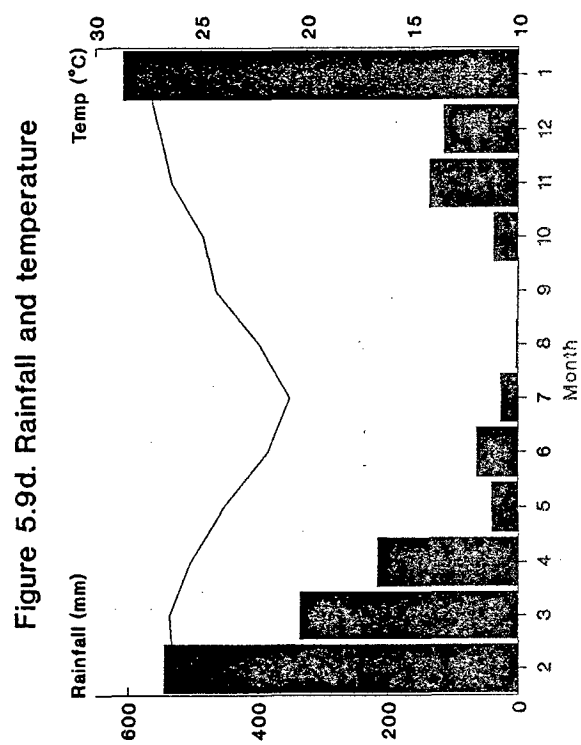
5.3.5. Nest composition.

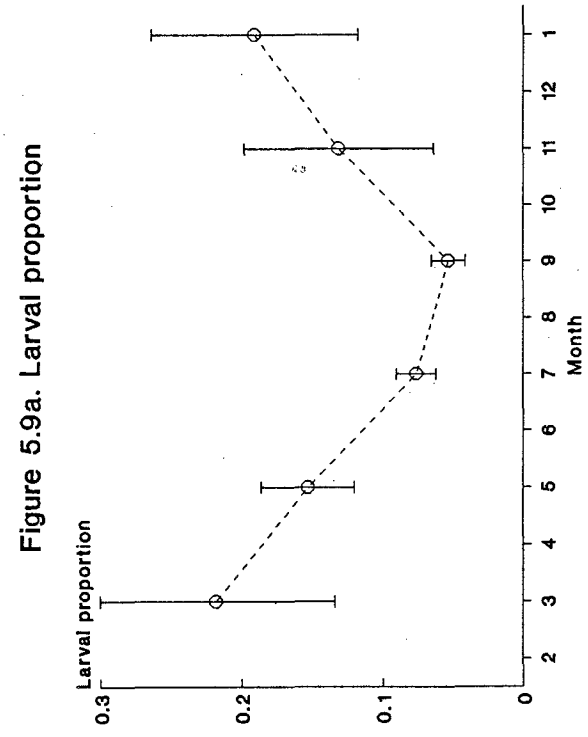
1984 - 1985:

The results of nest samples from March, 1984 to January, 1985 are displayed for the 6 sites in figures 5.9 to 5.14. In each figure, the first 2 plots show mean proportions of larvae and pupae of the 5 nests sampled per site per month, with 95% confidence intervals. A third plot displays seasonal patterns in the ratio of adult major caste worker

Figure 5.9. Temporal variation in nest composition and climate in Cairns.







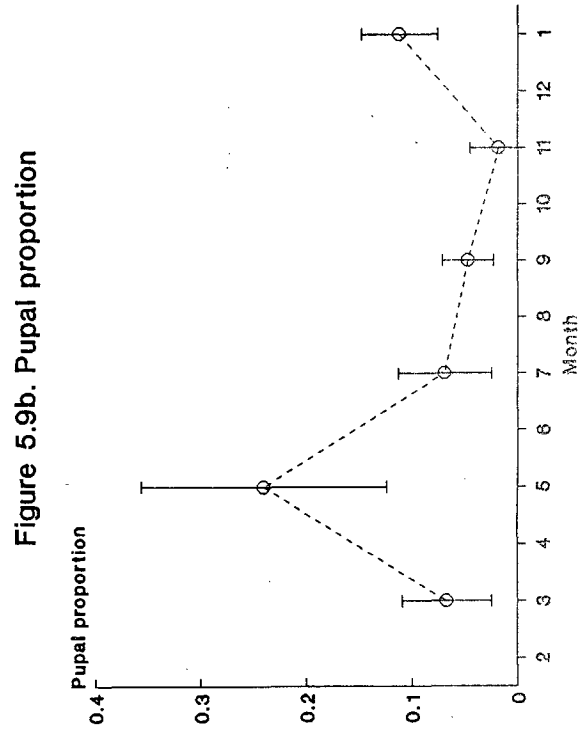


Figure 5.10a. Larval proportion

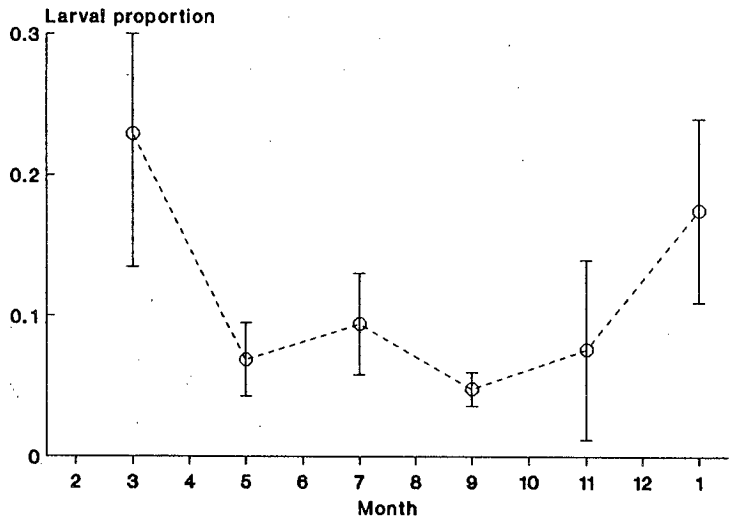


Figure 5.10b. Pupal proportion

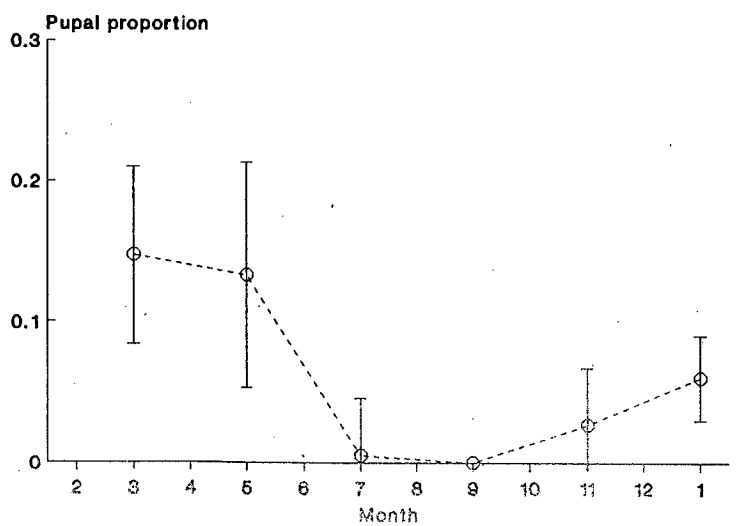


Figure 5.10c. Major/minor ratio and presence of sexual forms

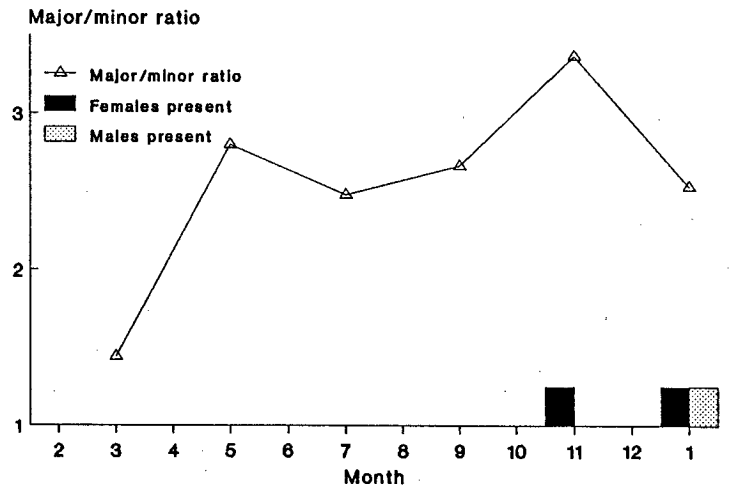


Figure 5.10d. Rainfall and temperature

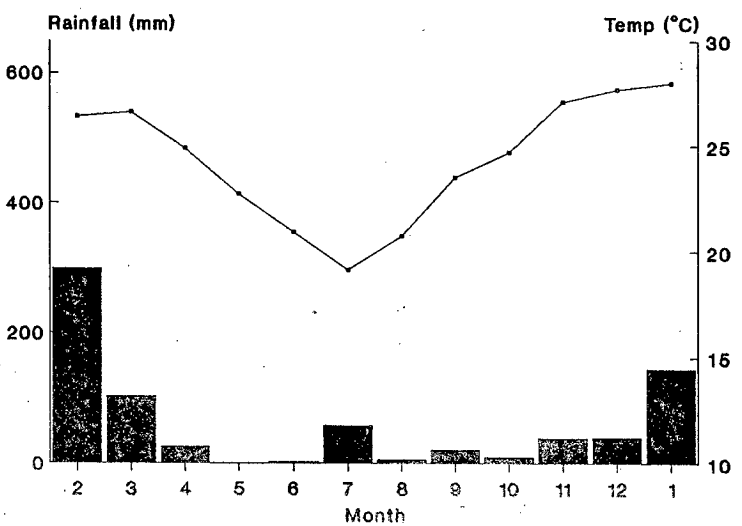


Figure 5.10. Temporal variation in nest composition and climate in Townsville.

Figure 5.11a. Larval proportion

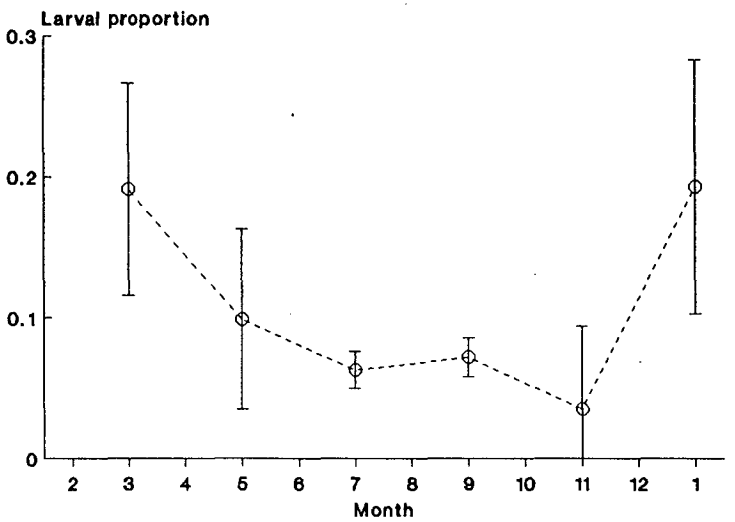


Figure 5.11b. Pupal proportion

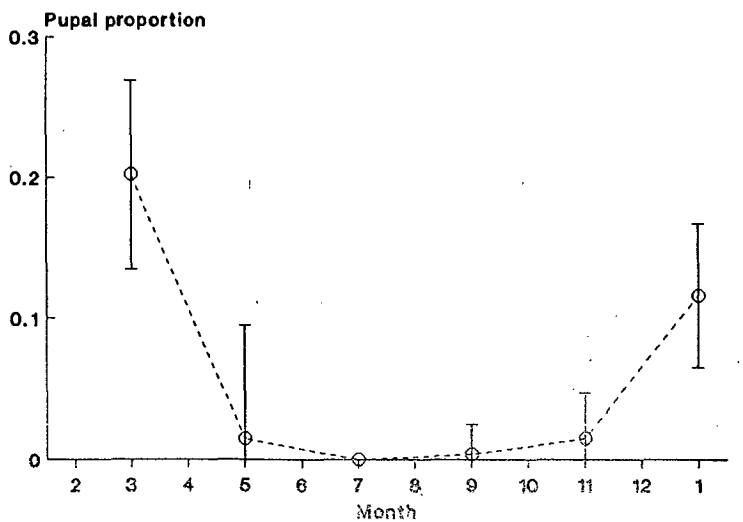


Figure 5.11c. Major/minor ratio and presence of sexual forms

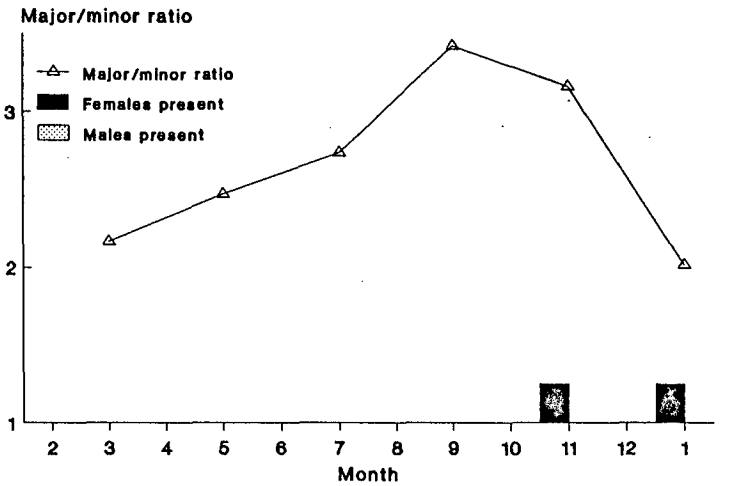


Figure 5.11d. Rainfall and temperature

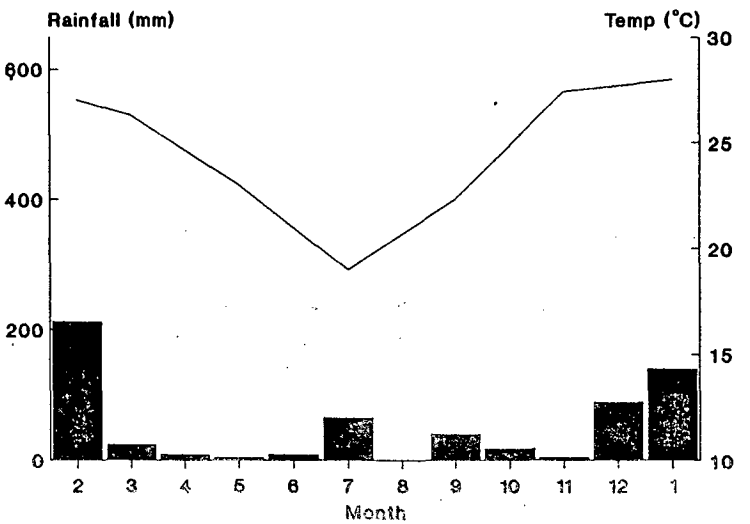


Figure 5.11. Temporal variation in nest composition and climate in Bowen.

Figure 5.12. Temporal variation in nest composition and climate in Proserpine.

Figure 5.12a. Larval proportion

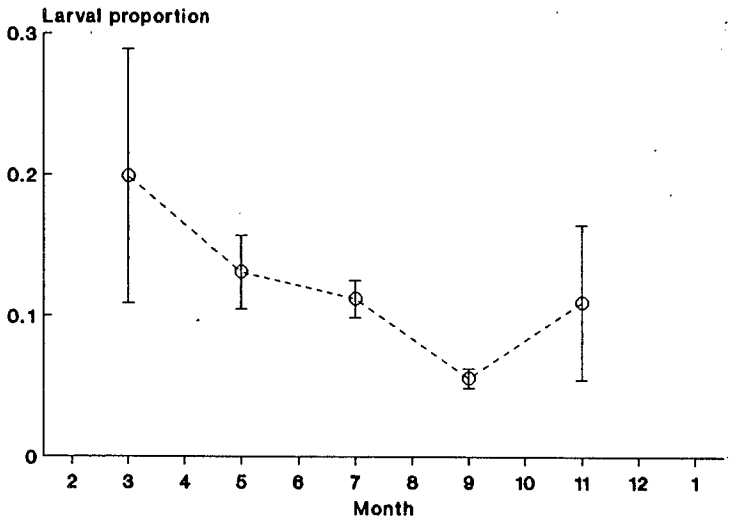


Figure 5.12b. Pupal proportion

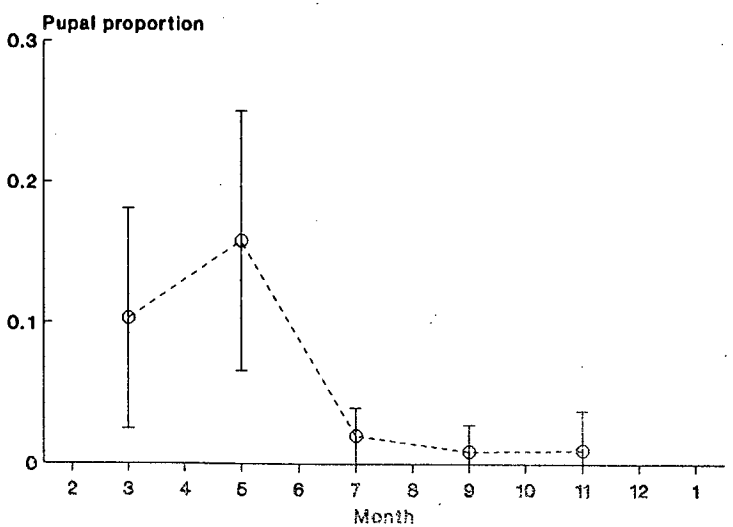


Figure 5.12c. Major/minor ratio and presence of sexual forms

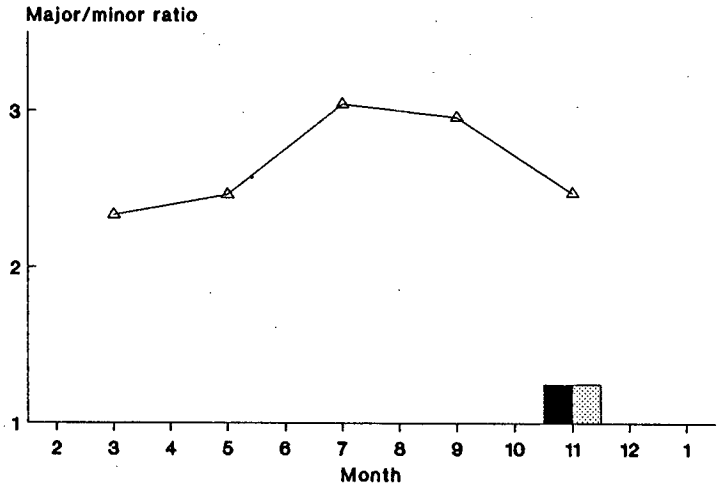


Figure 5.12d. Rainfall and temperature

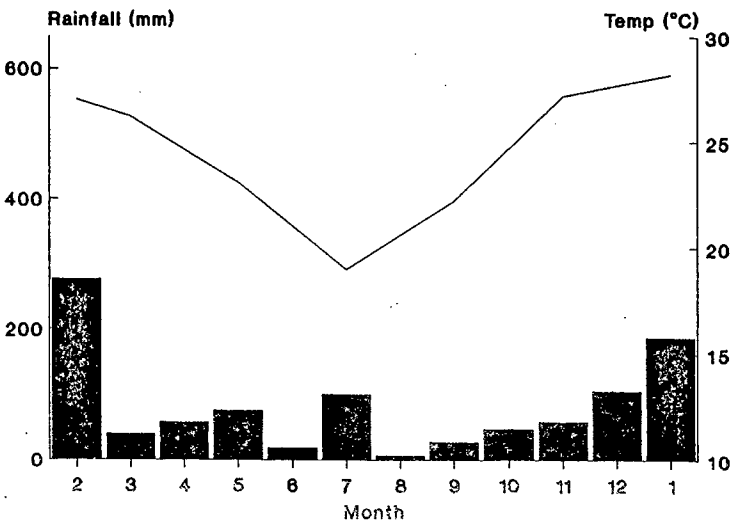


Figure 5.13a. Larval proportion

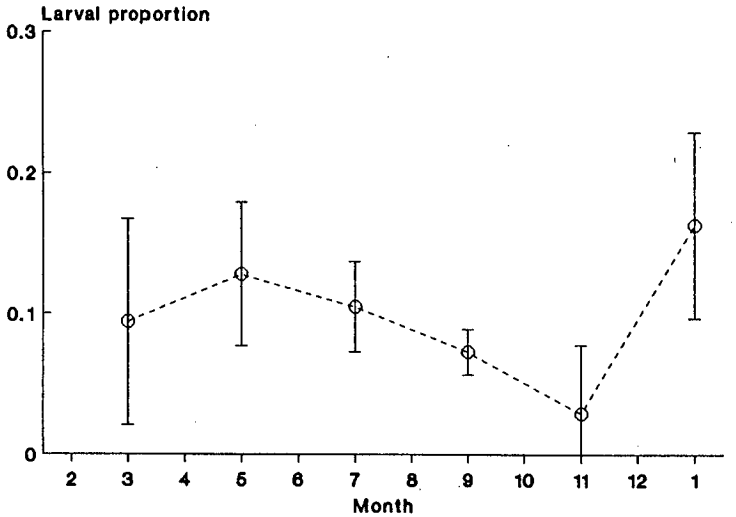


Figure 5.13b. Pupal proportion

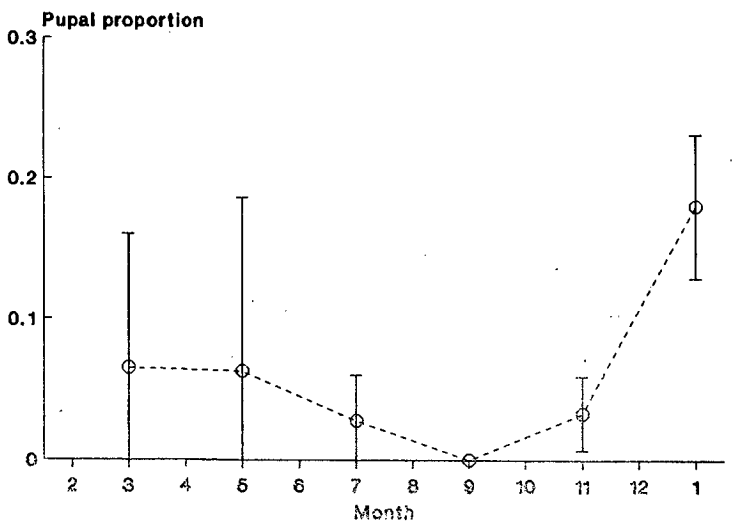


Figure 5.13c. Major/minor ratio and presence of sexual forms

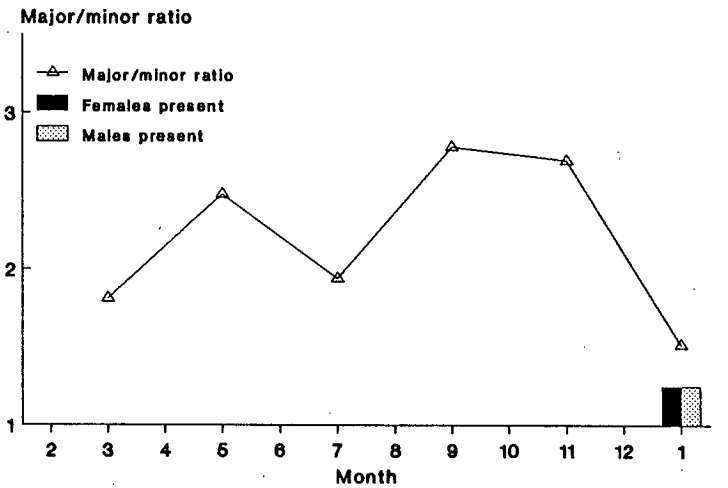


Figure 5.13d. Rainfall and temperature

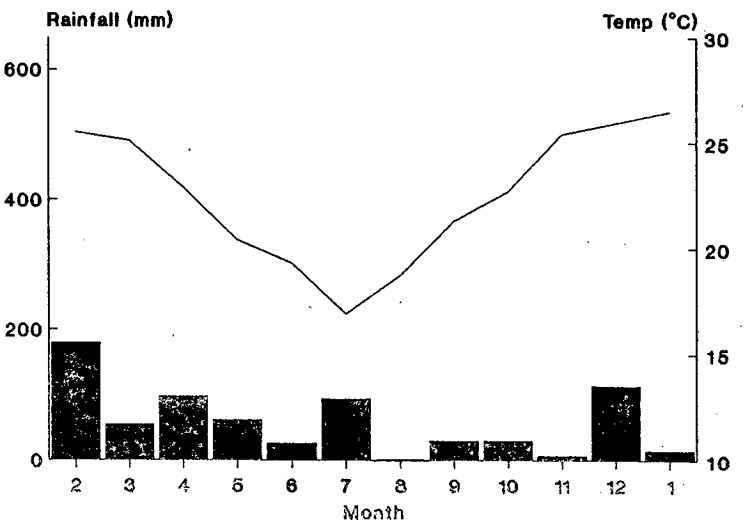
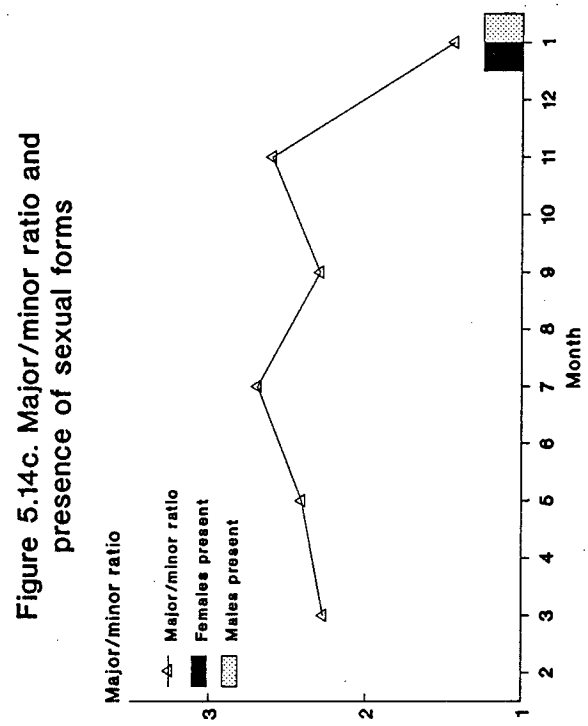
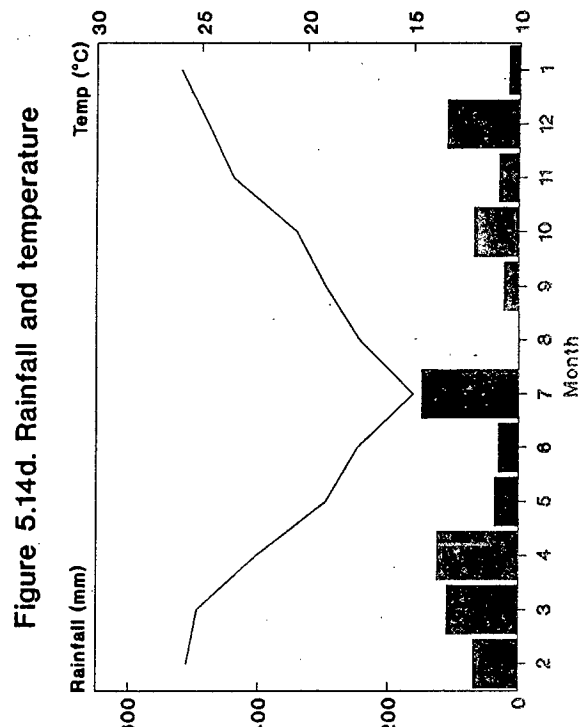
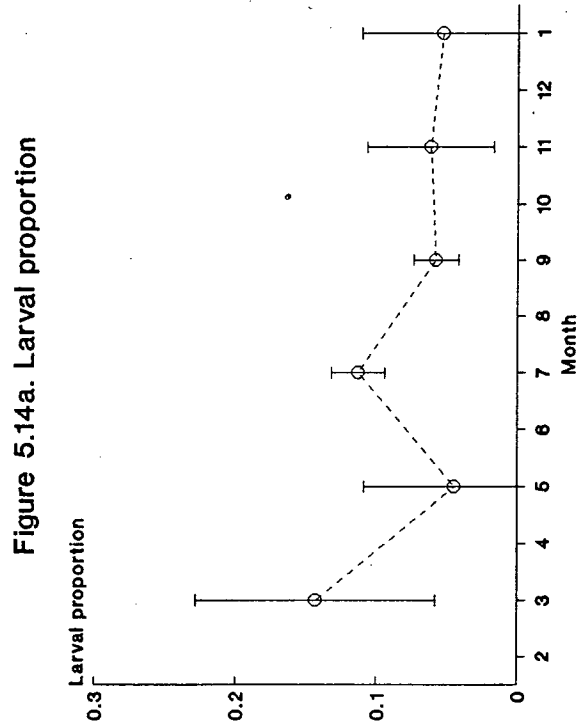


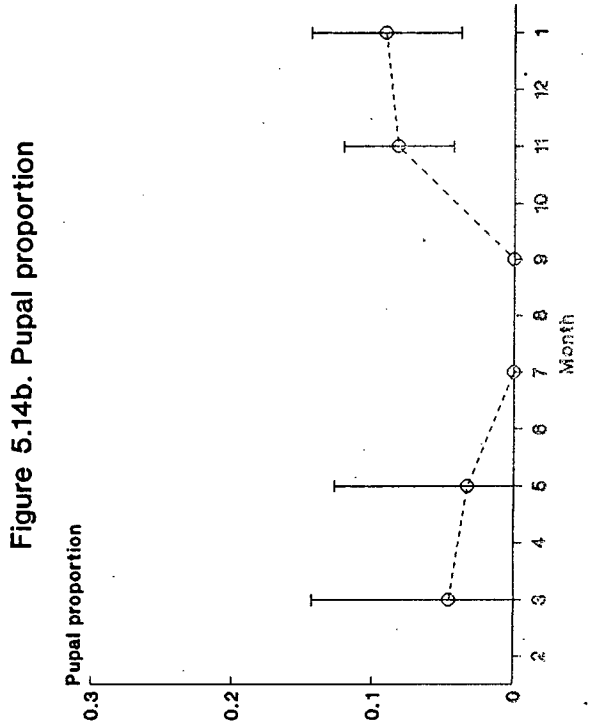
Figure 5.13. Temporal variation in nest composition and climate in Mackay.

Figure 5.14. Temporal variation in nest composition and climate in Yeppoon.









ants to minor caste worker ants (M/m), and indicates if male and/or female sexuals were present. The final plot describes the temperature and rainfall regime experienced by each site during the study.

Most nests had no or very few eggs. Only one nest, collected in 1986, contained large numbers of eggs, and a functionally reproductive queen was found in this nest. Presumably, only the queen's nest or a few adjacent nests contain eggs, and most brood are transported after hatching, as larvae, pupae, or young adults.

The most seasonally disjunct ant forms were the sexual castes, occurring only in November and January (figs 5.9c - 5.14c). When present, the numbers of sexuals varied greatly between nests, from 1 to over 1000. At least part of this variation was caused by the irregular levels of release of sexuals, even between adjacent nests within the same colony, following rain. Quantitative analysis of sexual proportions is thus pointless, without more frequent sampling.

Nests at all sites showed relatively similar patterns of larval proportions, with minimum levels from July to November, and maxima in January and/or March (figs 5.9a - 5.14a). When mean larval fractions were high, large inter-nest variation was also observed. Interestingly, all nests contained larvae, with 2% the lowest percentage observed. An analysis of covariance on arcsine square-root transformed data indicated larval proportion varied with month of year ($F=5.6$, 5x20df, $P=0.002$; table 5.1), but not between sites ($F=0.6$, 5x20df, $P=0.64$). It was also associated with the current month's rainfall in a parabolic relationship, with a significant rainfall term ($F=28.9$, 1x20df, $P=0.0001$) and rainfall squared term ($F=14.9$, 1x20df, $P=0.001$), but not with temperature.

Table 5.1: Analysis of covariance on proportions of larvae in nests.
Convention used in listing sources of variation:
A*B - factors A and B crossed. A(B) - factor A nested within B.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Location	5	0.00816	0.00163	0.64	0.6742
Month	5	0.07103	0.01421	5.54	0.0023
Rain	1	0.07416	0.07416	5.07	0.0001
$(Rain)^2$	1	0.03824	0.03824	14.92	0.0010
(-1/Temperature)	1	0.00710	0.00710	2.77	0.1111
Error	20	0.05126	0.00256		
Total	33	0.26979			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Rain	7.26×10^{-4}	3.2×10^{-4}
$(Rain)^2$	-1.18×10^{-6}	5.1×10^{-7}

Table 5.2: Analysis of covariance on proportions of pupae in nests.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Location	5	0.01326	0.00265	0.35	0.8753
Month	5	0.12402	0.02480	3.29	0.0251
Rain	1	0.17651	0.17651	23.39	0.0001
$(Rain)^2$	1	0.18929	0.18929	25.08	0.0001
(-1/Temperature)	1	0.04759	0.04759	6.31	0.0207
Error	20	0.15094	0.00755		
Total	33	0.70161			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Rain	1.37×10^{-3}	5.79×10^{-4}
$(Rain)^2$	-2.21×10^{-6}	0.80×10^{-6}
(-1/Temperature)	7.243	3.492

Table 5.3: Analysis of covariance on ratios of major to minor caste workers in nests.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Location	5	0.96294	0.19259	1.90	0.1396
Month	5	2.21493	0.44299	4.37	0.0075
Rain	1	3.44865	3.44865	34.00	0.0001
$(Rain)^2$	1	1.33157	1.33157	13.13	0.0017
(-1/Temperature)	1	0.04143	0.04143	0.41	0.5300
Error	20	2.02846	0.10142		
Total	33	10.0280			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Rain	-6.06×10^{-3}	2.15×10^{-3}
$(Rain)^2$	6.74×10^{-6}	2.95×10^{-6}

Monthly changes in average larval proportions (both with and without adjustment for rainfall) are shown in figure 5.15; individual data points are mean proportions at each site adjusted for rainfall effects. This plot demonstrates the large variability in January, March, and May, when mean larval levels were highest. Adjusting for rainfall effects did not substantially alter the seasonal pattern in larval proportions. Higher rainfall resulted in an increase in the larval fraction in nests, up to an asymptote which appeared to occur at around 200 mm rain/month. Unfortunately, little rain fell during the sample months, with rainfall over 200 mm occurring only on 2 occasions. Higher monthly totals were recorded during the months in between sampling (as can be seen from the range of rainfall figures plotted in fig 5.18, for the relationship of pupal number to previous month's rainfall). Because there were so few high rainfall data points, the curve fitted in figure 5.16, and used in the analysis of variance was the simpler parabola. This curve adequately fits the available data. More data during high rainfall periods are needed to determine the true form of this relationship, which may not be genuinely parabolic.

Pupal proportions were lowest from July to November, when nests also had fewest larvae (figs 5.9c - 5.14c). During July and September, many nests were totally devoid of pupae. Maximum pupal levels appeared to lag peak larval numbers by one sample period, with maxima at most sites in March and/or May. Very high variability was again observed at times of high mean pupal numbers. An analysis of covariance found transformed pupal proportion varied with month ($F=3.3$, 5x20df, $F=0.025$; table 5.2). It was related to the previous month's rainfall in a parabolic pattern (for rain term, $F=23.4$, 1x21df, $P=0.0001$; rain squared term, $F=25.1$, 1x20df, $P=0.0001$). A more distinct parabolic

Figure 5.15 - 5.16. Variation in larval proportions.

Figure 5.15. Seasonal variation (adjusted for rainfall effects)

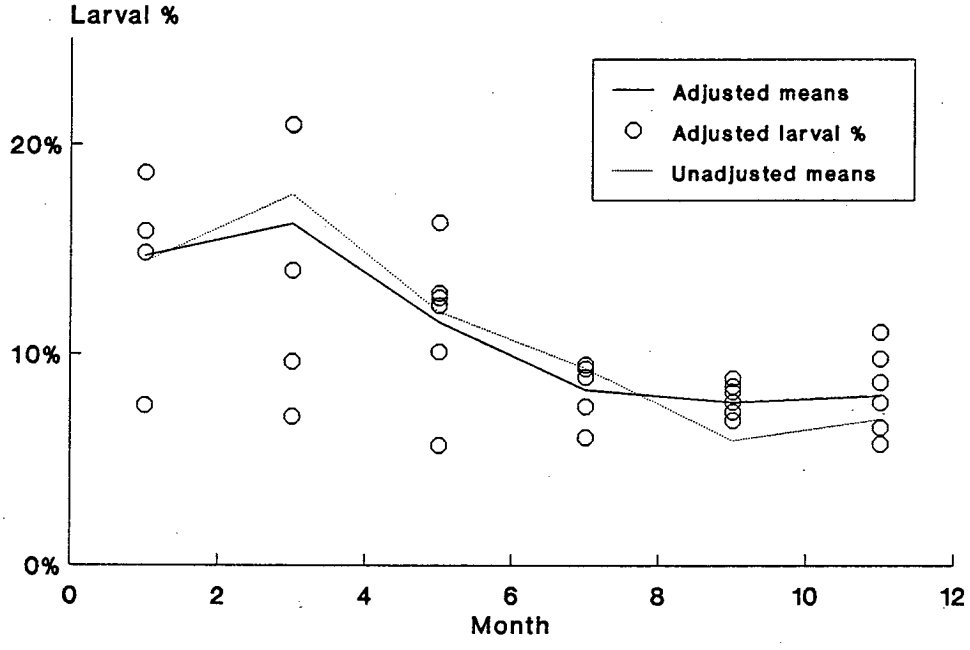


Figure 5.16. Effect of current month's rainfall (adjusted for seasonal trends)

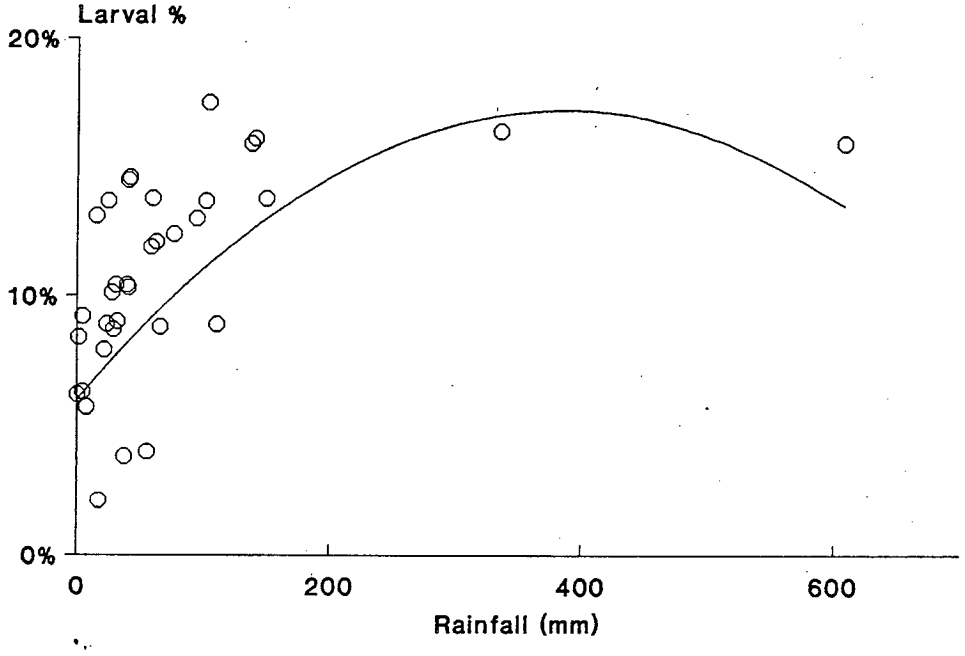


Figure 5.17 - 5.19. Variation in pupal proportions.

Figure 5.17. Seasonal variation
(adjusted for rainfall, temperature)

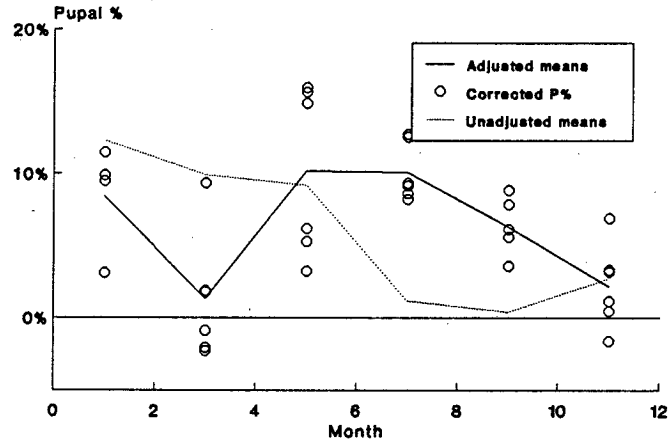


Figure 5.18. Effect of previous month's
rain (adjusted for month, temperature)

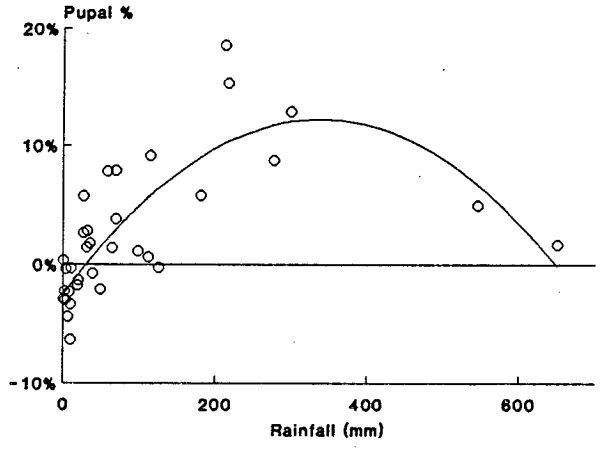
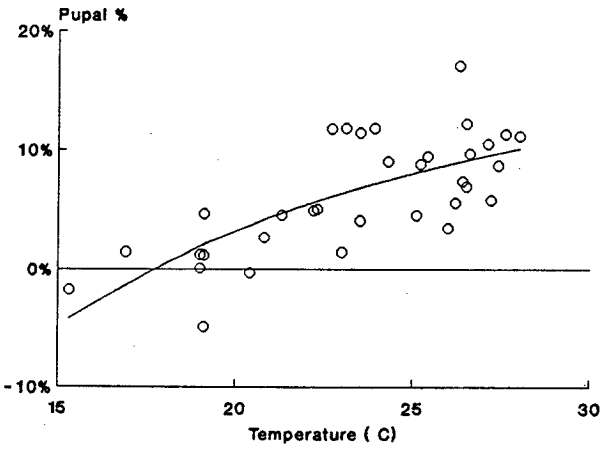


Figure 5.19. Effect of temperature
(adjusted for month, rainfall)



response is evident in this case (fig 5.18), with apparent declines in pupal proportions at rainfall levels both above and below an optimum of around 350 mm. Pupal fractions also varied with the current month's temperature in a negative hyperbolic relationship ($F=6.3$, 1x20df, $P=0.02$), although this relationship was less well-defined (fig 5.19).

After adjusting for rain and temperature effects, mean pupal proportions were highest during May and July, and lowest in March and November (fig 5.17). This pattern differs substantially from unadjusted means, which were high from January to May, and low from July to November. The marked reduction in March after covariate adjustment suggests that pupal production at this time may have been suppressed. In the months with highest variation, the distributions of adjusted data appeared to be bimodal, further suggesting that pupal production might "switch" between activated and suppressed states.

Seasonal variation in the ratio of major to minor caste workers (M/m) followed a pattern essentially the opposite to that occurring in pupal numbers ($r^2=-0.38$, 33df, $P<0.0001$). Major workers outnumbered minors in all nests sampled, with highest M/m usually from September to November, and lowest in January or March (figs 5.9d - 5.14d). An analysis of covariance indicated month ($F=4.4$, 5x20df, $P=0.007$; table 5.3), previous month's rain ($F=34.0$, 1x20df, $P=0.0001$), and rain^2 ($F=13.1$, 1x20df, $P=0.001$) were all significantly associated with M/m.

M/m adjusted for rain effects was reasonably constant from March to November, and dropped during January (fig 5.20). Data adjusted for monthly effects displayed an inverted parabolic response to the previous month's rainfall, with a minimum in M/m at 329 mm (fig 5.21). This relationship must be regarded as tentative, however, due to lack of high rainfall data.

Figure 5.20 - 5.21. Variation in ratio of minor to major worker adults.

Figure 5.20. Seasonal variation (adjusted for rainfall effects)

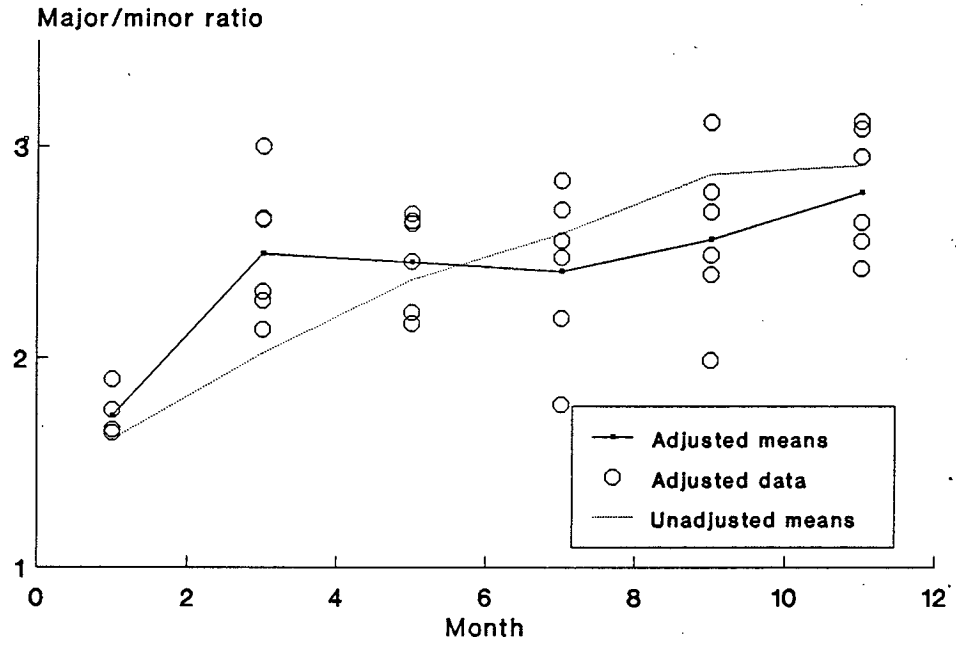
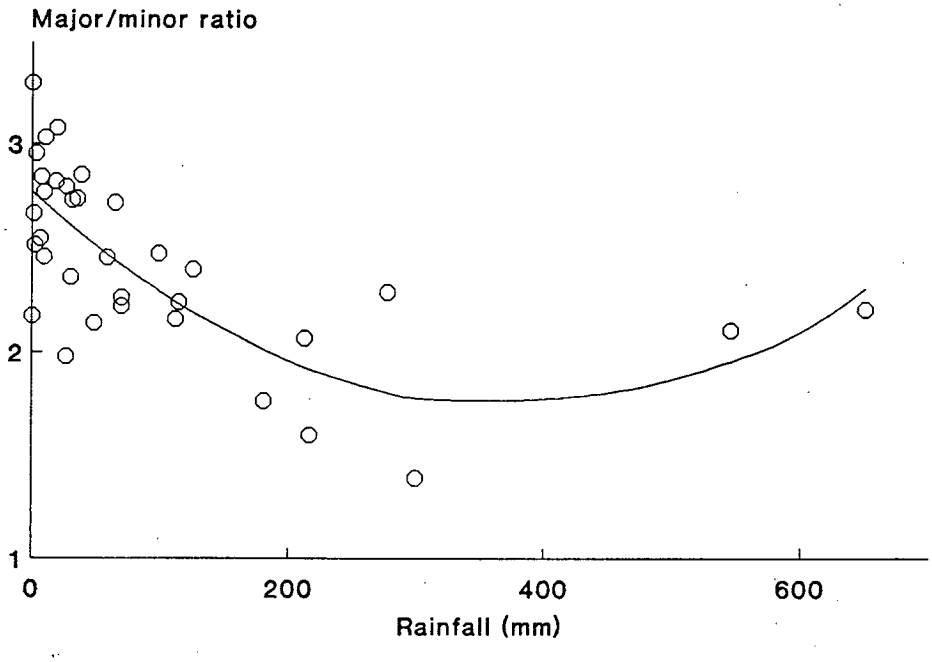


Figure 5.21. Effect of previous month's rainfall (adjusted for seasonal trends)



1986 - 1989:

The mean proportions of larvae and pupae, M/m ratios, and total nest population sizes for nests collected from November, 1986, till March, 1989, are given in figure 5.22. Using the models derived from the 1984/1985 data, predicted larval and pupal proportions, and M/m ratios were also plotted. Unfortunately, these models were only partially successful at predicting the observed patterns of nest composition from 1986 to 1989.

Observed larval proportions were relatively similar to predicted values in nests collected from 11/86 to 11/87, and 11/88 to 3/89 (fig 5.22a). During the intervening period, however, larval levels were much higher than predicted, and peaked in April, instead of January. The coefficient of determination between actual and predicted values was only 0.02 for the entire sampling period (16df, P=0.6), but reached 0.49 if data from 12/87 till 8/88 were omitted (9df, P=0.04).

The proportions of pupae in nests were poorly estimated by the derived model (fig 5.22b). The general patterns of both lines were roughly similar, but maxima and minima were displaced. For example, observed pupal levels in 1987 and 1989 peaked 2 months later than predicted. Also, a secondary peak in pupal levels in May, 1988 (caused by the extended period of larval production in this year) was not predicted. The coefficient of determination between calculated and actual values was only 0.11 for the entire trial (16df, P=0.21), and 0.27 if the period of anomalous larval production was deleted (9df, P=0.15). The large inter-nest variation in pupal proportions may have contributed to this poor fit.

Observed M/m ratios followed the pattern predicted reasonably well over all of the sampling period, except January (fig 5.22c).

Figure 5.22. Temporal variation in nest composition in Townsville study site. Values predicted by earlier analysis are also shown.

Figure 5.22a. Larval proportion

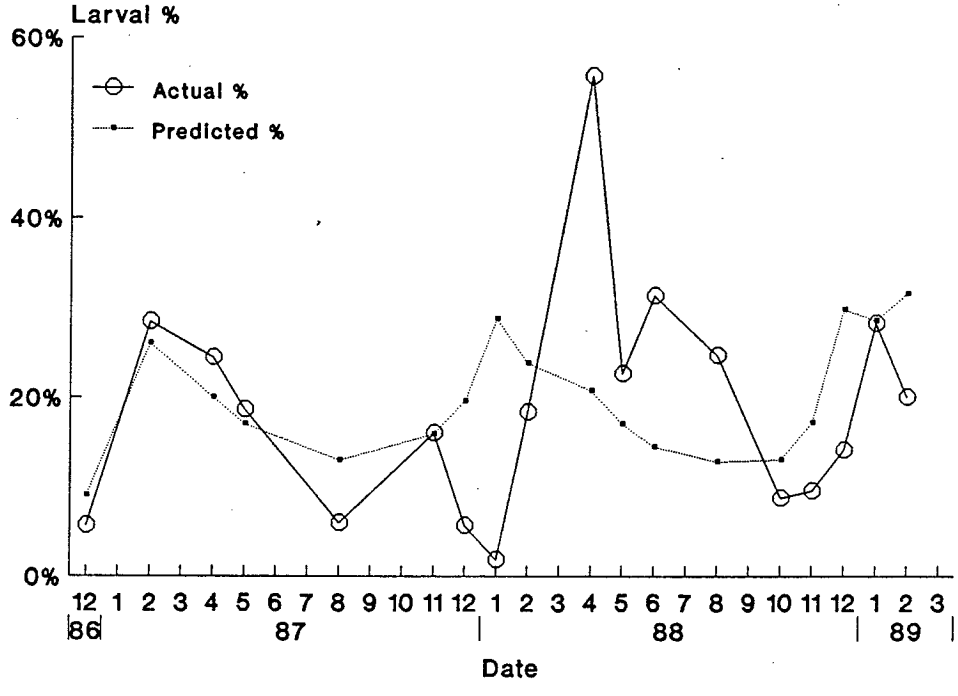


Figure 5.22b. Pupal proportion

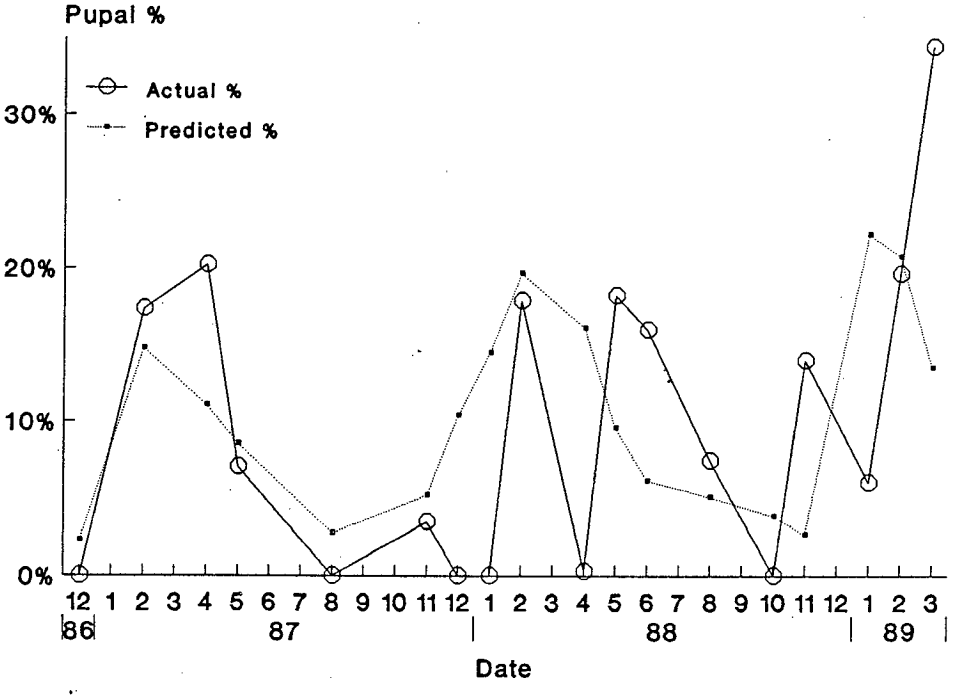


Figure 5.22 (continued).

Figure 5.22c. Major/minor ratio

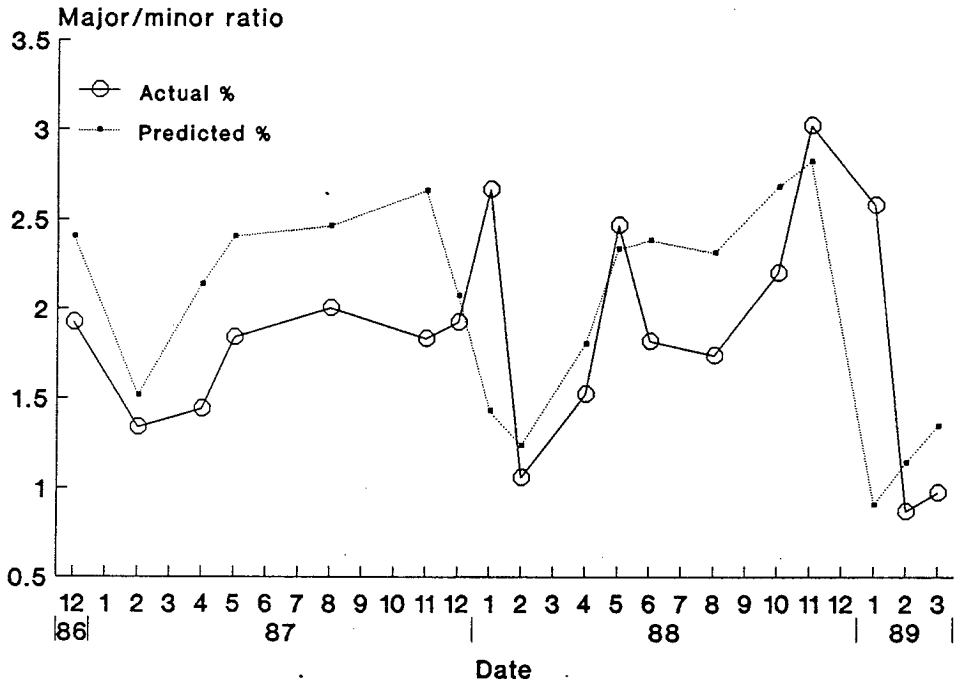
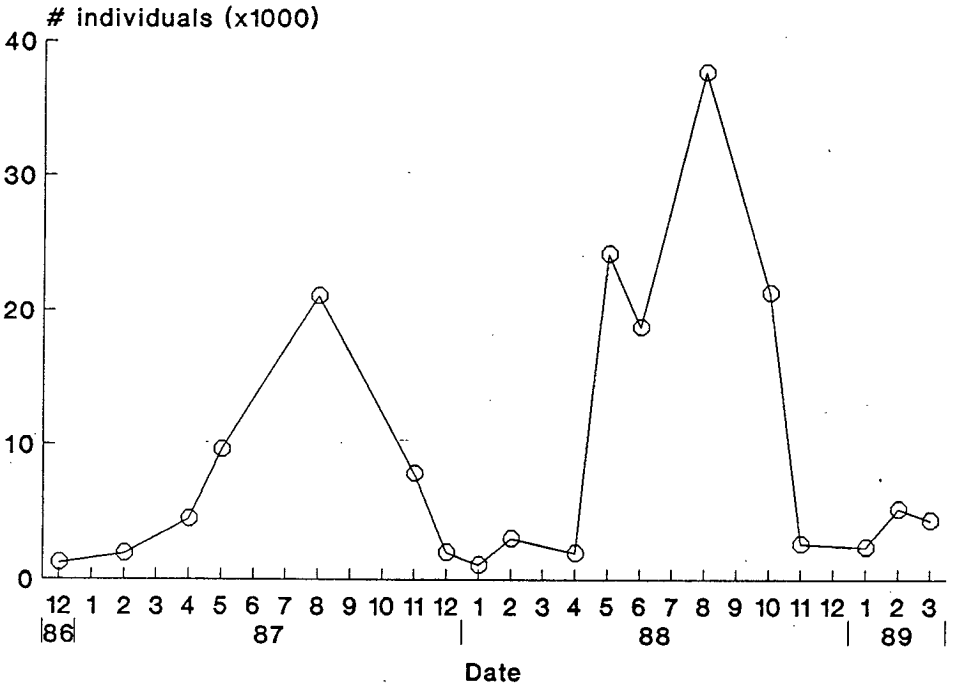


Figure 5.22d. Total nest population



The derived model predicted a sudden drop in M/m in this month, whereas actual values dropped a month later. The coefficient of determination including January data was only 0.17 (16df, P=0.12), but without these 2 values, rose to 0.75 (14df, P<0.001).

The total number of individuals in nests sampled from 1986 to 1989 also underwent a marked seasonal pattern, with maximum levels in August, and minimum from December to February (fig 5.22d). This noteworthy trend was masked in the 1984/85 trial by the artificial selection of large (>1 litre volume) nests, and may partially account for the substantial differences in patterns of nest composition between the 2 trials.

5.3.6. Worker size.

Green tree ant workers were readily classified into major and minor castes using thorax (alitrunk plus petiole) length, or scape length (fig 5.23). The 2 castes were mutually exclusive, with a gap of 0.35 mm in thorax lengths, and 0.63 mm in scape lengths, between the largest minor and smallest major worker. The relationship of scape to thorax length in minor workers was:

$$\text{Scape} = -0.80 + 1.16\ \text{Thorax} \quad (r^2=0.72,\ 47df,\ P<0.0001)$$

For major workers, the regression of scape to thorax length was:

$$\text{Scape} = 0.69 + 0.67\ \text{Thorax} \quad (r^2=0.62,\ 123df,\ P<0.0001)$$

Although thorax and scape lengths were highly allometric between castes (as demonstrated by the substantially different regressions), the relationship was quite consistent within each caste.

Figure 5.23. Scape and thorax lengths of major and minor caste workers.

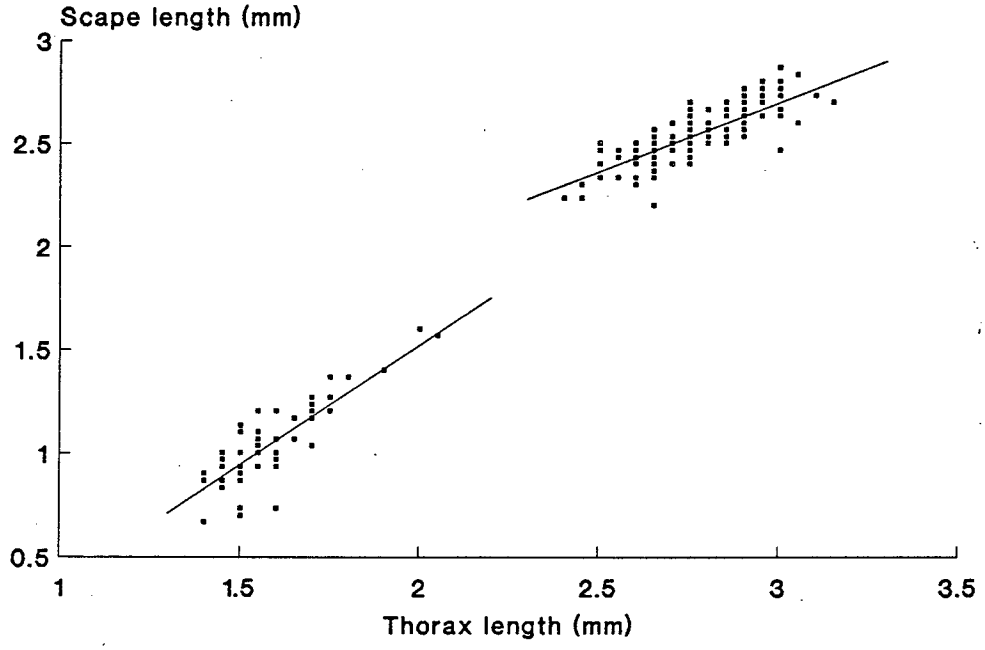
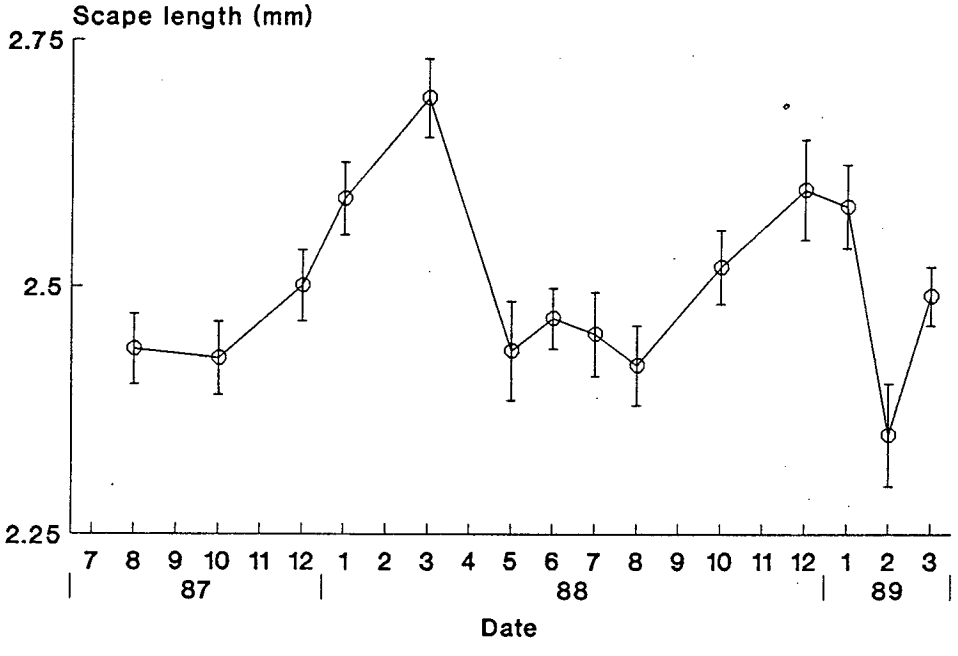


Figure 5.24. Temporal variation in scape lengths of major caste workers.



The mean scape lengths of major workers fluctuated markedly during the period from August, 1987, to March, 1989 (fig 5.24). However, the pattern of variation observed was rather erratic. Scape lengths peaked during summer, once in January to March, and again from December to January. Minimum scape lengths usually occurred in workers during winter (August to October, and May to August), but the smallest majors of all were recorded in February, 1989.

5.4. Discussion.

In native riparian forest, the average number of trees occupied by *O. smaragdina* colonies ranged from 45±9 trees in November, to 76±9 trees in May. Colony areas over the same period varied from 323±39 m^2 to 518±53 m^2. Hölldobler (1983) recorded relatively similar colony areas for this species in a higher rainfall locality 300 km further north, ranging from 400 to 1500 m^2 in forest, and 200 to 800 m^2 in mangrove habitat. However, the number of trees per colony were lower, 3 to 21 trees/colony in forest, and 12 to 44 trees/colony in mangrove. The average canopy size of trees in Hölldobler's site may have been larger and tree densities lower than in the Townsville site, which would account for his lower colony tree counts. Colonies of *O. longinoda* in forest habitat in Kenya show a similar trend with areas from 300 to 1600 m^2/colony, but only 6 to 17 trees/colony (Hölldobler, 1980).

Colony extents in the Major Ck mango plantation were much smaller, with 1.5±0.5 trees/colony in December (range 1-5), and 3.2±1.2 trees/colony in July (range 1-11). This difference in colony size was

attributed to the absence of canopy interconnections for movement of ants between trees, caused by the low tree density in the plantation. Access to all parts of the colony is essential for this strictly monogynous species, to transport brood among nests, and to maintain a uniform colony recognition odour. Brian and Adedoyin (1978) found that colony sizes of *O.longinoda* in Nigeria were also restricted by the need for interlocking canopies. Regular removal of understorey vegetation between mango trees may have contributed to the low colony size, by eliminating another pathway between trees, and destroying a potential food source, the homopteran and insect populations which inhabited the undergrowth.

Most weaver ant studies have been conducted in plantation habitats. Way (1954a) recorded *O. longinoda* colony extents in coconut and clove trees in Zanzibar, ranging from 1 to 12 trees. The largest colony covered an area of 800 m^2. Distribution maps of ant colonies in the same locality, by Vanderplank (1960), show colonies from 1 to 9 trees in size in March, 1955, and from 1 to 39 trees in March, 1956. The discrepancies in colony extents between the 2 years suggest that the largest colonies during 1956 were in fact a number of smaller colonies. Leston (1973) states colonies of weaver ants in cocoa plantations in Ghana can cover over 20 trees, and Taylor and Adedoyin (1978) assert that colonies in Nigeria may occupy over 100 cocoa trees.

These differences in colony sizes could be caused by vegetation influences, such as tree density, tree condition, levels of canopy interconnection, amount of understorey growth, and the proximity of native forest vegetation. Insufficient quantitative information on these variables is available to allow comprehensive comparisons between these studies and my data. Majer (1976a) observed that the distribution

of weaver ants was not correlated with a subjective index of cocoa canopy density. However, he did not examine colony extents, except to note that boundaries fluctuated seasonally with canopy condition. Bigger (1981) found that a population of *O.longinoda* in cocoa coincided with areas of tall undergrowth, which provided extra nesting sites and food, but he also did not differentiate colonies.

Trees may influence weaver ants directly by providing clusters of leaves for nest construction, and allowing inter-tree access when canopies interconnect. Indirectly tree condition can affect the abundance of arthropod fauna, both homopterans for honeydew, and other arthropod prey (Gibbs and Leston, 1970). The seasonality of arthropod abundance will be examined further in analyses of food intake (section 6.3.5), and of arthropod numbers in mango leaf samples (section 7.3.1). The density of tree cover may also alter the amount of understorey vegetation, which is a further source of nesting sites and food.

Another possible factor limiting colony extent is inter-specific and intra-specific competition between ants. As discussed in section 3.4, the distribution of weaver ants in tropical tree crops can be restricted by other aggressive territorial ant species. Various workers (e.g. Majer, 1976a; Vanderplank, 1960) have demonstrated that the mosaic distribution of ant colonies in tropical plantations is under compression. When ants were removed from areas of the mosaic, other colonies expanded rapidly into these gaps. Competitive compression has also been observed in some temperate ant communities (e.g Brian, 1956; Pontin, 1963, 1969; Rosengren *et al*, 1986).

The absence of other dominant ant species in the Townsville area (probably due to the drier, less equatorial climate; Greenslade, 1972) may contribute to the relatively large colony sizes in my native forest

site. Strong intra-specific competition did occur in certain areas of high tree density in the Townsville site from January to May, when colonies were expanding, suggesting some compression of colony size from the largest possible during these months. However, these interaction zones made up a relatively small proportion of the total colony boundaries. More typically, colonies were bounded by areas of low tree density. Aggressive territorial encounters with ground-dwelling ant species were very rare at these boundaries, except on 2 occasions, when an expanding *O. smaragdina* colony met an *Iridomyrmex purpureus* colony.

Seasonality of colony size in Townsville was correlated to the flowering and leaf flushing status of the inhabited trees. Majer (1976a) correlated a similar fluctuation in the number of cocoa trees occupied by weaver ant colonies in Ghana to seasonal changes in canopy density. Other workers (e.g Greenslade, 1971a; Brown, 1959) have ascribed seasonal variation in weaver ant distributions to seasonal changes in the distribution of more competitively dominant ant species, such as *Anoplolepis longipes*. The discrepancies between my results and research in wetter, more equatorial areas suggest that the controls on colony size and seasonality of *Oecophylla* differ between these regions. Distributions in the Townsville site appear to be determined primarily by the availability of suitable vegetation (and possibly some intra-specific competition), whereas in ant mosaics, colonies are limited more by inter-specific competitive interactions with other dominant ant species.

In a study of western North American ant communities, Bernstein and Gobbel (1979) observed a similar lack of inter-specific competition, which they postulated to be more prevalent in areas with

very diverse ant faunas, such as in tropical ant mosaics. This hypothesis is supported by research on southern Australian ant communities by Anderson (1986a,b). He found more intense inter-specific competition in arid regions, where ant abundance and diversity were higher than in wetter areas. Comparative studies of *O. smaragdina* colonies in habitats of varying ant diversities would help to elucidate the mechanisms controlling colony extent.

Reproductive effort also varied in distinct seasonal patterns. Nests contained sexual forms from November to March throughout the latitudinal range sampled. Wet season production of sexuals has been regularly documented in weaver ants (e.g. Greenslade, 1971b; Leston, 1973; Vanderplank, 1960; Way, 1954a; Yamauchi *et al*, 1987), and in some other tropical ants (Hölldobler and Carlin, 1985; Schneirla and Brown, 1952).

All sexuals had been released by April, and no more were produced until November. In contrast, Greenslade (1971b) recorded sexual adults throughout the year in nests of *O. smaragdina* in the Solomon Islands, although sexual brood occurred seasonally. He postulated that the retention of winged adults in the drier months inhibited the development of more sexual brood. No evidence of such a mechanism was observed in Queensland populations, which release all adult sexuals during the wet months.

Worker brood production was also highest in the wet season months. Larval proportions peaked from January till March in most localities. Larvae were surprisingly few in November, possibly because sexuals were produced at this time, at the expense of worker production. This inverse relationship between sexual and worker brood was reported by Greenslade (1971b). Larval proportions showed a positive linear

correlation with the current month's rainfall, in the range from 0 to 200 mm/month. Rainfall above 200 mm did not appear to influence larval levels, but unfortunately, few sample months had such high rainfall figures.

The proportions of worker pupae, unadjusted for weather factors, peaked in January to May. Pupal levels were affected by the previous month's rainfall in a parabolic pattern. Not surprisingly, the response of pupal production to rainfall lagged that of larval production. The interval is probably somewhat less than one month, as development from egg to pupa is only 22 days at 24°C, and 15 days at 30-35°C (section 4.3.1), but daily rainfall records were unavailable to improve the precision of this analysis. Pupae were most frequent when rainfall of 200 to 400 mm was recorded in the month prior to sampling, and were fewer below and above this figure. A switch to production of sexuals when rainfall levels are highest (and food is consequently abundant, see section 6.3.5.1) may account for the reduced pupal fraction at this time.

Low temperatures also depressed pupal proportions. This effect agrees with developmental rate results, which indicated that development during the larval stage was most restricted by low temperatures (section 4.3.2). The maintenance of a small larval population throughout the year is necessary to supply silk for nest construction and repair. Significantly, larval percentages never dropped below 2% in any nest sampled, while pupae were regularly absent from nests in the winter months.

The seasonal pattern of pupal proportions was markedly altered by adjustment for temperature and rainfall effects (whereas the pattern of larval proportions was not). March levels were much lower, and July

levels much higher than unadjusted levels. The low temperatures during July, and to a lesser extent, September, appear to be the primary cause of low pupal levels during this period. The March depression is less explicable, and could be caused by many factors, such as a diversion of effort to sexual production, the presence of several peaks of brood production (which cannot be detected with 2 month sample intervals), or changing food levels. During the wet season months, pupal proportions from different localities appeared to be distributed bimodally, with high production in some, and low in others. These results suggest the existence of some mechanism(s) which switch pupal production on and off. More detailed examination of the temporal variation in pupal green tree ant brood is needed to elucidate such a mechanism.

The ratio of major caste to minor caste adult workers also varied seasonally, in a pattern essentially the reverse of that seen in larval proportions. However, this measure is biassed by the unknown numbers of major workers foraging outside the nest at the time of sampling. The high proportion of majors when reproductive effort is low may thus be due to a decrease in the relative numbers of minor workers, or fewer major workers foraging outside the nest. Plans to estimate the size of foraging populations using mark recapture techniques had to be abandoned when no suitable marking technique could be found (section 6.2.3).

The nest composition models derived from the 1984/1985 data predicted the observed patterns of composition in subsequent nest samples reasonably well. However, a peak in worker brood production during the period, May to August, 1988, was not anticipated by the models. This unseasonal burst of reproductive effort is not explained

by any combination of temperature, rainfall, or seasonal patterns.

The total nest populations in the 1986 to 1989 sampling period (when nest size was less biassed by collection of large nests only) were large from May to October. The majority of nests sampled from November to April contained less than 5000 individuals, including brood. The density of small nests in trees peaked during this period, with maxima from November to March in *Pongamia pinnata*, and from February to May in *Zizyphus mauritiana*. During the wet season months, colonies thus appeared to be dispersed in larger numbers of nests with small populations, and later in the year were concentrated in fewer nests with large populations. Hölldobler and Lumsden (1980) demonstrated mathematically that the decentralization of nests in weaver ant colonies reduces defence costs in relation to net foraging benefits, at colony sizes beyond a certain minimum threshold. The increased dispersal of nests, during the season of colony expansion (December to May) may thus improve the defensibility of territories at a time when inter-colony encounters are most frequent. Decentralization also allows foragers to distribute more evenly throughout the territory, so encountering more food items, and reduces food transportation distance, from collection point to nest. Increased dispersion may hence improve the efficiency of food collection, when highest levels of food are necessary for brood development.

The temporal dynamics of green tree ant colony structure in Townsville can be tentatively described from these results. Colonies were most active during the wet season months, from November to March, and the early dry period until May. They were relatively dormant during the later dry months.

At the beginning of the active period, around November, colonies

extents were at their smallest, occupying a minimum number of trees. The density of small nests rose, and the average nest population dropped markedly, producing a more dispersed distribution of ants throughout the colony. Sexual brood were usually produced from November until March. Worker brood production occurred mainly from January till May. This season of high reproduction corresponded to the period of highest food intake, from December to May (chapter 6), and to the period of maximum flower and new leaf growth in most trees. Colony extents steadily rose until May, probably as a consequence of the influx of new workers into the colony. Nests remained low in population and highly dispersed until May.

After May, levels of reproduction dwindled, nest density dropped, and nest populations rose markedly. Colony extents slowly dropped, with ants gradually evacuating from peripheral trees into smaller core areas of high tree density. This trend was encouraged by the deciduousness of some trees and the general decline in tree condition during this period. The levels of ant activity outside the nest, examined in the next chapter, also followed this seasonal pattern.

6. Activity and food intake.

6.1. Introduction.

6.1.1. The components of activity.

The activity of an ant colony is the sum of all of the separate behavioural acts performed by its constituent ants. Although individual ants have a relatively limited behavioural repertoire (compared to that of vertebrates), complex patterns of synergistic activity can be produced. Estimates of the numbers of distinct behaviours in ant species include 27 in *Pheidole dentata* (Wilson, 1976b), 29 in *Leptothorax curvispinosus* (Herbers and Cunningham, 1983), 29 in the leaf cutter ant, *Atta sexdens* (Wilson, 1980), and 42 in the arboreal *Zacryptocerus varians* (Wilson, 1976a).

These behaviours can be grouped by location: inside and outside the nest. Intra-nest activity encompasses queen care, brood care, nest maintenance, and grooming. Food storage and trophallaxis are important behaviours inside nests of larger colonies. Workers of some species also tend populations of homopterans in their nests (e.g root aphids in *Lasius niger* nests, scales on leaves of weaver ant nests; Way, 1963).

Some activities are observed inside and outside the nest, such as trophallaxis and grooming. Tasks restricted to outside the nest include foraging, guarding, and defence. Foraging is generally considered to be the main extra-nest activity of ants, and will be described in detail later.

In polydomous colonies (i.e. colonies inhabiting more than one nest), worker migration between nests may form an important behaviour, ensuring a continual mixing of the colony recognition scent (e.g. in *Oecophylla*; Ledoux, 1950), and possibly also guarding against invasion by other ants (Hölldobler and Lumsden, 1980). Workers of polydomous colonies with only one functional queen (such as *Camponotus kiusiuensis*; Ito *et al*, 1988; *Oecophylla spp*; Way, 1954b) have the further task of transporting brood and/or callows from the queenright nest to other nests. Species which have strongly mutualistic associations with a homopteran species may also transport certain stages of the bug to favourable feeding sites. Way (1954a) observed *O. longinoda* workers transporting young *Saissettia zanzibarensis* nymphs to growing twigs near their nests. Similar records have been made for species of *Lasius*, *Acropyga*, *Crematogaster*, and *Dolichoderus* (Carroll and Janzen, 1973).

The division of these tasks among the workers of the colony can be controlled by age (age polyethism), size (size and caste polyethism), and individual preferences for tasks (idiosyncrasy; Lenoir, 1987). The commonest temporal sequence of polyethism begins with queen and young brood care by newly emerged workers, and progresses with increasing worker age, through older brood care to extra-nest tasks, and finally foraging. Mortalities of ants engaged in this last task are very high in some species, with life-spans averaging 14 days in *Pogonomyrmex owheei (Porter and Jorgensen, 1981)*, and 6.1 days in *Cataglyphis bicolor* (Schmid-Hempel and Schmid-Hempel, 1984). Foragers of *C. bicolor* in the laboratory could survive for months, suggesting that the dangers of foraging, not natural senescence, were responsible for this high mortality. Field survival rates may be higher

in some species, as evidenced by results such as the recapture of marked foragers of *Formica rufa* over 5 months later (Rosengren, 1971, 1977). A further stage of polyethism occurs in *O. smaragdina*, where old workers occupy "barrack nests" around the periphery of the colony's territory. These workers are the front-line defenders in territorial battles (Hölldobler, 1983).

Division of labour is also often observed between workers of different sizes, in species both with and without polymorphic castes. In most polymorphic species, the foragers generally belong to the smaller size classes, and the largest often perform a defensive role (Carroll and Janzen, 1973). In *Oecophylla*, however, workers of the larger major caste forage, while the smaller minors tend the brood, and both act in defence (Wilson and Hölldobler, 1977b). In the monomorphic acorn ant, *Leptothorax cuvispinosus*, the largest ants are foragers, and the smallest care for the brood (Herbers and Cunningham, 1983).

In many species, polyethism also occurs between workers of similar size and age. This idiosyncrasy of workers appears to be determined by stimuli during 2 sensitive periods, at the early larval and callow stages (Lenoir, 1987). Workers may also switch tasks in response to changing needs within the colony (Herbers, 1980; Gordon, 1989).

6.1.2. Food intake and its measurement.

Ants have evolved to exploit a wide range of foods. Many ant species are primarily scavengers on dead animal matter, and are opportunistic predators (Carroll and Janzen, 1973). Some are generalist predators of arthropods (e.g. army ants). Others specialize on a group of insects, such as termites (e.g. the genus *Termitopone*) or ants (e.g.

the tribe Cerapachyiinae).

A number of ant species forage on specific portions of plants. Some ants collect seeds (e.g. the desert dwelling seed harvesters such as *Pogonomyrmex*), and the leaf-cutter ants (tribe Attini) feed on fungus cultured on fragments of leaves or flowers of various plants. A few species, involved in obligatory mutualisms with plant species, feed on special food bodies produced by the plant (e.g. Beltian bodies on Acacia species are foraged by Pseudomyrmex spp. ants; Janzen, 1966).

Another commonly utilised food is sugar-rich exudate, from extra-floral nectaries, or honeydew producing homopterans. Although some species survive on these secretions alone, most ants (including *Oecophylla*) combine animal protein and honeydew, in varying proportions, in their diets. The analysis of feeding patterns is greatly complicated by this mixed foraging strategy, for reasons outlined later in this introduction.

Prey and large scavenged items are not consumed *in situ* by foragers of most species, but are carried back to the nest by one or more ants. By collecting ants holding items in their mandibles, many studies have monitored prey intake (e.g. Holt, 1955; Rosengren *et al*, 1985; Wehner *et al*, 1983). Unfortunately, some disturbance to other ants, and possibly to the nest population, is caused by this intrusion. Manual collection of prey items is also very labour intensive, especially if ants forage continuously day and night. A number of workers studying wood ants (Cherix, 1987; Rosengren *et al*, 1987; Skinner, 1980b) have used versions of an "automatic" prey collector (sometimes referred to as a Chauvin trap), based on earlier designs by Leplant and Chauvin (1966, quoted in Skinner). The nest was isolated with an ant-proof fence, and ramps were installed passing through the

fence in either direction, so that ants could pass in on one and out on the other by falling off the ramp ends. The returning ants were forced to travel through a box with a hole large enough for themselves, but not for large prey items. All prey items larger than the ants could thus be collected. This system is, however, very disorienting for many species, including *O. smaragdina*, which refused to travel along the ramps.

Liquid food intake has been monitored less frequently, usually by weighing workers moving to and from honeydew sources (e.g. Degen *et al*, 1986; Dreisig, 1988; Holt, 1955; Jensen, 1977; Skinner, 1980b). Dreisig (1988) found that the mean fresh weight gained by 4 European ant species (from homopteran populations), and 4 American species (from extra-floral nectaries) was highly correlated to their initial unfed weight. Fresh weight gain by the weaver ant, *Polyrhachis simplex*, however, varied both with time of day and month, while dry weight remained relatively constant. Degen and Gersani (1989) ascribed this loss in moisture content during hot periods to an evaporative cooling mechanism of the mealybugs or of the ants, in the hot, dry Judaean Desert region.

In many species, varying numbers of workers forage for other foods, also producing variation in the mean crop load of returning foragers. For example, Skinner (1980b) found higher numbers of *Formica rufa* foragers returning to the nest with honeydew-laden crops (i.e. replete) in spring and autumn, than in summer. These changes may be caused by the varying nutritional requirements of the brood and adults of the colony, and by changes in quantity and/or quality of honeydew and prey sources (Sudd, 1987). Recent studies (Brian and Abbott, 1977; Howard and Tschinkel, 1981; Petralia and Vinson, 1978; Sorensen et al,

1983, 1985; Traniello, 1989) indicate that different subcastes, and larvae, in dualistic feeding ants, can cause changes in requirements for protein and sugar. The presence of hungry larvae mainly increases protein uptake, whereas adult hunger stimulates collection of sugary food.

The volume and composition of honeydew can vary between different species, ages, and physiological states (e.g. seasonal flowering and leaf flushing) of the host plant (Auclair, 1963). Different species and strains of homopterans, and the length of time homopterans have fed on the plant can also affect honeydew (Way, 1963). Sudd and Sudd (1985) reported a sudden rise in the median acceptable concentration of sugar solutions offered to *Formica lugubris*, in mid-summer, corresponding to the appearance of certain obligate myrmecophilous aphids. Other workers have observed shifts in foraging from one tree species to another, with changes in homopteran populations (Ayre, 1958; Benzie, 1985; Skinner, 1980b).

The reliability of weight difference methods for monitoring liquid food intake is affected by additional factors, including size or task variation among foragers, trophallaxis during foraging, and honeydew production inside nests. Variability in forager size will increase the heterogeneity of intake estimates. Biased results may be produced if size changes with time. Minor workers of the alpine ant, *Formica neorufibarbis*, forage earlier in the day than major workers, a trend Bernstein (1976) attributes to the darker colour and higher surface-to-volume ratio of the minors. A simultaneous sample of incoming and outgoing workers of this species during mid-morning may thus collect exiting majors and returning minors. Colonies of the monomorphic harvester ant, *Pogonomyrmex badius*, also display circadian cycles of

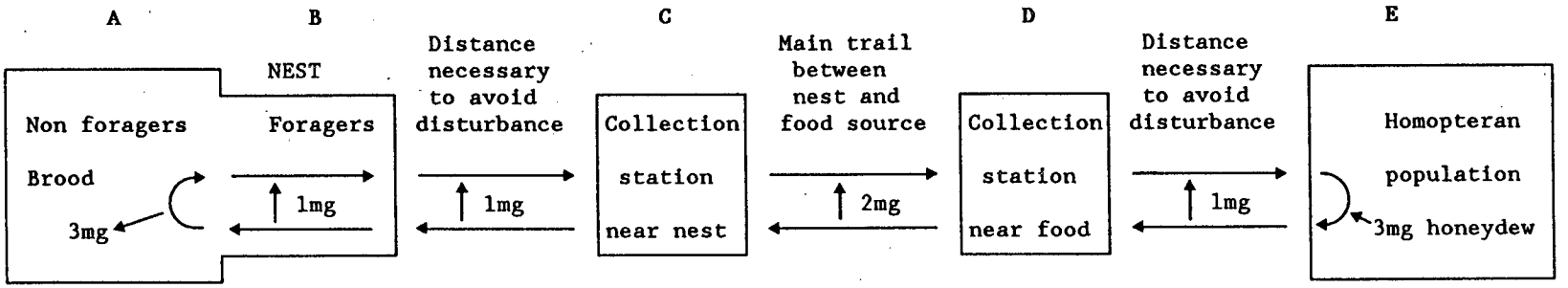
activity, which differ between the 5 tasks performed outside the nest. Patrolling ants, for example, are observed most frequently a few hours before foraging ant numbers peak (Gordon, 1983, 1986). Such changes in tasks throughout the day could easily bias measurement of crop weight. Rosengren (1977) found no evidence of diel subdivision in *Formica rufa*, but few studies have examined this aspect of activity.

Liquid food is also transferred trophallactically from returning workers to leaving workers, both on trails outside the nest, and within the nest (fig 6.1). Trophallactic exchanges means that the measurement of differences in weight between incoming and outgoing workers will underestimate the total amount of honeydew collected. This effect is demonstrated schematically in figure 6.1. Fully laden weight of an ant is set to 20 mg, and unladen weight to 12 mg, and a total of 5 mg is trophallactically passed from returning to leaving foragers. With equal inward and outward flow, weight difference at any one point is 3 mg, although total crop load is 8 mg. Nevertheless, the 3 mg value is an unbiased measure of the effective food input into the non-foraging nest population. If the outward ant flow is twice the inward flow, however, the estimate of food input varies with position of the monitoring point. No quantitative information on levels of forager trophallaxis have been published, to date.

Some species of ants have access to honeydew inside their nests. Some subterranean ants, such as *Lasius spp.* and *Acropyga spp.* tend populations of homopterans on roots within their nests (Way, 1963). Homopterans are often tended in the leaf nests of arboreal ants, such as *Oecophylla spp.* This source of food has also been little studied.

Figure 6.1: Schematic representation of potential food flow between foragers feeding on honeydew.

A, B, C, D, E: Sites from inside nest to homopteran honeydew source.
Weight of food entering non foraging nest population - 3 mg/ant
Forager weight when leaving nest - 12 mg
Forager weight when leaving feeding site - 20 mg



(a) Weights of inward and outward travelling ants when flow rates are equal.

Ant Direction	Weight into nest	Weight of ants at locations A to E				
		A	B	C	D	E
Out	3	12	13	14	16	17
In		15	16	17	19	20

(b) Weights when inward flow rate = 2 x outward flow rate.

Ant Direction	Weight into nest	Weight of ants at locations A to E				
		A	B	C	D	E
Out	3	12	12.5	13	14	14.5
In		15	16	17	19	20

In this study, food intake of the green tree ant, *O. smaragdina*, was monitored for a 2 year period. Prey were collected manually, and liquid food was monitored using the weight differential method. These results were analyzed for seasonal and circadian patterns in food intake. Some of the assumptions underlying the estimation of liquid food intake were also tested.

6.1.3. Foraging activity.

Foraging activity in an ant colony is influenced by conditions both inside and outside the nest. The level of hunger of ants inside the nest is the primary motivator of foraging behaviour, and originates from 3 sources - the brood, other adults, and the forager's own viscera (Vowles, 1955). Each hunger source may stimulate foraging to varying degrees, and for differing food types (e.g. hungry larvae increasing protein uptake, and adult hunger stimulating collection of sugary food).

Internal circadian rhythms may also regulate foraging activity in some species. Wood ants show a consistent pre-dawn peak in activity, in the field, and in constant laboratory conditions with 12 hours light, 12 hours dark photoperiod (Rosengren and Fortelius, 1986). This peak disappeared if a nest in the laboratory was subjected to continuous light (Rosengren, 1977). Lewis *et al* (1974b) found the start and end of foraging from a nest of the leaf cutter ant, *Atta cephalotes*, followed a persistent diel pattern for several weeks, but then underwent a major shift to a new diel rhythm. They suggested that the foraging cycle was re-set to different times of day (during which leaves contain varying levels of nutrients) in response to changing

nutritional requirements of the brood. The effects of varying hunger levels, and circadian clocks are very difficult to separate, in most cases.

External variables influencing foraging activity include the distribution of food resources in size, time, space, and quality; weather and climatic variation; and competition with other ant species (Traniello, 1989). Successful returning foragers can stimulate other ants to search for food, directly "exciting" them by vigorous antennation and other tactile messages. In some species, workers also leave chemical recruitment trails, which attract other foragers, to large or persistent food sources. The numbers of ants at a food source can, in many cases, be precisely adjusted according to the food quantity, quality, distance, using these recruitment systems (e.g. Cosens and Toussaint, 1985, 1986; Crawford and Rissing, 1983; Taylor (F.), 1977). Activity levels may thus respond to the levels of food encountered by foragers, especially in small colonies.

Temperature affects feeding activity in many species throughout the world. Different species of desert seed harvesters in America forage at distinct soil temperature ranges (Bernstein, 1979). Lynch *et al* (1980) observed 4 temperate ant species whose foraging activities correlated positively with high temperature, negatively with low temperature, or both. Rainfall was observed to reduce activity in *O. longinoda* (Brown, 1959), and *Formica rufa* (Skinner, 1980a).

The study of activity patterns in ants has been hampered by the difficulties in collecting records of movements on such a large scale. Earlier workers have manually observed ants moving to and from the nest (e.g. Holt, 1955; Ayre, 1958; DeBruyn and Kruk-deBruyn, 1972), but the presence of an observer can upset the behaviour of more perceptive

species. Manual counting also becomes very difficult when high flow rates occur (e.g. over 300 ants/minute in *Formica spp*; Skinner, 1980a), and requires a crew of workers in shifts to obtain continuous 24 hour records.

More recently, various automated counters have been developed, which record activity with much less disturbance (once the ants have habituated to the apparatus). Systems relying on weight changes (balance detector; Chauvin, 1965, in Skinner, 1980a), capacitive changes (McCluskey, 1958), or video scanning line comparison (Kruk-de Bruin and Tissing, 1975) work well in the laboratory, but are too fragile for outdoor use. Light beam detectors have been used successfully both in the laboratory (Rosengren, 1977, Rosengren and Fortelius, 1986; Siddorn, 1962), and in the field (Dibley and Lewis, 1972; Skinner, 1980a). Combining low initial cost, and low power consumption, light beam counters provide a reliable measure of ant activity, but often suffer from lack of accuracy. Underestimates are caused by ants passing through the beam together, and by very slowly moving ants. Overestimates occur when excited individuals break the beam repeatedly, or a large food item is carried through.

To study activity patterns in the tropical Australian green tree ant, *O. smaragdina*, a light beam counter which minimizes one major inaccuracy, underestimation due to ants passing through together, was developed. Results of activity monitoring for 2 years are presented, and analyzed for the existence of seasonal and circadian patterns. These patterns were compared to the cycles of prey and liquid food intake, and colony structure (chapter 5).

6.2. Methods:

6.2.1. Activity.

To study activity patterns in the green tree ant, *O. smaragdina*, a light beam counter which allowed continuous 24 hour/day recording was designed. The complete apparatus (fig 6.2) consists of three units - the sensor, interface circuitry, and a microcomputer. The sensor unit was designed to provide a pathway which directed the ants directly through the light beam, and restricted the number of ants which could pass through at once. Because this arboreal ant prefers to walk along twigs and edges, a 2 mm diameter monofilament nylon line was used, which provided good alignment, and allowed a maximum of 2 ants to pass together. Originally, a woven string was used to provide maximum grip for the ants, but the sensitivity of the system was found to slowly drop over a few weeks, from the build-up of pheromones and dust on the string. Replacement and realignment of the string was thus necessary every two weeks. Monofilament nylon was successfully negotiated by the ants, with no detectable reduction in running speed from a string path, and with minimal loss of sensitivity over a time span of 4 weeks.

The light beam was produced by an infra-red light emitting diode (LED), and detected by an infra-red phototransistor. Both were mounted in a blackened plastic pipe around the string path, to stop sunlight interfering with the beam. The supporting frame was built from aluminium for lightness and durability. To further reduce incident light on the beam, an adjustable joint was placed between the frame and the mounting plate. The counter could then be aligned on a horizontal north-south axis to prevent morning (eastern) and evening (western) sun from shining directly into the tube (see plate 6.1).

Figure 6.2. Design of light beam counter system for measuring ant activity in the field.

1 - Tree branch leading to ant nest.
2 - Electric grid (not powered if teflon coating diverted ant traffic through counter)
3 - Bolt for adjusting light beam alignment.
4 - Universal joint for adjusting orientation of counter.
5 - Coaxial lead to infra-red light emitting diode and receiver.
6 - nylon string.
7 - PVC pipe.
8 - Infra-red light beam.
9 - Counter frame.
10- 12 volt battery.
11- Voltage multiplier for grid.
12- Interface unit.
13- Microcomputer.

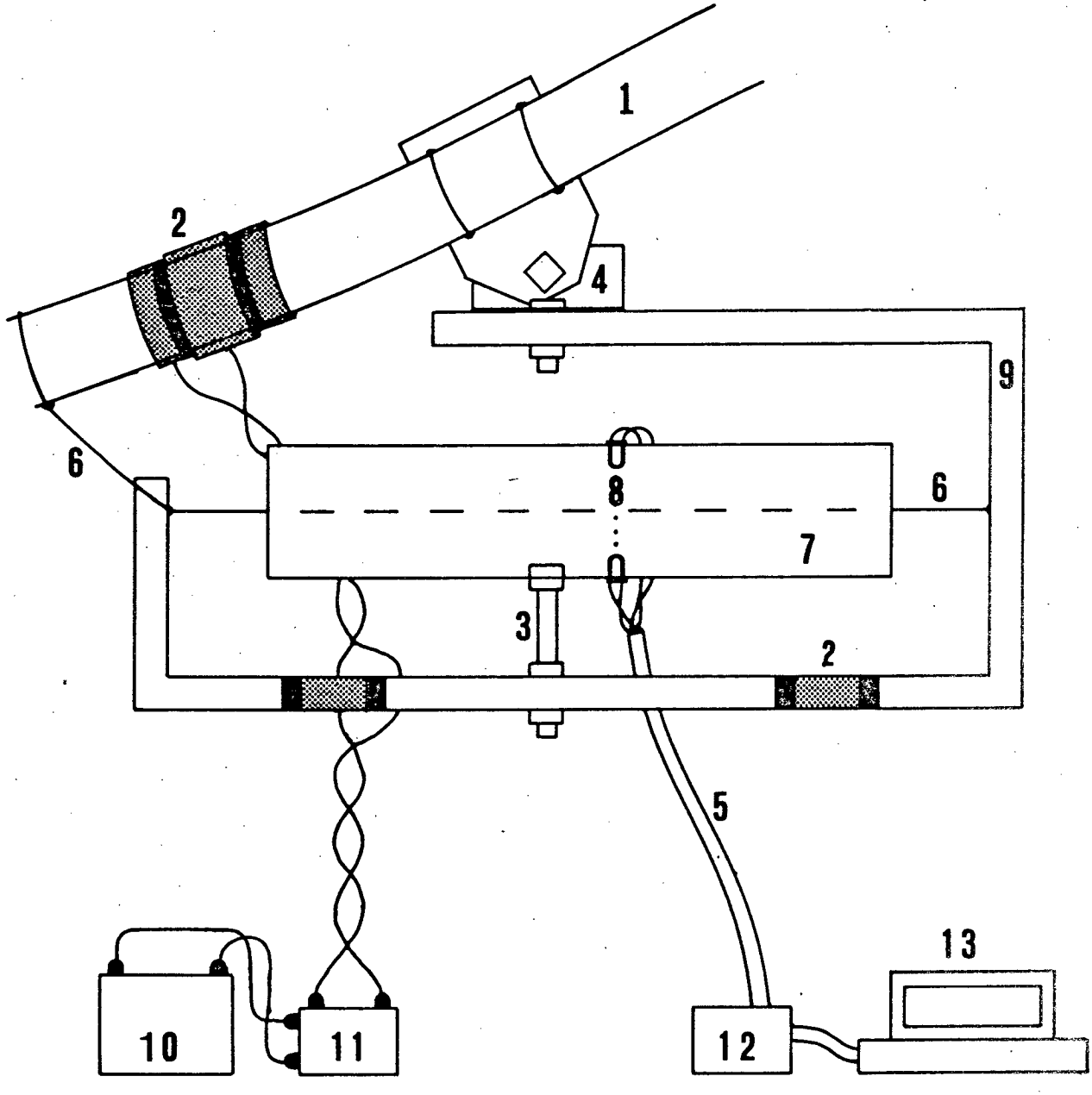


Plate 6. An ant counter operating in the field.

The complete sensor unit was attached to a branch leading to an ant nest (which consists of many leaves bound together with larval silk). Nests with few access branches were preferred, as these paths had to be blocked to coerce the ants into using the counter path. Many trail barriers were tested, including teflon, "tanglefoot" bird repellant, and various oils, but the only totally effective method was an electric "ant-fence". Each fence was made up of a base strip of aluminium-backed gutter sealant (flashband), and a thinner strip of aluminium foil, separated by an intermediate width, double-sided fabric tape. These grids, placed on each old access route and the counter frame, were powered by a voltage inverter/multiplier and 12 volt battery. For most activity trials, these grids were only necessary for a few days, until the ants discovered and pheromone-marked the string path, and the old pheromone trails dispersed.

In many trials, just the presence of the aluminium strips coated in teflon was enough to divert traffic to the new path. This technique was always tried first, as it involved much less equipment, and disturbed the ants much less. Over 25% of nests subjected to electric fencing were abandoned within a week, compared to only 8% of nests which were converted to the counter path using teflon-coated strips.

To record the sequence of beam cutting events, a microcomputer system was chosen over earlier mechanical methods (Dibley and Lewis, 1972; Rosengren, 1977; Skinner, 1980a). An interface circuit converted any signals from the light detector into an input compatible with the RS-232 serial port of a portable, battery operated Epson HX-20 microcomputer. A simple Basic program then stored this data as counts over set intervals, for 24 hours or longer. Power requirements for this equipment were very low, with one 12 volt lead acid battery lasting

over 10 days. The interface circuitry and microcomputer were stored in a weather-proofed plastic tote box, which provided sufficient protection, except during flash floods!

The accuracy and consistency of ant flow rates produced by this system were examined by comparing numbers of ants recorded by the counter to numbers observed manually, over 10 minute intervals. To test for biases due to variable flow rate, comparisons were conducted for rates ranging from 1/minute to 94/minute. Counts were also taken during light and dark periods to detect any variation in sensitivity with light level.

The major drawback of this counter system was its inability to differentiate inward and outward ant movements. To overcome this limitation, a more sophisticated sensor system, using 2 light beams, was developed. Direction could then be inferred from the order of beam cutting events. During periods of high flow rates, however, a false sequence could be triggered by 2 ants passing synchronously. Positioning the 2 beams very close together minimized this source of error, but increased problems with overlapping, uninterpretable signals. A more complex system with a storage buffer to cope with nearly simultaneous triggering, and which produces discrete, "clean" signals would be necessary to avoid these difficulties. Unfortunately, further development was halted by time, money, and technical limitations.

To assess the magnitude of variations between inward and outward flows, the numbers of ants moving in each direction were visually counted for nests in May, 1988, and December, 1988. The passage of ants in and out of each nest was monitored for ten minutes, every 2 hours, over a 24 hour period.

Earlier manual observations (Lokkers, 1982) suggested daily and seasonal variation in the activity of green tree ants, so I planned to compile counts of ants entering and leaving a nest over 10 minute intervals for at least 2 days, for each of 2 nests, every month for 2 years. This scheme was severely eroded by equipment problems (including power failures, battery problems, and microcomputer malfunctions), illness, and commitments to other research work. The numbers of days that nests were successfully monitored for activity in each month are given in table 6.1. From November, 1986, till March, 1989, 32 nests were observed, for a total of 74 nest-days.

Table 6.1. Numbers of days per month that activity trials were successfully completed from November 1986 to March 1989.

Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
86											2	2
87	3	-	-	-	2	-	-	6	-	5	-	4
88	3	-	5	-	5	4	-	7	-	5	4	5
89	4	4	4									

Before each activity study, at least 10 ant nests were selected for possible monitoring. Suitability criteria were:

(1) Accessibility (6 metre maximum height by ladder)

(2) Relatively few connections to rest of tree to fence off

(3) Not at edge of colony, as peripheral nests may be non-reproductive, "barracks" nests (Hölldobler, 1983)

(4) Not smaller than 125 cm^3, as small nests may be non-reproductive, "bivouac" nests around homopteran populations.

Activity sensor units were attached to 3 nests, randomly chosen from the 10 suitable nests. The third nest was prepared in case one was abandoned due to disturbance or natural senescence.

Each activity study was started at 0900-1000 and finished at 0850-0950 the following day. Physical data (temperature, wind speed, rainfall, and light level) were recorded concurrently, every hour during daylight, and every 3 hours at night. After at least 2 complete days of monitoring, the nest was collected, and the numbers of adults and brood counted, as described in section 5.2.3. Activity levels could then be expressed as a proportion of the total nest population, as nests varied dramatically in population size throughout the year (fig 5.22d).

The large size and unbalanced nature of the resultant activity data set made a single totally inclusive analysis impossible. These data were thus examined, using analyses of variance and/or covariance, at three levels:

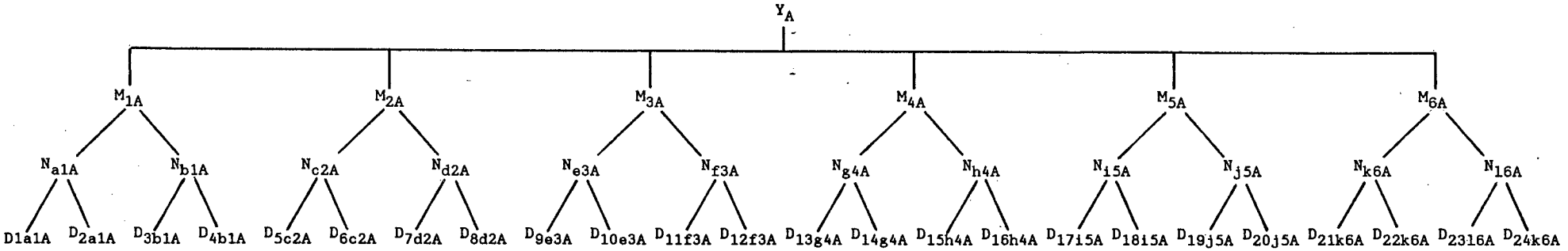
(1) Total day activity counts were examined for variation among 2 years (year 1 from 5/87-3/88, and year 2 from 5/88-3/89), 6 months (January, March, May, August, October, and December), and 2 nests within months, for 2 days per nest, using physical data as covariates, in a mixed model analysis of covariance (table 6.2).

(2) Circadian effects were tested in a mixed model analysis of variance, the factors being year, month, time of day, and nest within month, for 2 days per nest. Times of day were grouped into 2 hour periods (called "hour" in the analysis of variance tables). This analysis allowed interactions between the crossed factors, month, year, and hour to be examined, but computing memory problems prevented the inclusion of covariates.

(3) For separate months, 2 hourly periods were examined for effects of nest, and hour crossed with nest, for 2 days per nest (table 6.3). Physical data were added as covariates.

Table 6.2. Analysis of variance design for total day activity counts.

Year (Y): 2 levels (A-B).
Month (M): 6 levels (1-6).
Nest (N): 2 levels (a-x) nested within month and year.
Day (D): 2 levels (1-48) nested within nest within month and year.



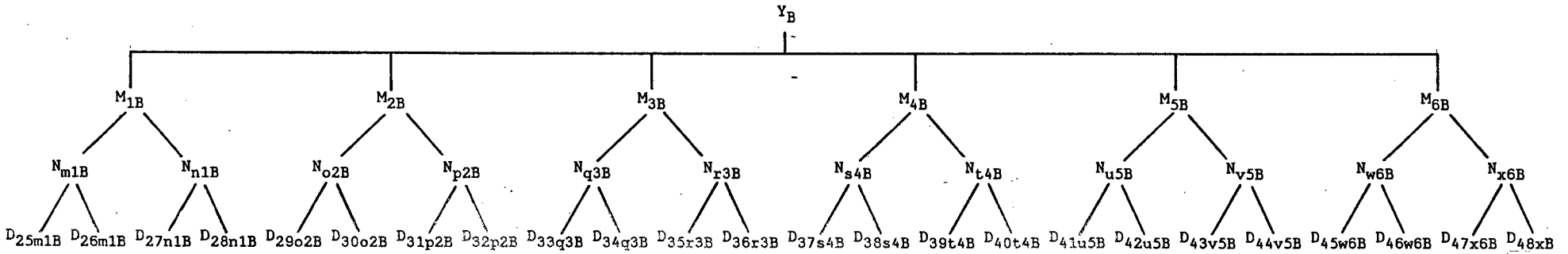
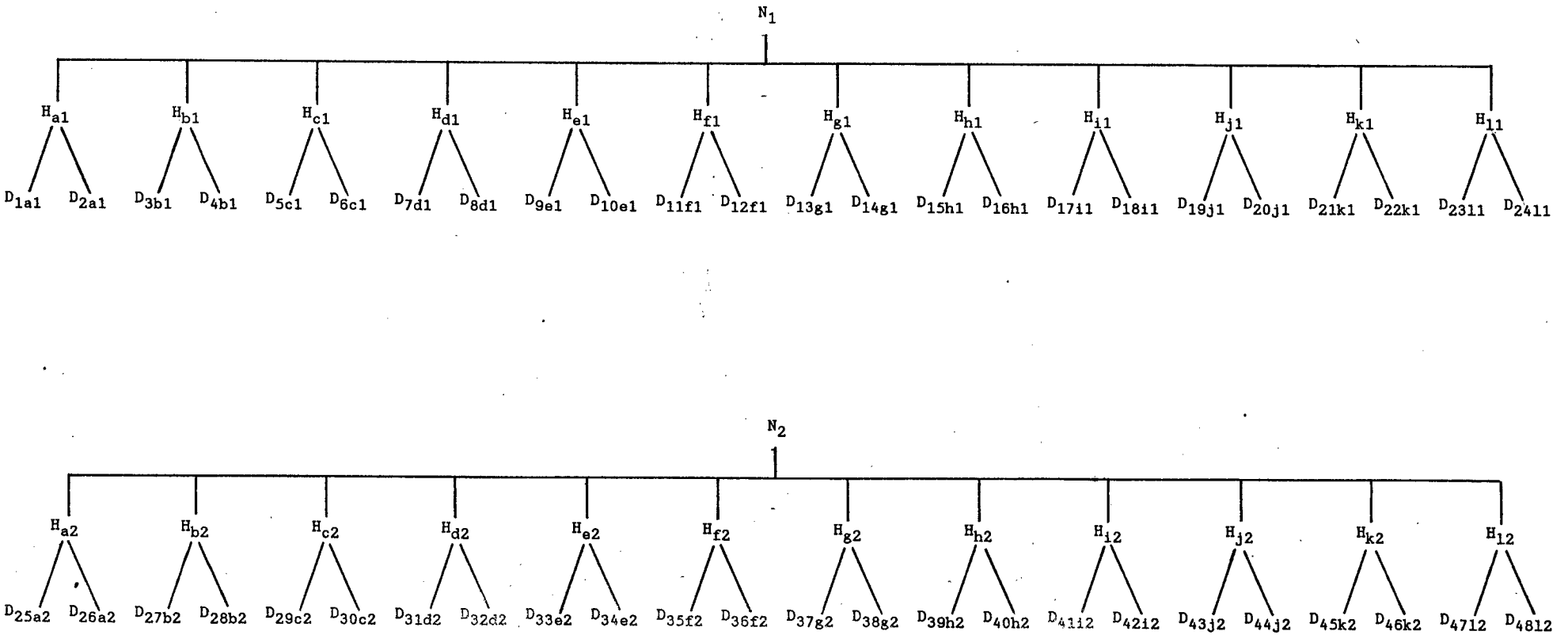


Table 6.3. Analysis of variance design for 2 hourly activity counts on individual nests within each month.

Nest (N): 2 levels (1-2).
Hour (H): 12 levels (a-l).
Day (D): 2 levels (1-48) nested within hour and nest.



Activity patterns of several populations of green tree ants were measured in laboratory conditions, using the experimental design shown in figure 6.3. Nests were collected, and placed in the nest area, along with an artificial nest (described in section 4.2). Escape from the nest and foraging areas was prevented by electric ant fences. A string path provided access between the 2 areas, and directed passing ants through the infra-red beam of a counter. A box was placed over the entire apparatus to reduce disturbance, and to allow accurate photoperiod control. All trials were run at a constant temperature of 24±1°C. Artificial ant diet (Bhatkar and Whitcomb, 1970) was provided for the duration of trials.

Only 1 of 5 nests introduced to this system survived for over one month. Large numbers of ants in the other 4 nests were regularly found electrocuted on the grids every morning. Activity patterns of the longest surviving nest were monitored for 4 days with a 12 hour light, 12 hour dark photoperiod, and 2 days with continuous light.

A young queenright colony from the developmental trials (chapter 4) was also reared in a laboratory counter box. Teflon strips were used to contain the colony, rather than electric grids, which killed many ants. The colony increased from a population of 10 adult workers in February, 1987, to a maximum of 500 workers in January, 1988. Unfortunately, the queen stopped producing brood in February, 1988, and died in March. In preliminary trials during August and September, activity data were collected for 6 days with a 12 hour light, 12 hour dark light cycle. The numbers of ants outside the nest at different times of day were also monitored during this period.

Figure 6.3. Design of laboratory ant activity counter system.

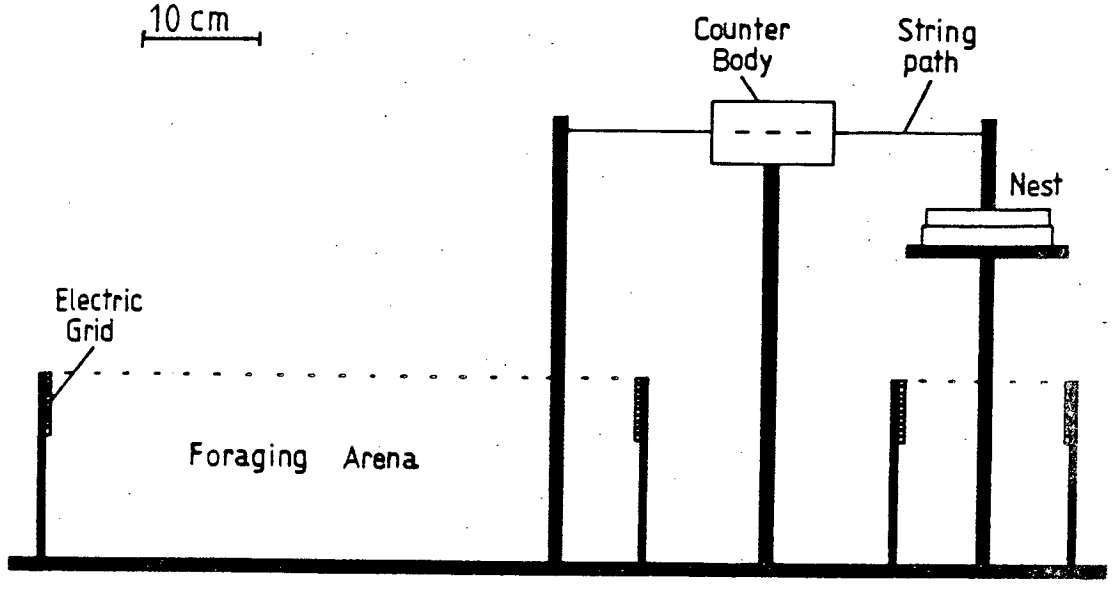
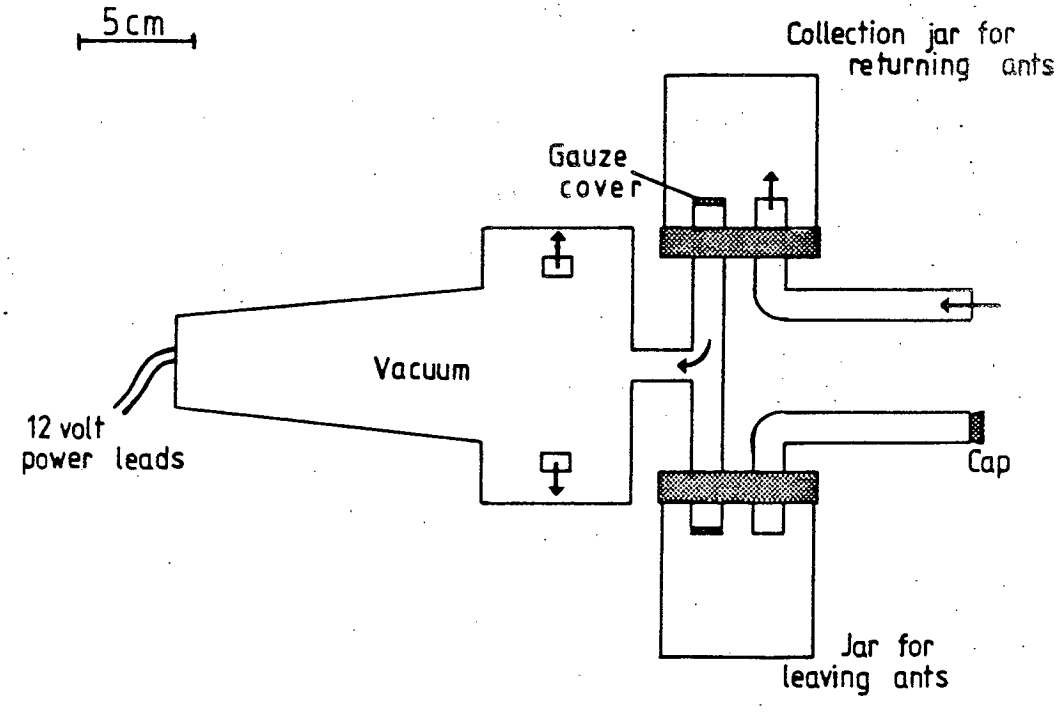


Figure 6.4. Design of vacuum-powered ant aspirator.



6.2.2. Food input.

Food collected by foragers was monitored on the first day that the activity of each nest was recorded. Food data could not be collected from the activity trial nests without excessive disturbance (see section 6.3.1), so food input was observed at the nearest of the 10 previously selected nests to each activity trial nest.

Food intake was measured in 2 ways. Liquid food brought into the nest in the crop of returning ants was monitored by collecting 50 leaving and 50 returning ants in separate chambers of a mechanical aspirator (fig 6.4). Suction was provided by an adapted portable vacuum cleaner, powered by a 6 volt lead acid battery. The ants were then anaesthetized, split into groups of 25, and weighed to the nearest 0.1 mg using a microbalance. The weight difference of the returning and leaving ants gave a measure of liquid food entering the nest. All insect prey was also collected from 100 workers returning to the nest, identified as far as possible (often only to order), and weighed. The number of brood carried by these workers was also recorded.

Food input was monitored at 9 times of day during each trial - 1100, 1300, 1500, 1700, 1900, 2400, 500, 700, and 900. Analysis of data was similar to activity analysis, but with one factor omitted (day within nest), as only one day of food data was recorded. Analyses were thus less complex, and separate analyses for each month were not possible.

A number of assumptions underlie the validity of the liquid food intake results (section 6.1.2). Data collected in March, 1989, examined the influence of body size on crop loads, and foraging activity. Fifty ants leaving and 50 ants returning to a nest were collected by

aspirator. The entire nest was then collected, and a random sample of 50 major workers taken. Each of these ants was individually weighed, and its scape (1st antennal segment) length measured, using a binocular microscope with graduated eyepiece. The correlation of weight to scape length was calculated for the 3 groups, to determine which was most variable. An analysis of variance was used to detect variation in scape length between inward bound, outward bound, and nest ants. Weight differences between the 3 groups, after adjusting for scape length differences, were tested for using an analysis of covariance.

The influence of different foraging paths on crop load was monitored in July, 1986. Groups of 50 ants leaving and returning to a nest were collected from 2 major trails, one leading up into the tree canopy, and the other down to the ground. After 4 days, both trails had been sampled on 8 occasions: every hour from 1100 to 1800. Weight differences of incoming and outgoing ants were calculated, and compared between the 2 trails using a paired t-test.

6.2.3. Ant tagging.

To examine some aspects of the activity and foraging behaviour of *O. smaragdina*, a method of differentiating between individual, or at least groups of workers was necessary. Aspects requiring this approach included:

-Length of foraging trips, in space and time.

-circadian variation in foragers outside the nest.

-Fidelity of foragers to feeding sites, and to nests.

-Constancy of foraging on either food type.

-Rate of dispersal of ants throughout the colony.

-Lifespan of foragers, and age when foraging commences.

A wide variety of techniques for tagging green tree ant workers, either with individually recognizable tags, or with a group mark, were tried, with little success. Individual tags tested included:

1. Various paints applied with a fine brush to the abdomen or thorax, either with or without anaesthesia, and with varying holding times to allow for drying, and dissipation of foreign odours, before returning to the colony (e.g. Davidson, 1977; Holt, 1955; Hölldobler, 1983; Lewis *et al*, 1974b).

2. Small (about 2 mm^2) waterproofed paper tags with numbers, glued to the abdomen or thorax of workers, while anaesthetized, with varying holding times (Meudec and Lenoir, 1982; Seeley, 1979).

3. Wire rings tied around the petiole of workers, while under anaesthesia (Carlin and Hölldobler, 1986; Kruk-deBruyn *et al*, 1977; Mirenda and Vinson, 1979).

In each trial, at least 2000 ants were marked, with mortality due to marking never exceeding 2%. Marked ants kept in the laboratory accepted the tag after a short time, and appeared to behave normally. However, when they were returned to their home colony, the resident workers could be observed attempting to remove the tag. Within one week, no marked individuals could be found, even with wire rings, which appeared to be removable only by pulling off the marked ant's abdomen! Similar marking techniques were successfully applied to 2 other species of ant, *Iridomyrmex purpurea*, and *Camponotus sp.*

These external tags appeared to provoke the highly developed colony recognition system of this species. Hölldobler (1983) successfully tagged *O. smaragdina* workers with enamel paint, but he was marking ants in guard nests, which he concluded were a physiologically

discrete, old subset of the worker population. Many of these workers have missing or damaged appendages, and may well have been ejected from the interior regions of the colony previously.

Mass marking of ants was also attempted, using 2 methods:

1. Spraying a fine mist of fluorescent dye or paint over a group of anaesthetized ants, with various holding times before returning to the home colony (Porter and Jorgensen, 1980).

2. Feeding ants honey solution with fluorescent or vital dyes, in the field (Brian and Abbott, 1977; Petralia and Vinson, 1978; Wilson *et al.*, 1971).

The spraying technique gave similar results to those observed for other external marks, that is, none at all. The dye feeding trials were the most successful, with no signs of ants reacting adversely to the internal colouring of the crop. However, ants would only feed on the dyed food for a few days, even if fresh solutions of varying concentrations were supplied. Lanza (1984, 1988) found ants could discriminate between nectars with different amino acid contents; differences in composition of homopteran honeydew and bee honey may account for the abandonment of honey sources by green tree ants. As these dyes were visible through the abdomen wall for only about one week, this mark had a very limited lifespan. Also, trophallactic exchange of the dyed food may produce an overestimate of ant dispersal. However, as no other marking techniques were found, a number of dye dispersal trials were conducted.

6.3. Results.

6.3.1. Activity counter calibration.

The use of a monofilament string ant path, and modern electronic components produced a consistently high level of accuracy in ant counts. A calibration curve (fig 6.5), comparing visually observed flow rates with those measured by counter, shows that electronic counts always fell within 10% of the visual counts. Regressing counts obtained by counter (C) with observed counts (F) gave the following equation:

$$C = 2.26 \pm 6.68 + 0.99 \pm 0.02\ F \qquad (r=0.997,\ P<<0.001)$$

As the confidence limits of the constant term (-4.42 to 8.94) included 0, and the slope (0.97 to 1.01) included 1, the flow rate recorded by the counter was an accurate unbiased measure of actual flow rate throughout the range observed (1 to 90 ants/minute).

Recorded and observed flow rates in dark and light conditions were also compared (fig 6.6). Counter efficiency , calculated as the ratio of recorded to actual counts, was used in this plot, to display the spread of data more effectively. Efficiency did not vary with actual flow rate in either light ($r=0.11$, $P=0.52$), or dark conditions ($r=0.23$, $P=0.10$), over the range examined. Efficiency during daylight was $101.1 \pm 1.6\%$, and at night was $99.5 \pm 1.1\%$; these were not significantly different ($t=1.15$, 52df, $P=0.25$), and confidence limits of both include 100%. The accuracy of the counter was thus unaffected by light levels.

A typical record of ant activity generated for *O. smaragdina* (figure 6.7) in May shows a diurnal pattern, with peaks in the morning and late afternoon, and some activity throughout the night. A notable

Figure 6.5. Calibration of light beam and manually recorded ant flow

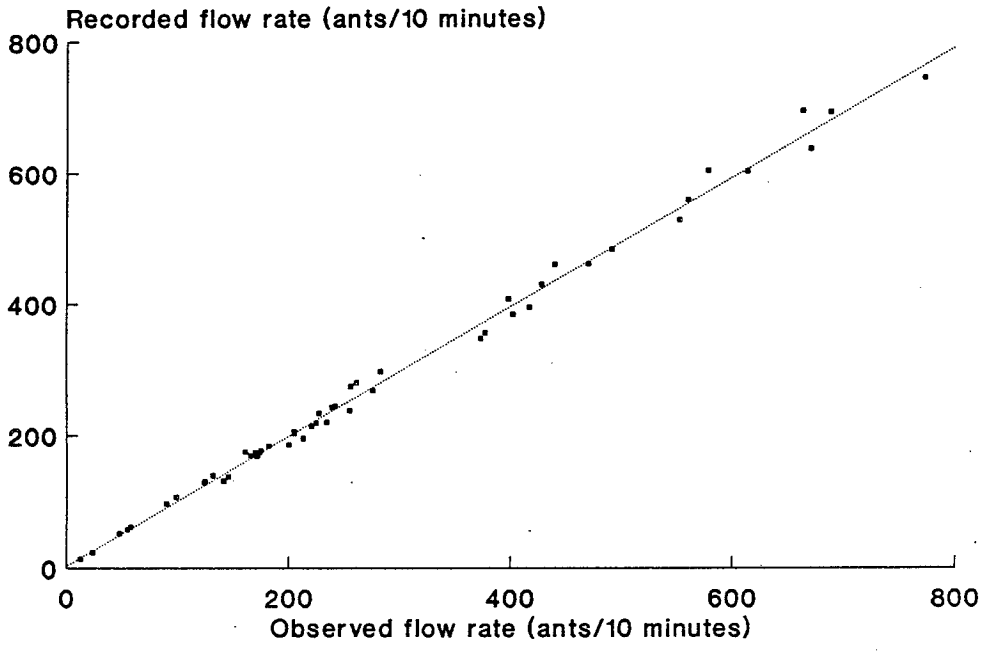


Figure 6.6. Efficiency of light beam counter in light and dark conditions

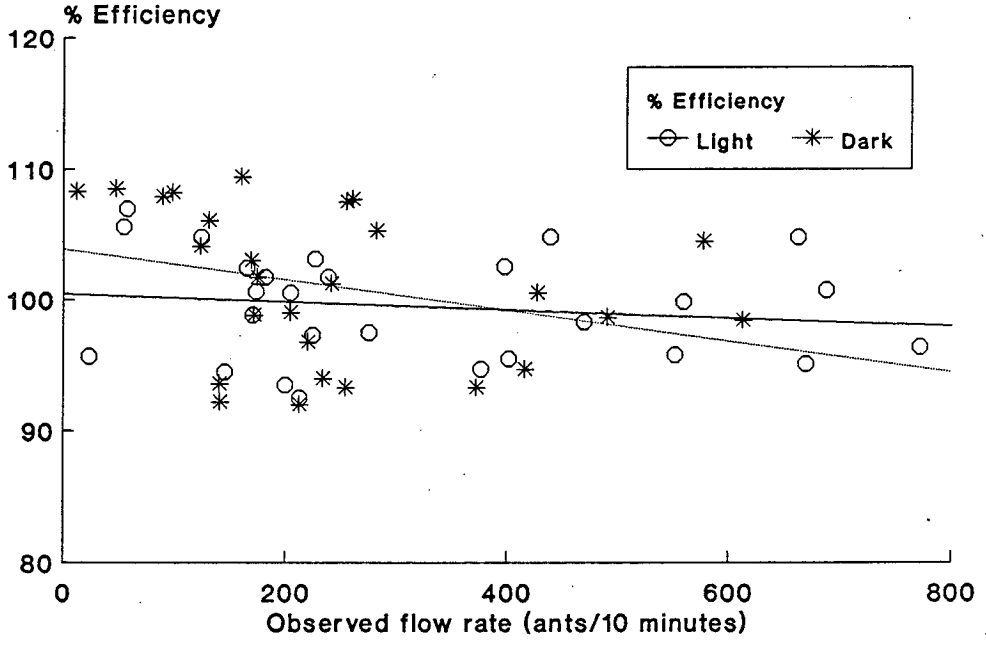
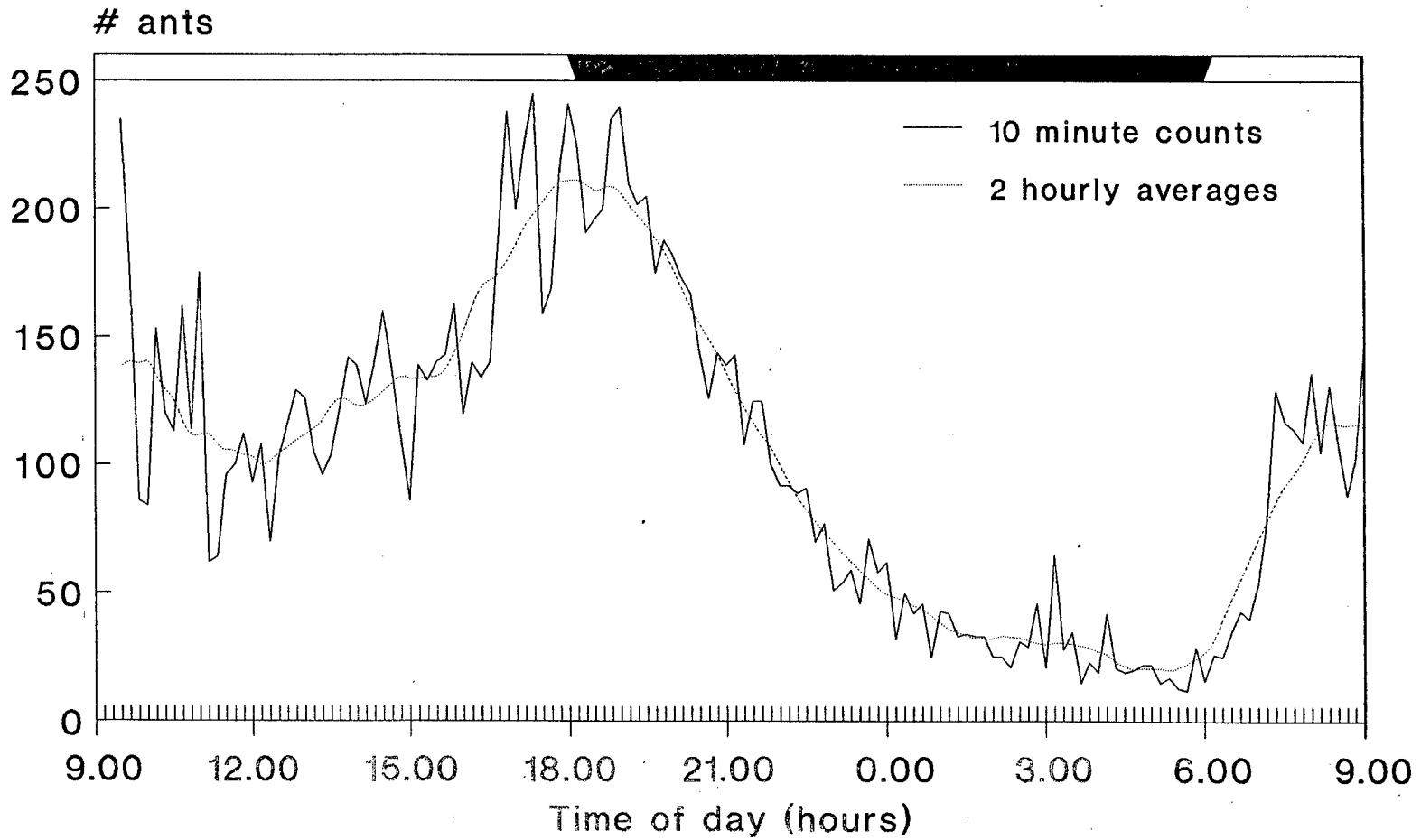


Figure 6.7. Ant activity recorded from 9.30 am, 20 May to 9.10 am, 21 May. (Photoperiod shown in top bar)



feature of this graph is the unusually high activity measured in the first 10 minute interval. This excitation period, of variable duration and level, appears to be caused by the disturbance of switching on the counter system, and was subsequently minimized by keeping well away from the nest area. Similar activity pulses could be produced by approaching within about one metre from the nest, provoking an alarm/defence recruitment response from the ants (as described by Wilson and Hölldobler, 1978). The counter system thus produces measures of activity unbiased by the observer effects which occur during visual counts.

6.3.2. Comparison of inward and outward flow.

The numbers of ants leaving the nest in December, 1988, were slightly lower than numbers returning from 0700 till 2100, and were slightly higher in the dark period from 2300 to 0500 (fig 6.8a). The proportion of ants outward bound varied little from the equal flow fraction of 50%, ranging from a minimum of 40% at 1100, to a maximum of 57% at 0500 (fig 6.8b).

However, a sizeable difference in ant numbers inside and outside the nest could be generated by these slightly different flow rates. To illustrate this point, the numbers of ants moving in and out every 10 minutes for 24 hours were interpolated from the 2 hourly data. During the period from 0600-2200, the higher inward flow resulted in an increase of 2403 ants in the nest population. The opposite trend from 2200-0600 resulted in a nest population drop of 1372, producing a total nest gain over 24 hours of 1032 ants. Considering that the numbers of major workers during the wet season months varied from 600 to 2000

Figure 6.8a. Inward and outward ant flow in December, 1988.

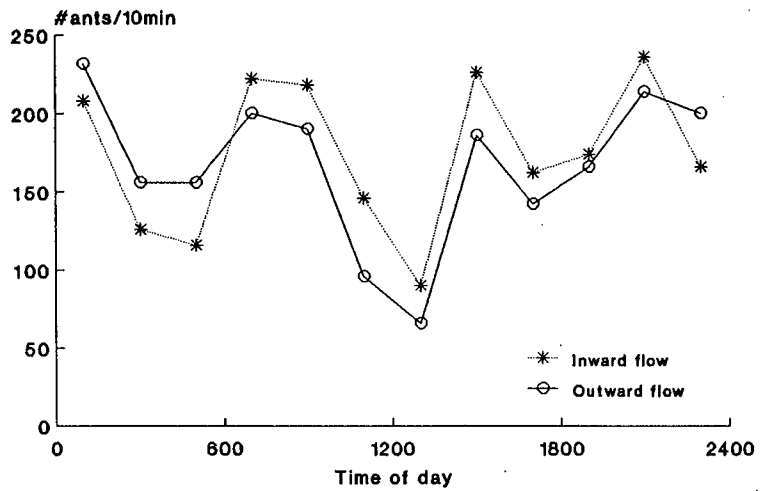


Figure 6.9a. Inward and outward ant flow in May, 1988.

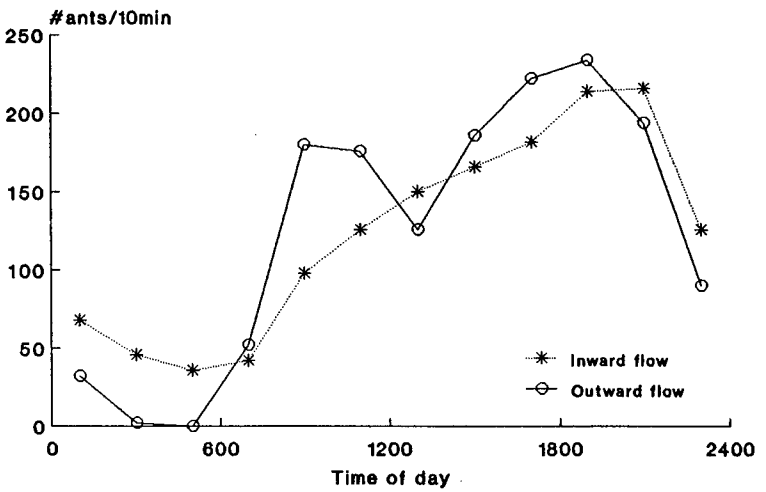


Figure 6.8b. Proportion of total flow outward bound in December, 1988.

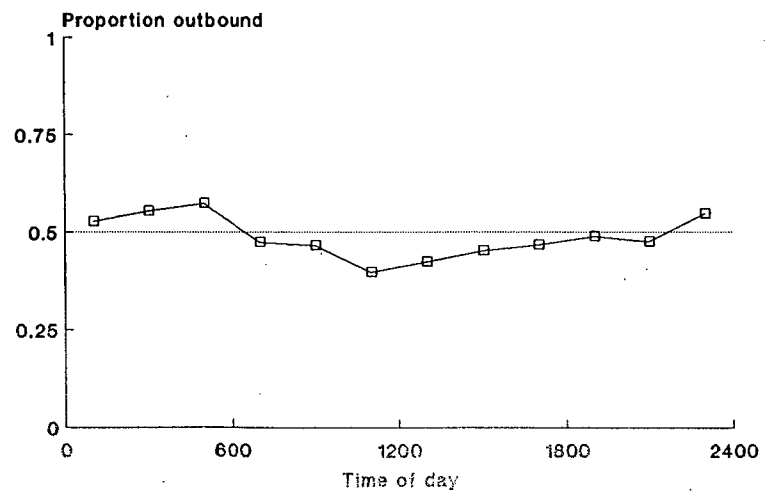
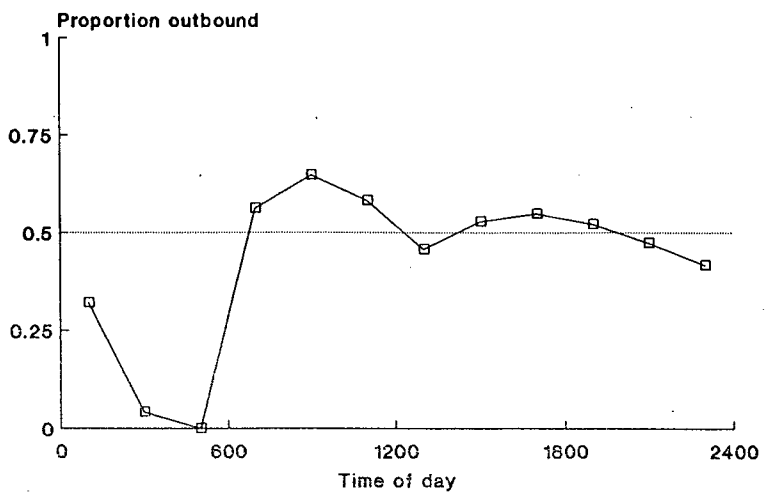


Figure 6.9b. Proportion of total flow outward bound in May, 1988.



workers (section 5.3.5), these changes could dramatically alter the forager populations inside (and presumably also outside) nests.

Circadian variation between inward and outward flows was higher in May (fig 6.9a). Little ant activity occurred in the cold early morning hours, and the proportion of departing ants was very low (reaching 0% at 0500; fig 6.9b). However, the impact of the divergent flow rates during this period was relatively minor, due to the low total flow rates compared to other times of day. The proportion of outward bound ants reached a peak of 65% at 0900, when both the temperature and total ant flow had risen substantially. Flow rates in both directions were similar for the remainder of the day, with outward fractions ranging from 42% to 58%.

The higher outward flow rate from 0630-2000 resulted in a potential drop of 2267 ants in the nest population. The opposite trend from 2000-0630 added 1979 ants, so a net loss of 288 ants was estimated for this nest over 24 hours. Nest populations were much larger in May, with 5000 to 15000 major workers, so these changes would have much less effect on nest forager populations than during December.

The possible consequences of variable flow rates for patterns of foraging activity in December were examined using a simulation model (appendix B). A total population of 500 foragers was created, each of which could be located either inside or outside the nest. The model calculated 2 probabilities: P(l) was the probability that an ant currently inside the nest would leave it, and P(r) was the probability that an ant presently outside the nest would return home. At each time increment (1 hour), a random number between 0 and 1 was generated for each ant; if this was less than or equal to the relevant probability, the ant would return or leave, as appropriate.

The average probability of an ant leaving the nest to forage per hour was estimated as the mean number of ants leaving the nest per hour divided by the mean major worker population per nest = 1000/1500 = 0.67.

Circadian changes in P(l) were estimated from observed flow rates as:

$$P(l) = \frac{\text{average } P(l) \times \text{observed out flow}}{\text{observed in flow}}$$

No information on the probability of foragers returning [P(r)] was available (as no marking system was successfully developed), so 3 alternative scenarios were simulated:

(1) $P(r) = \frac{0.67 \times \text{in flow}}{\text{out flow}}$	$P(l) = \frac{0.67 \times \text{out flow}}{\text{in flow}}$
(2) P(r) varied as in (1)	P(l) = 0.67
(3) P(r) = 0.67	P(l) varied as in (1)

Initially, the entire simulated forager population of 500 ants was inside the nest. The simulations were run in hourly steps for 150 hours (about 6 days), by which time a relatively stable cycle had developed in all cases.

Figure 6.10 shows the patterns of average foraging trip lengths, the numbers of foragers outside the nest [F(o)], and the proportions of inward bound workers (i.e. inward flow/total flow) for the second scenario - P(l) constant, P(r) variable. Predictably, minimum foraging trip lengths coincided with highest P(r). However, maximum trip lengths lagged the minimum in P(r) by a few hours, because P(r) remained smaller than the constant P(l) for 11 hours after P(r) bottomed out. A similar pattern was created when both probabilities varied inversely. Trip length also cycled, although less precisely, when P(r) was constant and P(l) varied (with minimum trip length when P(l) peaked).

Figure 6.10a. Probabilities of foragers leaving and returning

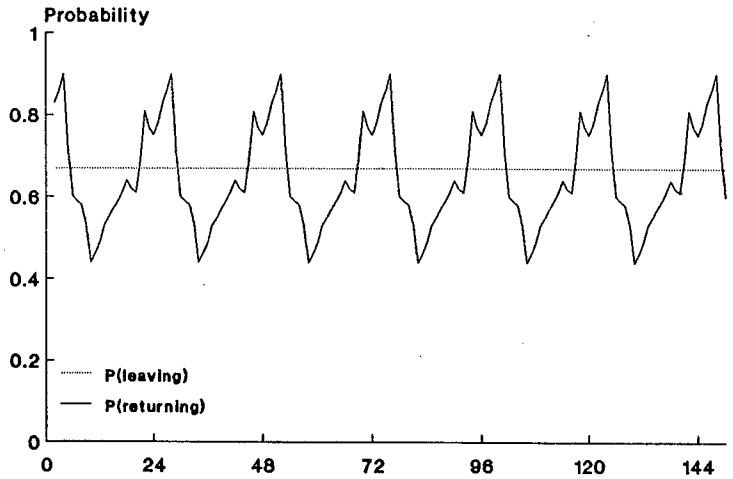


Figure 6.10b. Foragers outside nest

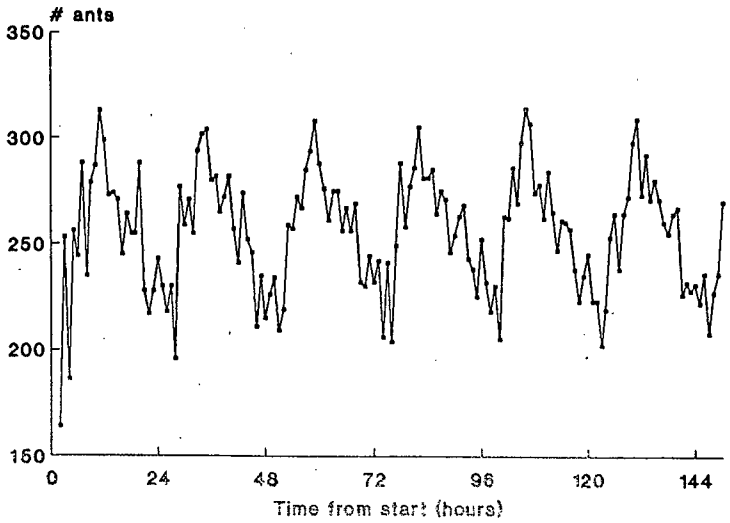


Figure 6.10c. Foraging trip length

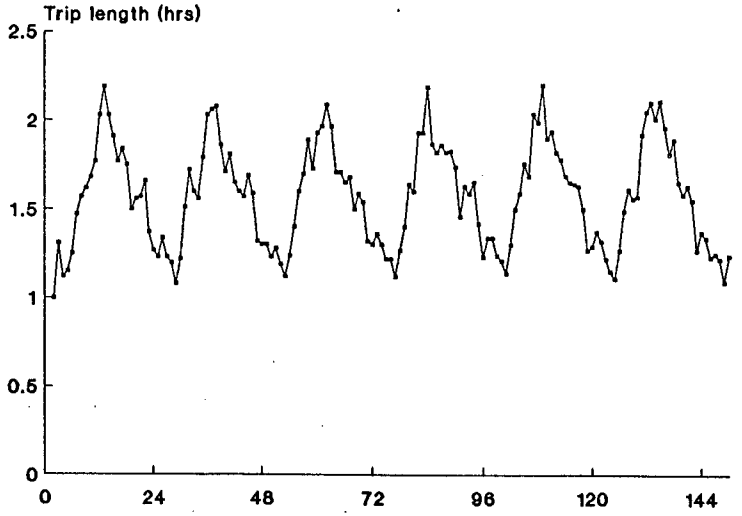


Figure 6.10d. Proportion of total ant flow returning to nest

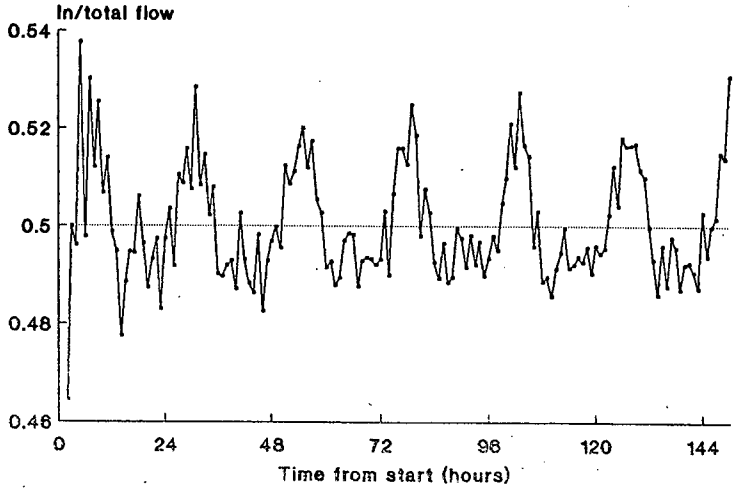


Figure 6.10. Temporal patterns in foraging activity generated by simulation model.

Mean trip length over a 24 hour period was about 1.6 hours in all cases, indicating that trip length averaged over a day or more is not affected by circadian cycles in probabilities. Simulations varying the average values of the 2 probabilities demonstrated that average trip length was solely controlled by P(r) in an inverse relationship. Unfortunately, this probability cannot be estimated from the available data.

Forager populations outside the nest varied in synchrony with transition probabilities, whether either P(l), P(r), or both varied, and did not lag probability cycles as trip length did. F(o) varied inversely with variable P(r), and directly with variable P(l). The magnitude of F(o) changes was related to the magnitude of the differences between P(l) and P(r). Thus, the largest cycles in F(o) occurred when both probabilities varied inversely.

The proportions of inward bound ants were highly variable; this was partially due to the hour increment steps used by the simulation. When moving averages of 5 adjacent means were plotted, distinct patterns became evident. Surprisingly, highest inward proportions occurred after P(r) peaked. This is due to the low F(o) at maximum P(r); i.e. there were few ants outside the nest to be recalled after the probability of returning had been high for a few hours. This simulation clearly shows that the proportion of ants moving inward (and outward) is related to leaving and returning probabilities, and to inside and outside populations, in a complex interactive pattern. The cyclical patterns of inward bound proportions (which occur in the field) could be generated by all 3 simulations.

The usefulness of these simulations is limited by the lack of additional information. Measurement of trip length, or ant numbers

outside the nest, would allow activity dynamics to be more effectively modelled. Unfortunately, trials assessing these variables had to be abandoned when no suitable mark could be developed.

6.3.3 Field activity patterns.

The large variation in individual nest sizes (1546 to 37680 individuals/nest) made comparisons of absolute activity counts between nests meaningless. All activity data presented in this section were thus divided by their respective total nest populations to produce corrected activity values. The term activity will be used for these corrected values, unless otherwise specifically stated. In all analyses, the natural logarithm of this value (plus 1) was used, to produce more homogeneous variances.

6.3.3.1 Yearly and monthly variation in activity.

The total ant activity occurring over 24 hours, averaged for all nests monitored in each month, showed a regular seasonal pattern, with peaks occurring from November till March (fig 6.11a). An analysis of covariance on total day activity (table 6.4a) showed a highly significant month effect ($F=90.7$, 5x6df, $P<0.0001$), and also an interactive effect between year and month ($F=11.8$, 5x6df, $P=0.005$). The interactive term resulted from lower January activity in year 2 compared to year 1, while all other months showed higher activity in year 2 (fig 6.11b). A similar analysis deleting January showed no interactive effect ($F=2.7$, 4x5df, $P=0.15$; table 6.4b), but a significant yearly difference was found ($F=16.6$, 1x5df, $P=0.01$), with

Figure 6.11a. Temporal patterns in daily activity

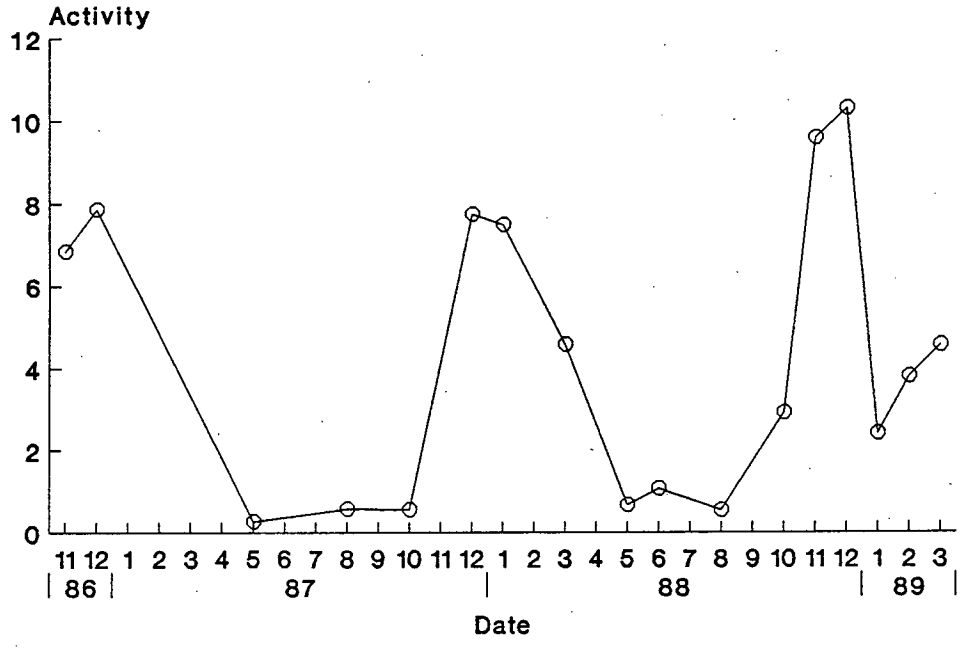


Figure 6.11b. Seasonal patterns in daily activity

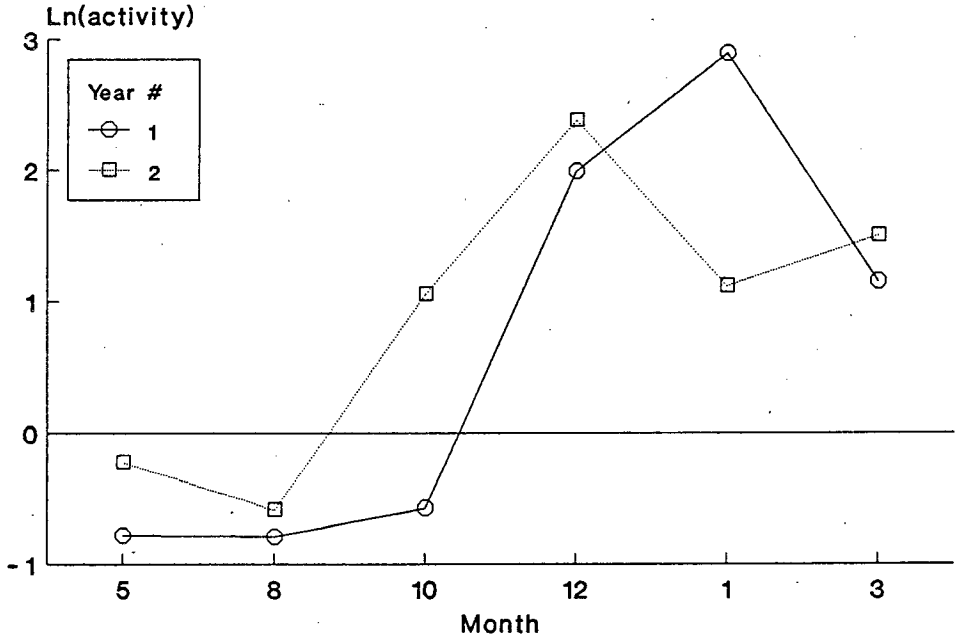


Table 6.4: Analyses of covariance for total day activity counts.

Convention used in listing sources of variation:
A*B factors A and B crossed.
A(B) factor A nested within factor B.

a) All months including January.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Month	5	65.387	13.077	59.81	0.0000
Nest(Month)	6	0.7735	0.1289	0.59	0.7315
Year	1	0.7172	0.7172	3.28	0.1201
Month*Year	5	11.365	2.2730	10.40	0.0064
Nest(Month*Year)	6	1.3119	0.2186		
Rain	1	0.2952	0.2952	4.62	0.0429
Residual	22	1.4062	0.0639		

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Rain	-0.01735	0.008075

b) All months except January.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Month	4	50.316	12.579	148.97	0.0000
Nest(Month)	5	0.4222	0.0844		
Year	1	3.9379	3.9379	16.63	0.0096
Month*Year	4	2.5603	0.6400	2.70	0.1523
Nest(Month*Year)	5	1.1837	0.2367		
Rain	1	0.26632	0.26632	4.94	0.0386
Residual	19	1.0245	0.05391		

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Rain	-0.01702	0.007656

lower activity in year 1. Within each year, highest activity was observed in December, January, and March, and lowest in May and August (fig 6.11b). The only physical variable found to significantly affect activity in this analysis was daily rainfall (F=4.9, 1x19df, P=0.04), which depressed ant activity.

6.3.3.2 Monthly and circadian variation in activity.

A further level of analysis incorporated 2 hourly observations of activity for each day, bringing the number of records in the data set to 564. This total is composed of:

2 years x 6 months x 2 nests x 2 days x 12 2-hour periods

= 576 records - 1 day x 12 periods (in January, 1988)

= 564 records.

This unbalanced design was too large to analyze on the statistical packages available on the Zoology Department microcomputers (Statistix or SAS), with an estimated memory requirement of 22 megabytes, using SAS.

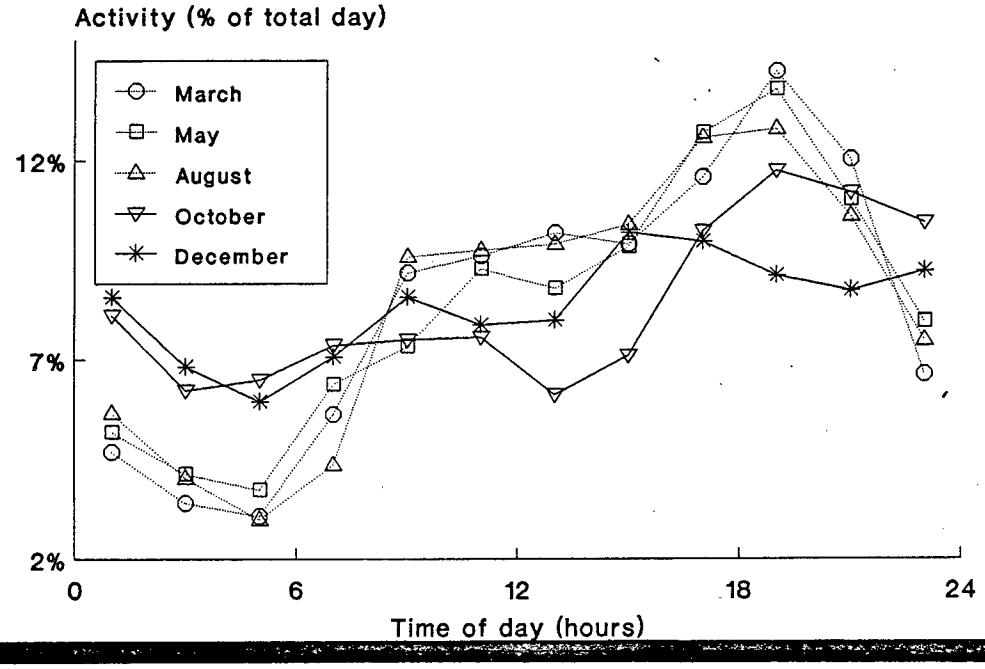
Without January, the data set was reduced to 480 records, and was balanced, so it could be analyzed using simpler algorithms (procedure ANOVA on SAS, which, unfortunately, does not allow covariates to be included in the model). As in the previous analysis, activity varied with month and year (table 6.5). Both hour (F=12.5, 11x55df, P=0.0001) and an interaction between hour and month (F=3.0, 44x55df, P=0.0001) also influenced activity.

Circadian variation in each month is shown in figure 6.12, standardized by displaying activity in each 2 hour interval as a percentage of the total day's activity. Thus, in this graph, the sum

Table 6.5: Analysis of variance for 2 hourly activity counts.

Source	DF	Sum of Squares	Mean Square ($x10^{-4}$)	F ratio	Pr>F
Mth	4	0.1934	483.62	312.30	0.0001
Nest(Mth)	5	0.00077	1.5486	0.31	0.8939
Day(Nest(Mth))	10	0.00494	4.9417	2.65	0.0062
Nest(Mth*Year)	5	0.00082	1.6303	0.87	0.5006
Day(Nest(Mth*Yr))	10	0.00622	6.2195	3.34	0.0008
Yr	1	0.00683	68.276	41.88	0.0013
Yr*Mth	4	0.00500	12.501	7.67	0.0232
Nest(Mth*Hour)	55	0.00424	0.7713	0.41	0.9998
Day(Nest(Mth*Hour))	110	0.01142	1.0383	0.56	0.9988
Hour	11	0.01061	9.6448	12.51	0.0001
Hour*Mth	44	0.01025	2.3301	3.02	0.0001
Yr*Hour	11	0.00153	1.3946	1.33	0.2341
Yr*Hour*Mth	44	0.00359	0.8154	0.78	0.8058
Nest(Yr*Hour*Mth)	55	0.00577	1.0497	0.56	0.9902
Error	110	0.0205	1.8636		
Total	479	0.28594			

Figure 6.12. Monthly variation in circadian activity patterns. (standardized so that activity over 24 hours = 100%)

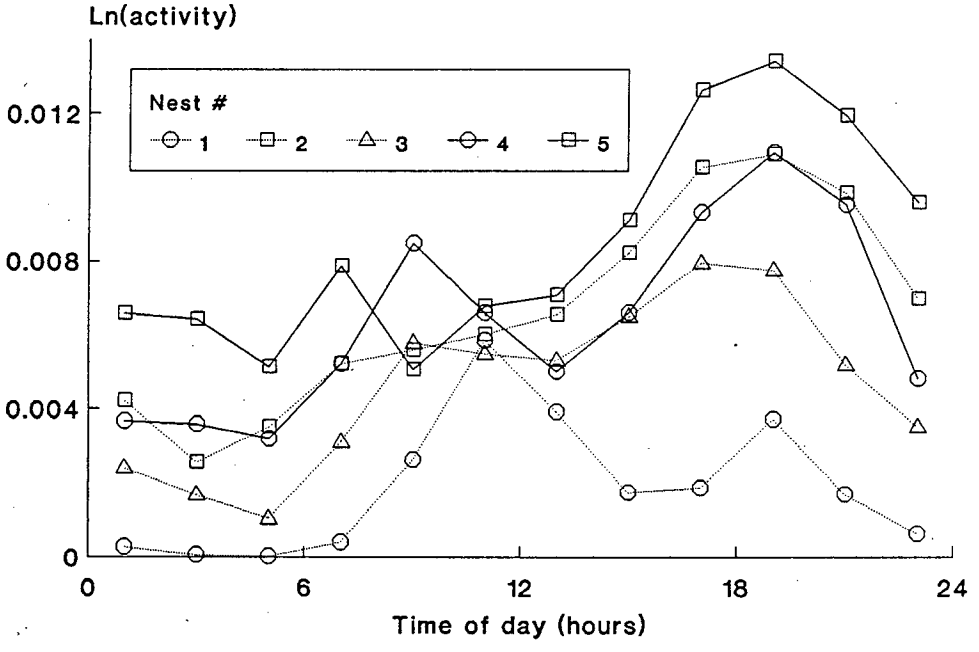


Figures 6.13 - 6.18. Circadian activity patterns of individual nests during each month.

Legend for figures 6.13 - 6.18:

Dotted lines: nests monitored during first year (5/87 to 3/88)
Solid lines: nests monitored during second year (5/88 to 3/89)

Figure 6.13: Circadian activity patterns during May.



of the 12 two hourly values for each month totals 100%. March, May, and August show very similar trends, with minimum activity from 0100 to 0500, followed by a fairly rapid rise till 0900. Relatively constant activity was observed from 0900 till 1500, and then rose steadily to a maximum at 1900. After this time, activity decreased fairly rapidly. Both October and December showed much less circadian variation, with a less pronounced early morning minimum in activity. Activity in October showed a small peak at 1900, and a much broader, shallower trough from 0100 to 1500. December activity varied least, with a gradual rise in the 12 hours from 0300 till 1500, followed by an equally slow fall during the next 12 hours.

6.3.3.3 Circadian variation in activity during each month.

A number of shortcomings were evident in the previous combined monthly analysis. The effects of physical variables were untested, and, even if included in this analysis, might show differing responses between months, as nest composition and the foraging requirements of the ants changed (see chapter 5). Also, activity in January could not be tested. Separate analyses were thus performed on data for each month. Unfortunately, computer memory requirements were too large to allow inclusion of year as a variable into these analyses, so the factor "nests" includes values from both years. Yearly differences were therefore confounded with variation between nests. However, it usually proved possible to detect yearly variation visually in suitable plots. Circadian patterns in activity for each monthly analysis are thus shown separated into individual nests, to display any differences between years.

May:

In May, activity was not significantly correlated with any of the physical variables measured. A stronger temperature effect might have occurred, if trials had coincided with cooler weather, as I observed a complete halt in ant movements below 12°C; the minimum temperature recorded during May trials was 14.3°C. An analysis of variance (table 6.6) revealed a strong relationship between activity and time of day ($F=11.2$, 11x44df, $P<0.0001$). The pattern of circadian variation (fig 6.13) was similar to that described for May in the earlier combined monthly analysis (fig 6.12), and was relatively consistent among nests (as demonstrated by the lack of interaction between nest and hour, $F=1.26$, 44x55df, $P=0.21$). An almost significant difference in activity between nests ($F=3.7$, 3x4df, $P=0.09$) was due primarily to the depressed activity levels recorded in nest 1, 1987, compared to other nests (fig 6.13). The other nests examined in 1987, and all nests in 1988, showed remarkably similar activity patterns, suggesting that yearly differences were negligible during May trials.

August:

Activity varied with temperature in August (table 6.4b), when the temperature ranged from 11.6 to 29.8°C. The best fitting analysis of covariance model incorporated temperature and temperature squared terms ($F=11.2$, 1x64df, $P=0.0014$, and $F=7.14$, 1x64df, $P=0.0095$, respectively; table 6.7b), suggesting that ant activity exhibited a curvilinear response to temperature, with a maximum positive effect at 28.2°C. Time of day, and an interactive effect of nest and hour explained highly significant amounts of variation in activity, either with (table 6.7b), or without (table 6.7a) the temperature terms.

Table 6.6: Analysis of variance for 2 hourly activity counts during May.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	4	5.9111	147.78	3.73	0.0905
Day(Nest)	5	1.9784	39.568		
Hour	11	5.0491	45.901	14.11	0.0000
Hour*Nest	44	1.7987	4.0880	1.26	0.2093
Error	55	1.7888	3.2523		
Total	119	16.526			

Table 6.7: Analyses for 2 hourly activity counts during August.
(a) Analysis of variance.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	5	28.753	5.7506	0.86	0.5540
Day(Nest)	6	39.920	6.6534		
Hour	11	2.7430	24.937	58.35	0.0000
Hour*Nest	55	76.088	1.3834	3.24	0.0000
Error	66	28.206	0.4273		
Total	143	4.4727			

(b) Analysis of covariance.

Source	DF	Sum of Squares ($x10^{-5}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	5	0.996	1.99	0.56	0.7291
Day(Nest)	6	2.138	3.56		
Hour	11	5.436	4.94	5.43	0.0001
Hour*Nest	55	5.028	0.91	2.81	0.0001
Temperature	2	0.364	3.64	11.20	0.0014
$(Temperature)^2$	1	0.232	2.32	7.14	0.0095
Error	64	2.082	0.33		
Total	143	44.73			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Temperature	$1.28x10^{-3}$	$3.83x10^{-4}$
$(Temperature)^2$	$-2.27x10^{-5}$	$8.48x10^{-6}$

Figure 6.14a. Circadian activity patterns: August

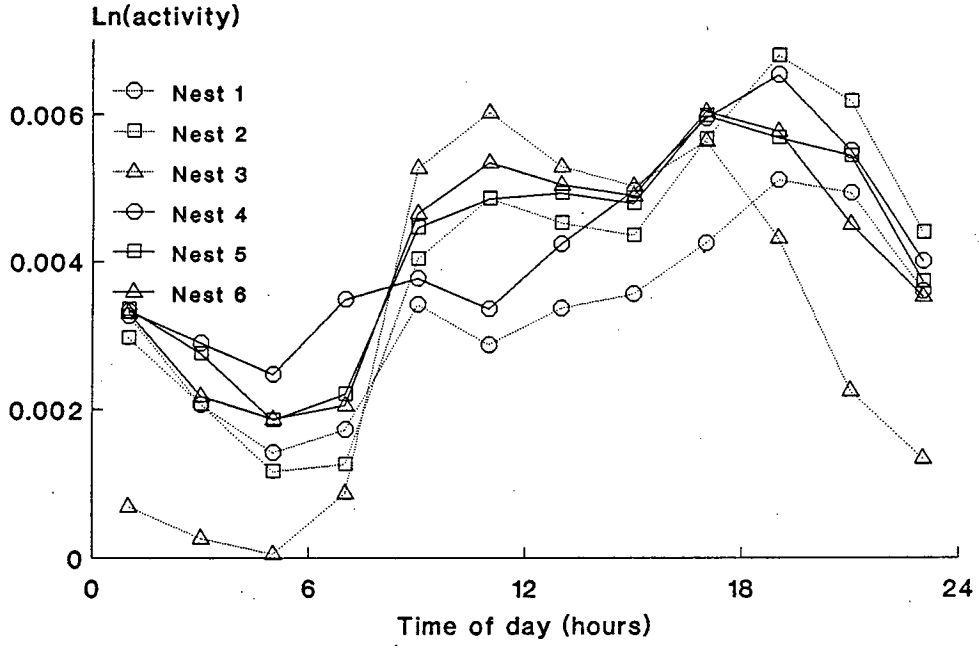
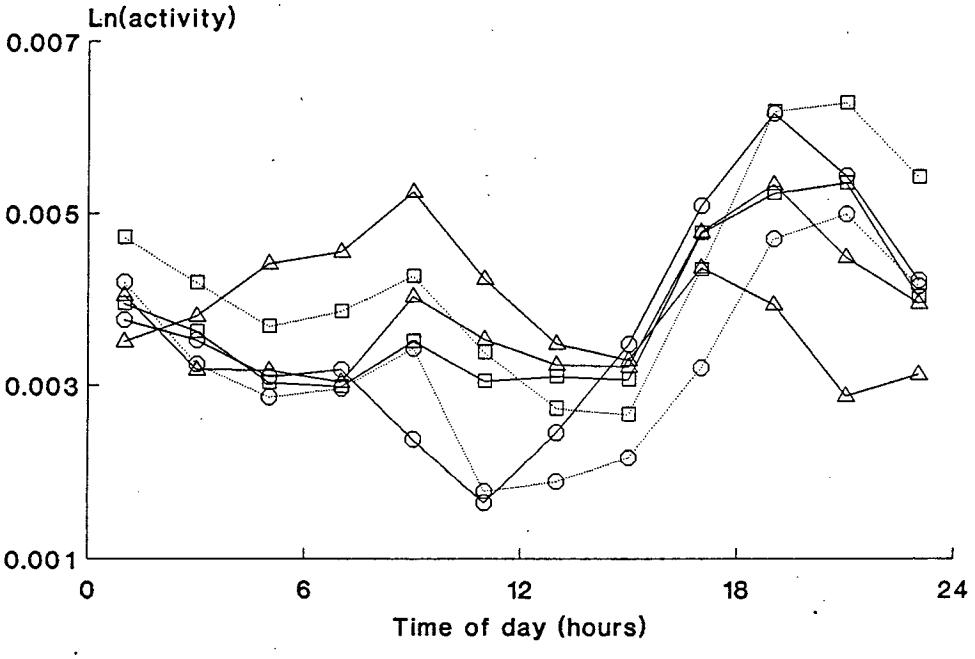


Figure 6.14b. Temperature adjusted circadian activity patterns: August



Plots of circadian variation calculated by both of these analyses are shown for 2 nests in 1987, and 4 nests in 1988 (fig 6.14). Variation between nests appears to be similar in magnitude to the differences observed between years in both cases. Interaction effects between nest and hour were caused primarily by nest 3, 1988, which showed a lower nocturnal activity, and a higher late morning peak, than the other nests.

Ignoring temperature effects (fig 6.14a), most nests showed a similar circadian variation to that described in the combined monthly analysis, except for a slightly raised activity at 1100. When temperature effects were included (fig 6.14b), a new minimum activity was seen at 1300 to 1500, but maximum activity still occurred from 1900 to 2100. The early morning trough in ant activity might thus be due to low temperature inhibition of ant movement. However, temperature did not appear to influence the early nighttime activity peak.

October:

In October, no physical variables were correlated with activity. In an analysis of variance (table 6.5), large inter-nest differences were found ($F=44.3$, 3x4df, $P=0.002$). These correspond mainly to the higher levels of activity in nests monitored in 1988, compared to 1987 (fig 6.15). Activity was also affected by time of day ($F=6.1$, 11x33df, $P<0.0001$), and by nest and hour in an interacting pattern ($F=1.9$, 33x44df, $P=0.03$). The latter effect may be due to differences in circadian patterns between years (fig 6.15). In 1987, activity varied little, gradually rising from a minimum in early morning to a maximum at 2300. In 1988, peak activity occurred at the more typical time of 1900, and was uniformly low from 0100 till 1500 (essentially the

Table 6.8: Analysis of variance for 2 hourly activity counts during October.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	3	64.78	2135.9	44.26	0.0016
Day(Nest)	4	1.930	48.256		
Hour	11	7.356	66.873	11.30	0.0000
Hour*Nest	33	3.614	10.953	1.85	0.0284
Error	44	2.604	5.9197		
Total	95	79.58			

Table 6.9: Analyses for 2 hourly activity counts during December.
(a) Analysis of variance.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	3	280.09	9336.5	4.04	0.1054
Day(Nest)	4	92.432	2310.8		
Hour	11	22.527	204.79	0.33	0.9733
Hour*Nest	33	79.375	240.53	0.39	0.9968
Error	44	269.82	613.22		
Total	95	744.24			

(b) Analysis of covariance.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	3	382.94	12765	5.65	0.0648
Day(Nest)	4	90.494	2262.		
Hour	11	61.573	559.7	1.75	0.1053
Hour*Nest	33	105.59	320.0	1.11	0.3718
Temperature	1	148.68	14868	51.55	0.0001
$(\text{Temperature})^2$	1	140.07	14007	48.57	0.0001
Error	42	121.14	288.4		
Total	95	744.24			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Temperature	$1.09x10^{-1}$	$1.516x10^{-2}$
$(\text{Temperature})^2$	$-1.63x10^{-3}$	$2.339x10^{-4}$

Figure 6.15 Circadian activity patterns: October

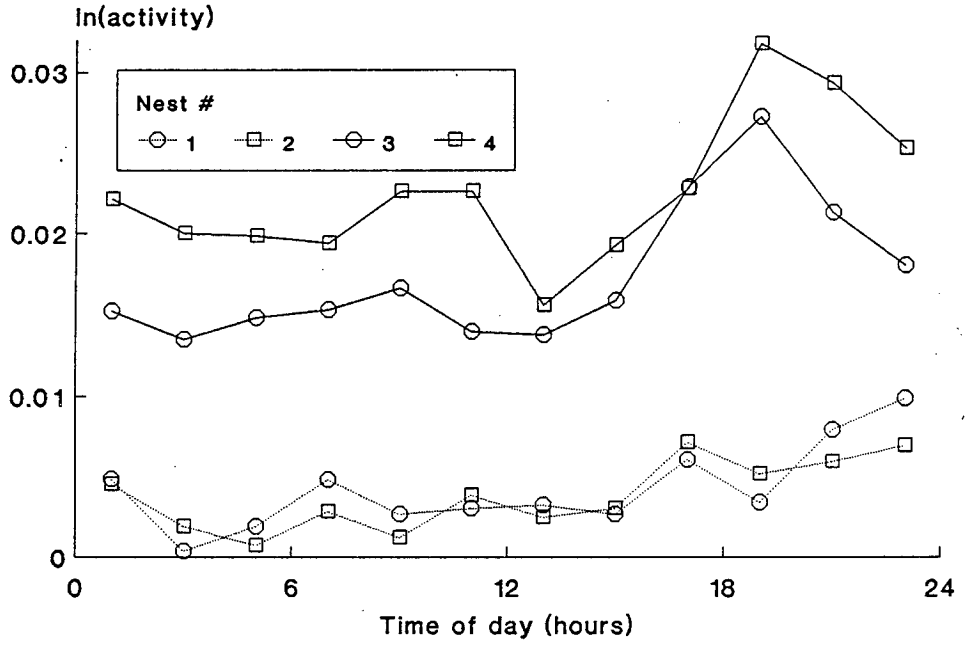
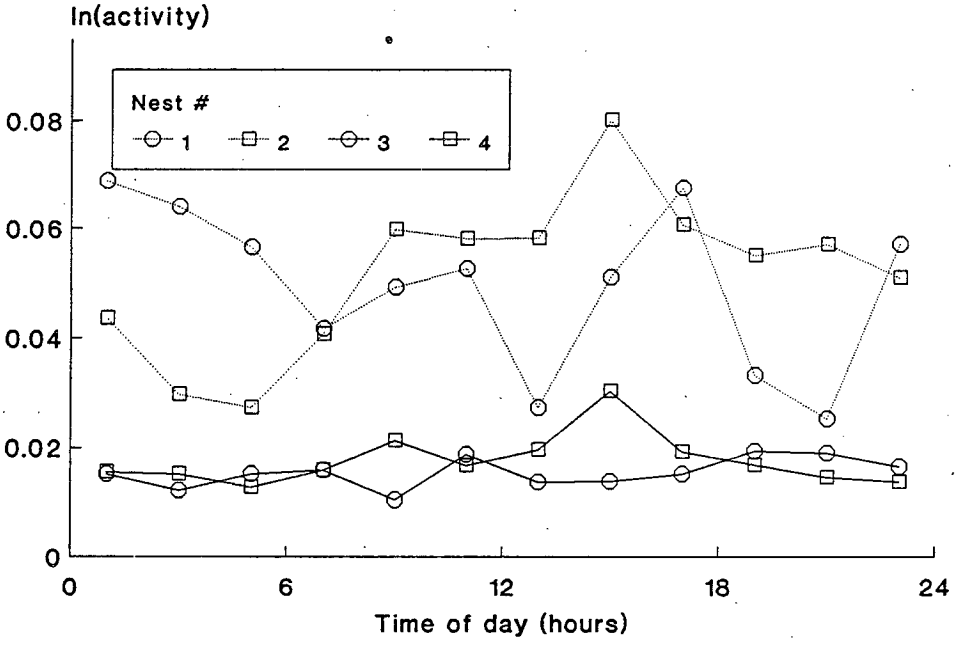


Figure 6.16. Circadian activity Patterns: December



pattern described in the earlier combined monthly analysis). October thus appeared to be characterised by much more variable patterns of activity than recorded in the winter months.

December:

Activity in December showed no significant relationship with time of day or nest, whether physical factors were included (analysis of covariance, table 6.9b), or excluded (analysis of variance, table 6.9a, fig 6.16). In an analysis of covariance, temperature and temperature squared were highly significantly associated with activity ($F=51.6$, 1x42df, $P<0.0001$, and $F=48.6$, 1x42df, $P<0.0001$) with maximum activity occurring at 33.4°C. Ant movements in December were not related to any other physical or biological variable measured, including rainfall (using levels recorded during preceding periods, ranging from 1 day to 4 weeks), proportions of brood inside the nests, and food intake levels from a nearby nest (section 6.3.5).

January:

January trials produced divergent patterns of activity between years, similar to those observed in October. In an analysis of variance (table 6.10a), significant variation was explained by time of day ($F=3.3$, 11x33df, $P=0.004$), and an interaction between nest and time of day ($F=2.1$, 33x44df, $P=0.011$). Yearly variation in circadian patterns of activity probably account for most of the interactive effect. A uniform low level of activity occurred in nests monitored in 1988, whereas a pattern reminiscent of winter month activity (i.e. August and May) was observed in 1989 nests (fig 6.17a).

Table 6.10: Analyses for 2 hourly activity counts during January.
(a) Analysis of variance.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	3	23.156	771.87	2.38	0.2101
Day(Nest)	4	12.951	323.77		
Hour	11	35.020	318.36	6.90	0.0000
Hour*Nest	33	31.929	96.753	2.10	0.0110
Error	44	20.292	46.118		
Total	95	123.35			

(b) Analysis of covariance.
(for 1989 nests only)

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	1	0.0006	0.06	0.00	0.9629
Day(Nest)	2	1.5731	78.65	2.73	0.0892
Hour	11	14.521	132.00	4.59	0.0016
Hour*Nest	11	4.6816	42.56	1.48	0.2151
Temperature	1	9.8878	988.78	34.37	0.0001
$(\text{Temperature})^2$	1	9.5022	950.22	33.03	0.0001
Error	20	5.7538	28.77		
Total	47	84.714			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Temperature	0.154652	0.026380
$(\text{Temperature})^2$	-0.00253	0.000441

Figure 6.17a: Circadian activity patterns: January

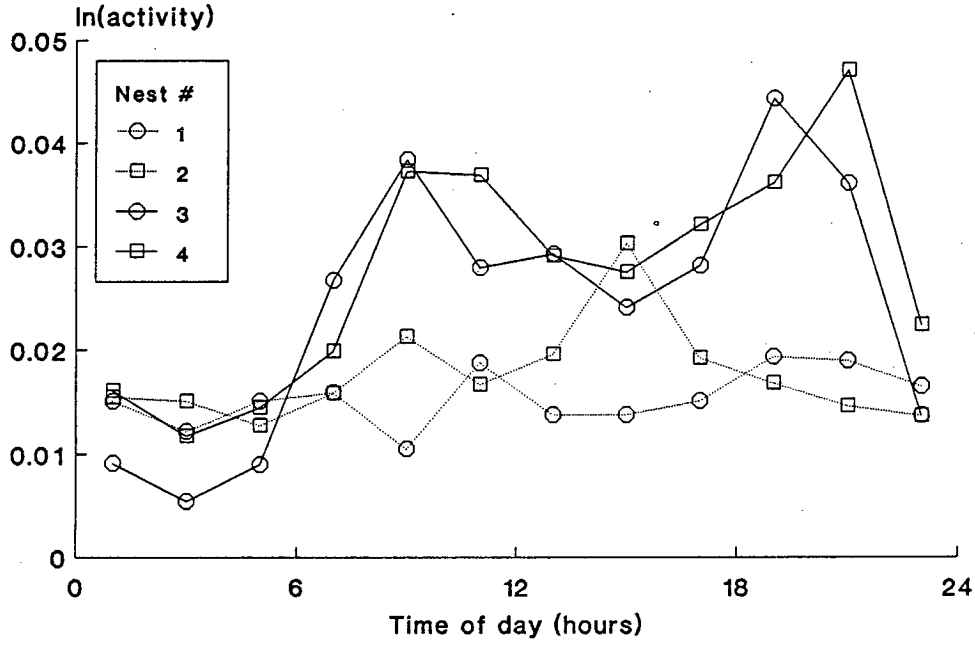
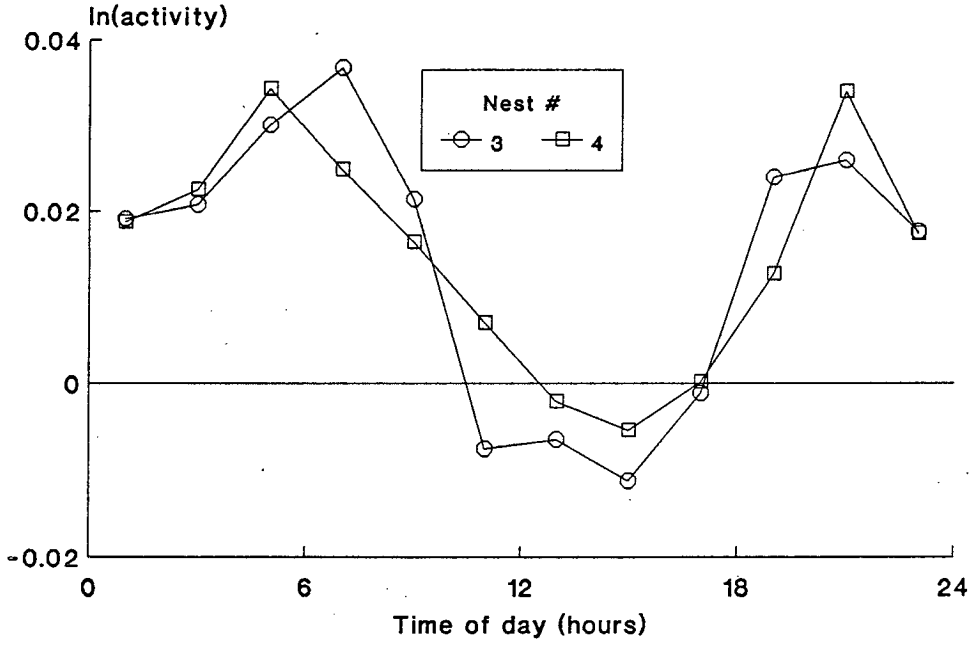


Figure 6.17b: Temperature adjusted circadian activity patterns: January



An analysis of covariance (table 6.10b) suggested that temperature again had a non-linear effect on activity (for temperature, F=20.91, 1x42df, P=0.0001; for temperature^2, F=20.62, 1x42df, P=0.0001), with a maximum response at 31.2°C. Significant variation in temperature-adjusted activity was explained by a combination of nest and time of day (F=3.61, 33x42df, P=0.0001). Much of this variation was attributable to the differing activity patterns between years.

An analysis using only January, 1988 nests indicated that activity during this month had no significant relationship with temperature, time of day, or nest. This minimal activity variation was similar to the pattern observed in October, 1987.

A strong temperature effect (for temperature, F=34.4, 1x20df, P<0.0001; for temperature^2, F=33.0, 1x20df, P<0.0001) and a weak circadian effect (F=3.10, 11x20df, P=0.037) were found in a similar analysis on 1989 nests. Temperature-adjusted activity displayed a circadian pattern similar to the winter months, with minimum activity around midday, with a maximum in the early evening (fig 6.17b). However, a second maximum seen in January around dawn did not occur in winter trials.

March:

In March, by contrast, circadian patterns of activity were similar for different nests and years (fig 6.18a). This observation was confirmed by the non-significant nest by hour interaction term (F=1.14, 44x55df, P=0.32) and nest term (F=0.84, 4x5df, P=0.55) in an analysis of variance (table 6.11a). Activity varied with time of day (F=13.97, 11x44df, P<0.0001), showing a circadian pattern very similar to May and August nests.

Temperature was again significantly related to activity ($F=3.43$, 3x53df, $P=0.039$; table 6.11b), although not as strongly as in August or December (the months when trials were conducted in hottest and coolest conditions). In contrast to other months when temperature was correlated with activity, adjusting for temperature in March trials increased differences between nests (fig 6.18b), with all terms reaching significance (table 6.11b). Some of the nest differences were attributable to yearly variation, with the three 1988 nests exhibiting generally lower activities than the two nests in 1989. However, one very large peak in temperature adjusted activity occurred in the early morning in nest 3, 1988. Unseasonally low temperatures occurred during this trial, reaching 20°C at dawn, compared with a range of 25 to 26°C seen at dawn in other March, 1988 trials. A similar, but less pronounced elevated activity was seen in the early morning in 1989 trials, when dawn temperatures were 23 to 24°C. Thus, ants maintained a relatively uniform actual activity level throughout a range of dawn temperatures from 20 to 26°C.

Temperature adjusted activities were more consistent in the second half of the day, with low levels at midday, and a peak in most nests at 1900 to 2100. The magnitude of this peak was, however, much higher in 1989 nests, and did not occur at all in nest 3, 1988. The inconsistent relationship of temperature with activity patterns suggests either that the correlation of March activity with temperature was a spurious relationship, or that other unrecorded factors were also influencing activity.

Table 6.11: Analyses for 2 hourly activity counts during March.
(a) Analysis of variance.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	4	23.606	590.15	0.84	0.5543
Day(Nest)	5	35.098	701.97		
Hour	11	142.35	1294.1	15.92	0.0000
Hour*Nest	44	40.742	92.595	1.14	0.3209
Error	55	44.703	81.278		
Total	119	286.49			

(b) Analysis of covariance.

Source	DF	Sum of Squares ($x10^{-4}$)	Mean Square ($x10^{-6}$)	F ratio	Pr>F
Nest	4	27.362	684.05	2.17	0.2096
Day(Nest)	5	15.753	315.07		
Hour	11	63.772	579.74	5.75	0.0001
Hour*Nest	44	44.353	100.80	1.35	0.1477
Temperature	1	4.8947	489.47	6.55	0.0133
$(\text{Temperature})^2$	1	4.6179	461.79	6.18	0.0161
Error	53	39.579	74.678		
Total	119	286.49			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Temperature	$6.659x10^{-2}$	$2.601x10^{-2}$
$(\text{Temperature})^2$	$-1.135x10^{-3}$	$4.565x10^{-4}$

Figure 6.18a: Circadian activity patterns: March

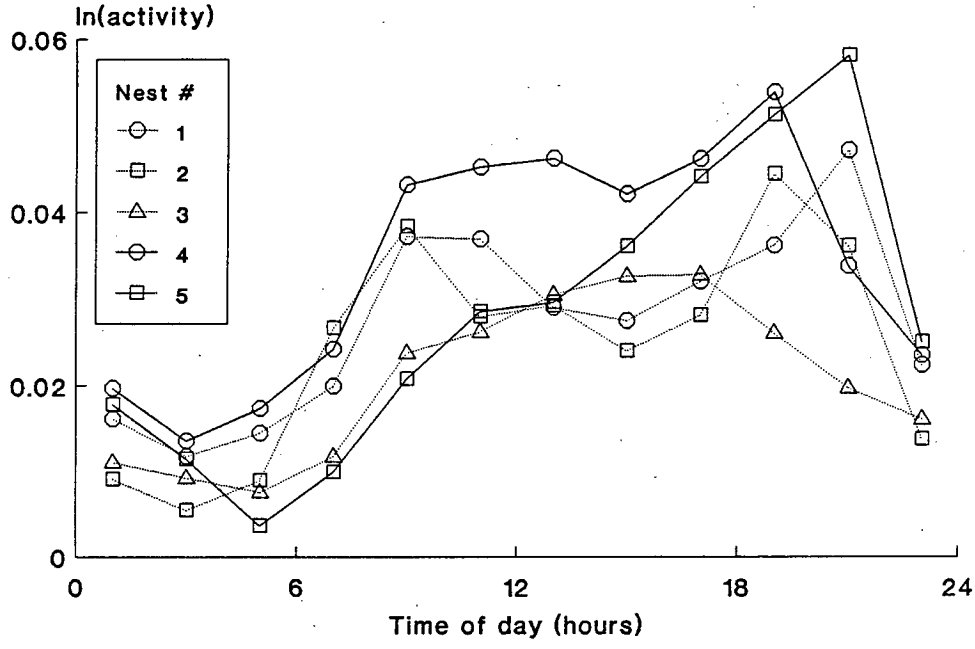
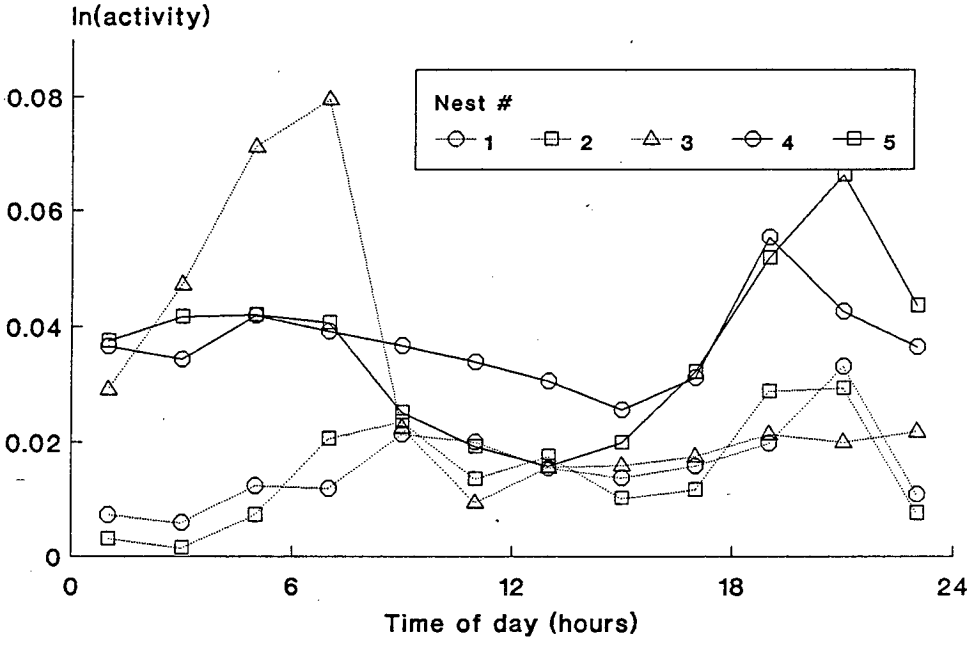


Figure 6.18b. Temperature adjusted circadian activity patterns: March



6.3.3.4 Field activity: a summary.

Activity of *O. smaragdina* worker ants leaving and entering nests varied between years, months, time of day, and nests in complex interacting patterns. Levels of ant activity were higher in the second year of the study, in all months except January.

A summary of some aspects of monthly variation is presented in table 6.12. Highest activity was recorded in the summer months of December, January, and March, and lowest in the winter months, May and August. Trials during March, May, and August gave very consistent results at the yearly and inter-nest levels, with a regular activity peak during the early night (1700-1900), and minimum activity in the early morning before dawn (0300-0500). In October and January, activity patterns were highly variable between nests, with some nests displaying very little circadian variation, and others showing cycles similar to those in March, May, and August. No circadian patterns were detected in nests monitored during December.

During March, August, December, and January, 1989, temperature was significantly related to activity in a parabolic fashion, maximum activity coinciding with temperatures from 28.2 to 33.4°C. Temperature was not correlated with activity in May, October, or January, 1988. In December, activity was affected by temperature, but not by any other recorded factors (i.e circadian patterns, rainfall, wind, light, or brood levels).

In March, August, and January, 1989, activity adjusted for temperature variation generally dropped to a minimum around midday (1100-1500). The early morning minimum (0300-0500) in unadjusted activity in these months may therefore be caused primarily by low

Table 6.12: Seasonal and circadian patterns of activity in nests of *Oecophylla smaragdina*.

Levels of activity, variability in circadian patterns between nests, and times of day when maximum and minimum activity occurred are displayed for each month. The optimum temperatures (at which maximum activity occurred) are given.

Legend:
- \- low level
- \+ medium level
- ++ high level
- -+ variable levels
- ? indistinct circadian pattern
- * significant temperature effect
- § 1989 nests only

	Month					
	May	August	October	December	January	March
Activity level	-	-	-+	++	++	++
Without temperature covariates:						
Variability between nests	-	-	++	++	++	-
Time of minimum	3-5	3-5	?	?	1-5§	3-5
Time of maximum (24 hour time)	17-19	17-19	?	?	19-21§	17-21
With temperature covariates:						
Variability between nests	-	-	++	-	+	+
Time of minimum	13-15	11-15	?	?	11-17§	13-15
Time of maximum (24 hour time)	19-21	19-21	?	?	19-21§ 5-7§	19-21
Optimum temp.(°C)	26.7	28.2*	30.3	33.4*	31.2*	29.7*

temperatures. Maximum temperature-adjusted activity occurred from 1900-2100; this minimal shift from the original peak during 1700-1900 suggests that temperature influenced maximum activity very little. In January, 1989, a second peak in temperature-adjusted activity occurred at dawn.

The temperature coinciding with maximum activity in each month appeared to be correlated quite closely with the maximum temperature recorded during the trials of that month (fig 6.19). This correlation applies even to those months which did not have a significant association with temperature (although these data points are of dubious value). Nests of *O. smaragdina* thus appeared to alter their thermal activity optima in response to changing temperatures. All significant optima were within 2°C of the maximum temperatures, so high temperatures did not greatly reduce activity; rather activity reached a plateau level at higher temperatures. Activity was reduced markedly by low temperatures.

6.3.4. Laboratory activity patterns.

The movement of ants from the nest area to the foraging area in a young queenright colony (Q1) maintained at constant temperature (24±1°C) was generally higher during the light period than during the dark (fig 6.20). The highest peaks, of variable duration, often occurred at "dusk" and "dawn". The activity cycle of Q1 most closely resembled the pattern observed in nests in the field during January, 1989 and December. Trials examining the effects of temperature on laboratory activity were abandoned when the colony's queen unexpectedly died.

Figure 6.19. Seasonal patterns in optimum activity temperature and maximum temperature during trial

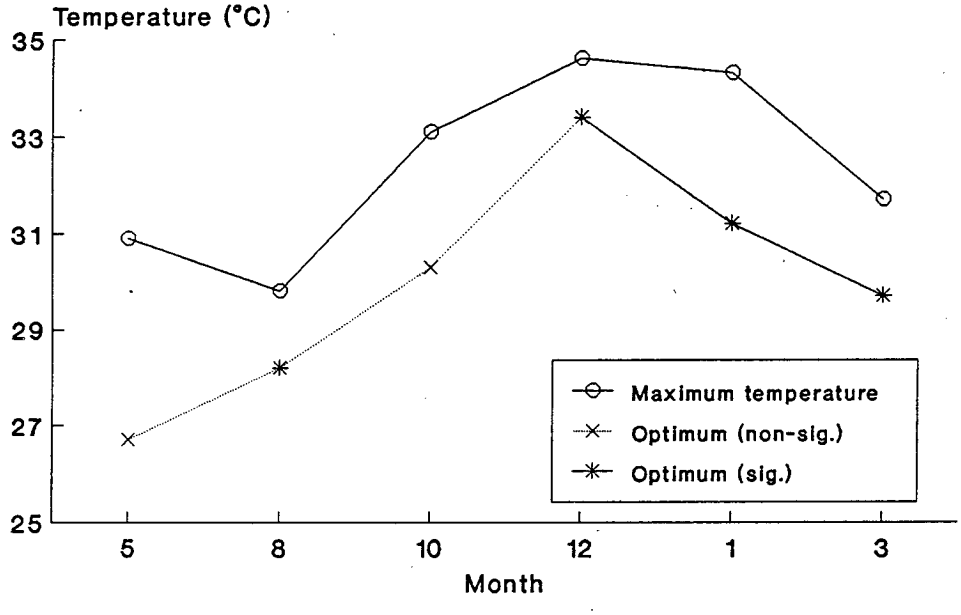


Figure 6.22. Temporal variation in number of ants outside nest of queenright colony in laboratory

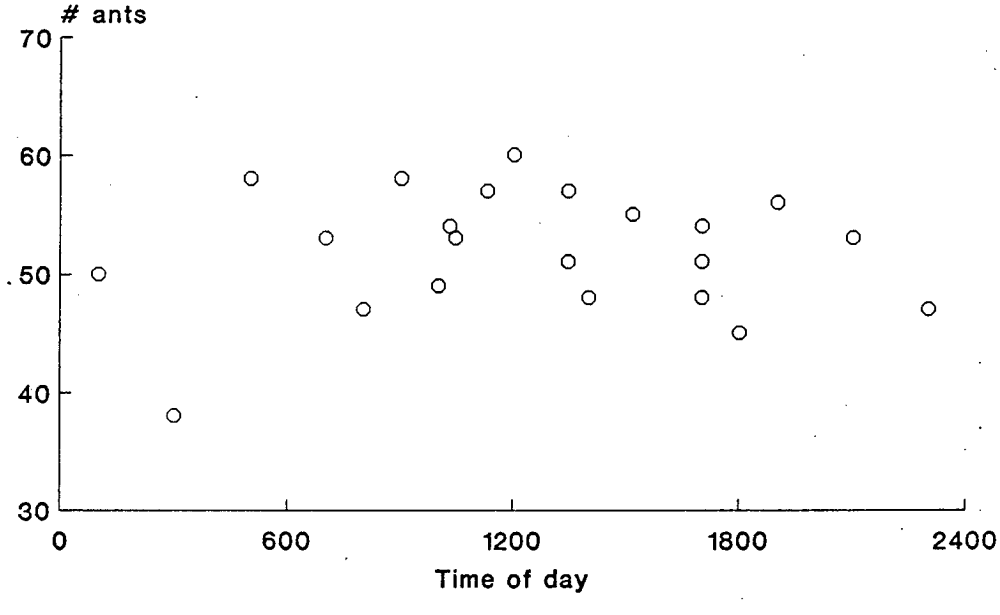


Figure 6.20. Temporal variation in activity of queenright colony in laboratory conditions.

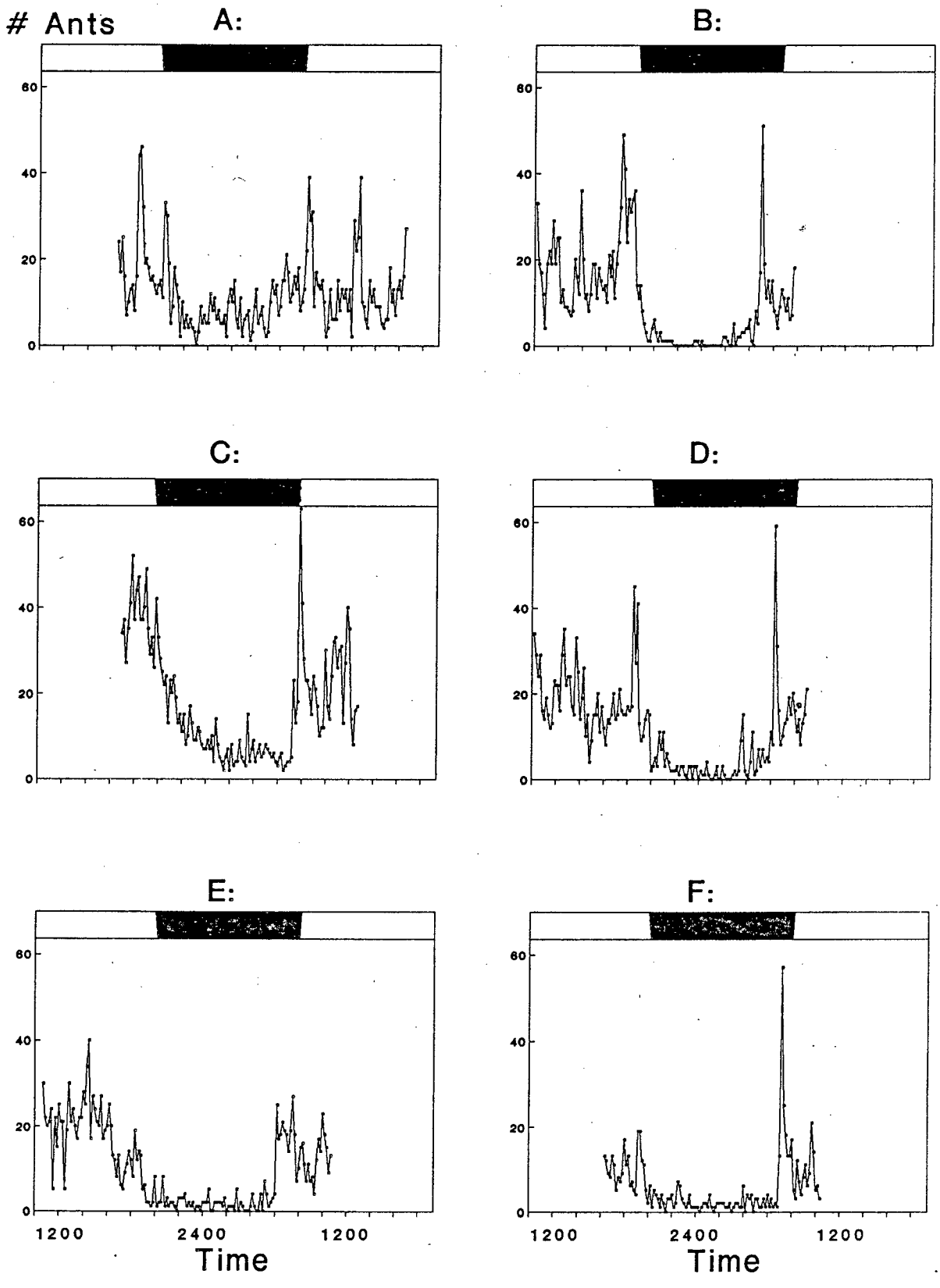
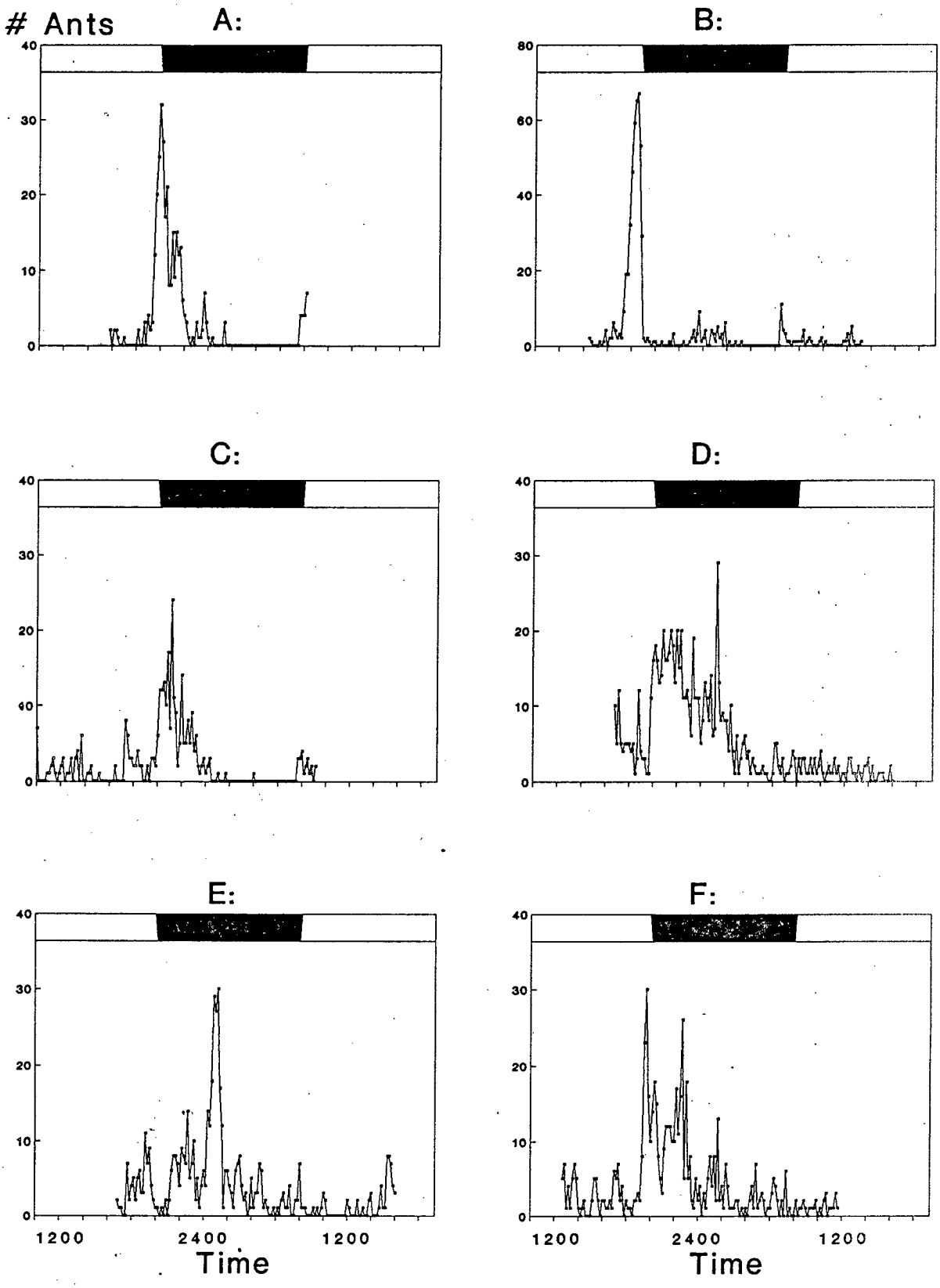


Figure 6.21. Temporal variation in activity of queenless colony fragment in laboratory conditions.



A markedly different pattern was observed in a queenless colony fragment (N1), with the only substantial activity period during dusk or early night. This peak corresponds to the early evening (1900-2100) peak observed in the field. The highly exploratory behaviour of ants during this period, and the proliferation of electrocuted ants along the electric grid by morning, suggests that these ants were attempting to relocate and return to their parent colony at this time. Food input results (section 6.3.5) indicate that the early evening peak in field activity did not correspond to high food intake, and might thus perform some other function, such as inter-nest movements and/or brood transport (section 6.3.5.3).

The last 2 plots in figure 6.21 show activity cycles 1 and 3 days after a continuous 24 hour light photoperiod was initiated. The characteristic early evening peak was still evident even after 3 days, suggesting that circadian activity cycles in this species are at least partially maintained by biological rhythms.

The numbers of ants in the queenright colony found outside the nest during August, 1987, varied from 38, at 0300, to 60 at 1200, and showed no evidence of circadian variation (fig 6.22). This continuous "outdoor" population throughout the day might allow continual territorial surveillance, in this highly aggressive, territorial ant. In the field, a similar situation was implied by the persistence of inward and outward ant flows, except in very cold weather (section 6.3.2).

6.3.5. Food Input.

Foragers of *O. smaragdina* collect two main food types. They tend homopterans for honeydew, and prey on small animals, mainly arthropods, for protein. These tasks are not performed exclusively by different ants, as an ant tending a homopteran would often kill and carry back a prey item, if encountered. The possibility of differing tendencies towards these two functions cannot be ruled out, however. By tagging ants, I hoped to examine the fidelity of individual ants to each food type, to foraging areas and times, and to each nest. Unfortunately, no suitable persistent mark was devised for workers of *O. smaragdina* (section 6.2.3).

6.3.5.1 Prey intake.

Green tree ant foragers preyed on a wide variety of arthropod species (table 6.13). The great majority (47.6% of the total number) were ants of other species, such as *Opisthopsis haddoni*, *Iridomyrmex purpurea sanguinea*, and species of *Crematogaster*, *Camponotus*, and *Polyrhachis*. All of these species forage in trees to some extent. Other common insects collected were homopterans (7.9%), coleopterans (7.6%), dipterans (4.5%), hymenopterans other than ants (4.5%), and larval lepidopterans (3.5%). A further 15.6% of prey items were unidentified insect fragments, either dismembered from a large insect, or scavenged insect remains.

A total of 1549 prey items were carried by 28800 ants observed returning to nests, so the average ratio of ants to prey was 19:1. The numbers of ants involved in prey transport varied from 1 for a small

Table 6.13: Frequencies of arthropod prey collected by foragers.

Arthropod group.	Number collected.	%
Formicidae	738	47.6
Other Hymenoptera	69	4.5
Homoptera	123	7.9
Heteroptera	24	1.6
Coleoptera	118	7.6
Diptera	69	4.5
Larval Lepidoptera	54	3.5
Isoptera	44	2.8
Orthoptera	39	2.5
Aranae	25	1.6
Blattodae	5	0.3
Unidentified items	241	5.6
Total	1549	100.0

item, to over 10 for a large insect, such as a grasshopper. The average number of ants/item was usually around 2. Only about 11% of returning ants were thus involved in prey transport, although a larger proportion might have participated in prey capture, and more again in unsuccessful searching for prey.

The total weight, number of items, and average item weight of prey collected by foragers showed distinct seasonal patterns (fig 6.23). Each monthly value displayed in this graph is a measure of the prey intake of 900 returning ants per nest, averaged for all nests monitored in that month. Well defined peaks in total prey weight occurred in the beginning of 1988 and 1989 (fig 6.23a). The less obvious peak observed in early 1987 might be an artifact of irregular monitoring at this time, or due to the very poor wet season during this summer. Lowest prey weight intake occurred in the winter months of July and August.

Highest numbers of prey items did not coincide with highest total prey weights, with less distinct peaks occurring just before and after maxima in prey weight (fig 6.23b). Numbers of other ants preyed on by *O. smaragdina* were also plotted in this graph. Two obvious bursts of ant predation in May, 1988, and March, 1989, formed a substantial part of the peaks occurring after each prey weight maximum. These peaks in predation on ants, which are relatively small insects, help explain the combination of high prey numbers, but only intermediate prey weights, during these periods. Minimum numbers of prey occurred in July and August, coinciding with lowest prey weights.

Two very sharp peaks in average prey item weight corresponded closely to maximum total prey weights in early 1988 and 1989 (fig 6.23c). Prey collected during these periods were thus much larger than at other times of year. Foragers in months before and after these

Figure 6.23a. Temporal patterns in total prey weight per 1000 ants

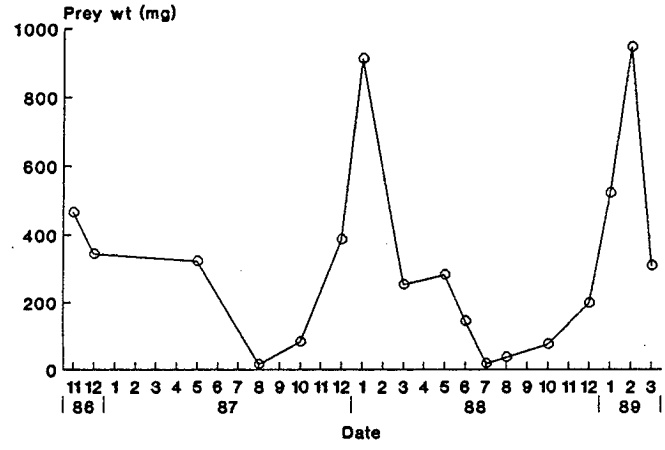


Figure 6.23b. Temporal patterns in number of prey collected per 1000 ants

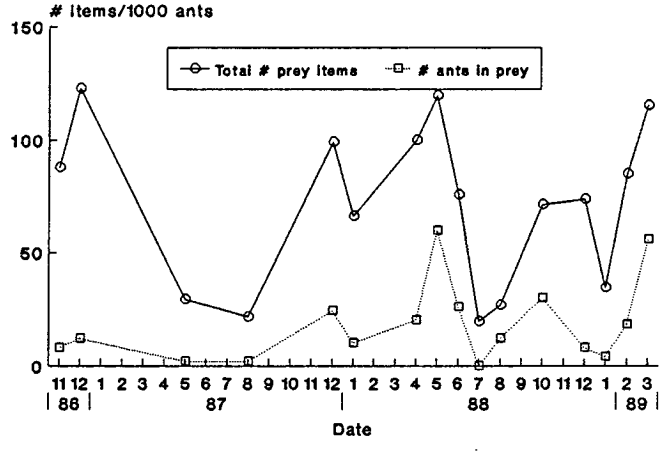
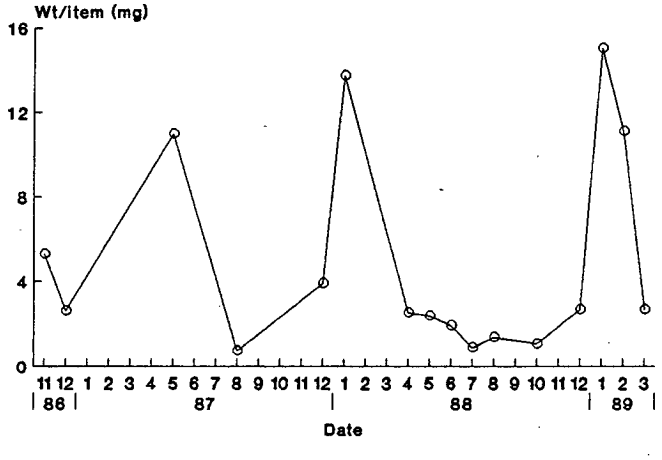


Figure 6.23c. Temporal patterns in average prey item weight



periods collec
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6.14a) did not
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Prey number
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tems, but of much smaller size, so
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rge orthopteran.

more formally using analyses of
May, 1987, to March, 1989. In all
rey values (plus 1) were used, to
s. No physical variables were
easures. Total prey weight (table
37, 1x12df, P=0.55), but was very
.6, 5x12df, P=0.0001). Lowest prey
, and highest levels from December

cantly with month (F=3.85, 5x12df,
ion was less marked than for prey
of prey items were collected in
fewer were gathered (fig 6.24b).
ms was strongly associated with
ble 6.14c), and may be weakly
, P=0.063). The latter effect
n 1988 were on average slightly
nce was not significant. A large
ry, and low weights were seen in

Table 6.14: Analyses of variance for daily prey intake measures.

(a) Total Prey weight.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Year	1	0.1761	0.1761	0.37	0.5540
Month	5	32.305	6.4609	13.59	0.0001
Year*Month	5	3.3593	0.6718	1.41	0.2877
Error	12	5.7039	0.4753		
Total	23	41.544			

(b) Total prey number.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Year	1	0.8901	0.8901	2.34	0.1521
Month	5	7.3308	1.4662	3.85	0.0258
Year*Month	5	3.5380	0.7076	1.86	0.1757
Error	12	4.5673	0.3806		
Total	23	16.326			

(c) Average prey weight per item.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Year	1	1.0353	1.0353	4.26	0.0634
Month	5	11.167	2.2333	9.19	0.0012
Year*Month	5	2.8702	0.5740	2.36	0.1090
Error	11	2.6721	0.2429		
Total	22	17.744			

Figure 6.24a. Seasonal pattern in total prey weight collected

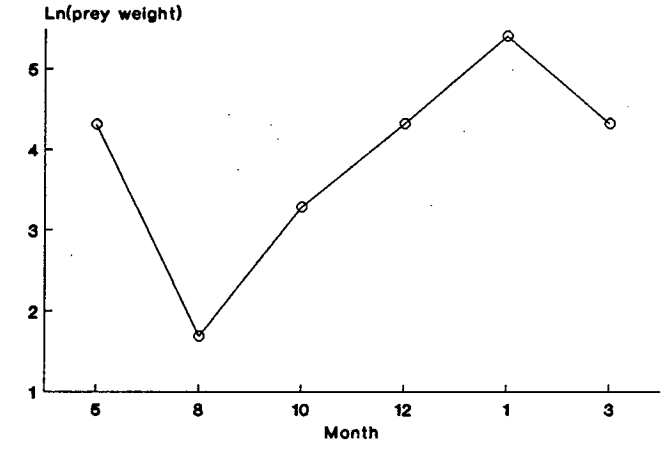


Figure 6.24a. Seasonal pattern in number of prey items collected

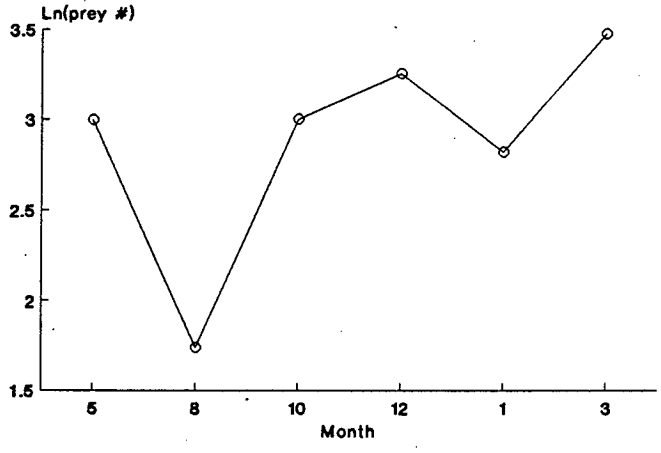
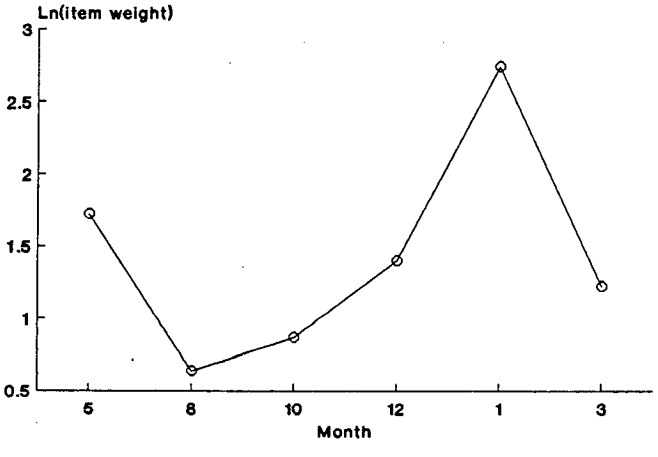


Figure 6.24a. Seasonal pattern in average weight of prey items



More detailed analyses, including time of day, were next performed. Year was excluded, as it showed no significant association with prey intake in the previous analyses. All 3 prey measures were again related to month (table 6.15), and also varied significantly with time of day. Circadian variation followed very similar patterns in the 3 prey measures (fig 6.25). High levels were observed during daylight hours, from 0900 to 1700, with a pronounced depression at night. The nocturnal activities of green tree ants thus do not appear to be associated with prey hunting. These circadian patterns occurred consistently throughout the year, as demonstrated by the non-significant interaction terms between month and hour (table 6.15).

6.3.5.2 Liquid food intake.

O. smaragdina workers tended large populations of homopterans inside their leaf nests, and in various locations throughout occupied trees. Dense aggregations often occurred on shoots with flowers and young fruit, where sap flow was presumably highest. The most commonly tended homopterans were coccids and pseudococcids, although other groups such as aphids and membracids were also occasionally visited for honeydew.

6.3.5.2.1. Assumptions of liquid food intake analysis.

Liquid food collected by foragers was measured as the weight difference between leaving and returning ants. An unknown amount was also gathered from homopterans inside the nest. This internal production was probably directed to workers remaining inside the nest,

Table 6.15: Analyses of variance for circadian patterns of prey intake.

(a) Total Prey weight.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Month	5	22.639	4.5278	4.12	0.0035
Hour	8	85.751	10.719	9.76	0.0001
Month*Hour	39	54.386	1.3945	1.27	0.2171
Error	46	50.511	1.0981		
Total	98	221.66			

(b) Total prey number.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Month	5	5.2243	1.0449	2.50	0.0437
Hour	8	35.612	4.4515	10.66	0.0001
Month*Hour	39	16.136	0.4137	0.99	0.5080
Error	46	19.202	0.4174		
Total	98	80.569			

(c) Average prey weight per item.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Month	5	13.385	2.6770	3.67	0.0071
Hour	8	20.362	2.5453	3.49	0.0032
Month*Hour	39	26.044	0.6678	0.92	0.6086
Error	46	33.548	0.7293		
Total	98	97.122			

Figure 6.25a. Circadian pattern in total prey weight collected

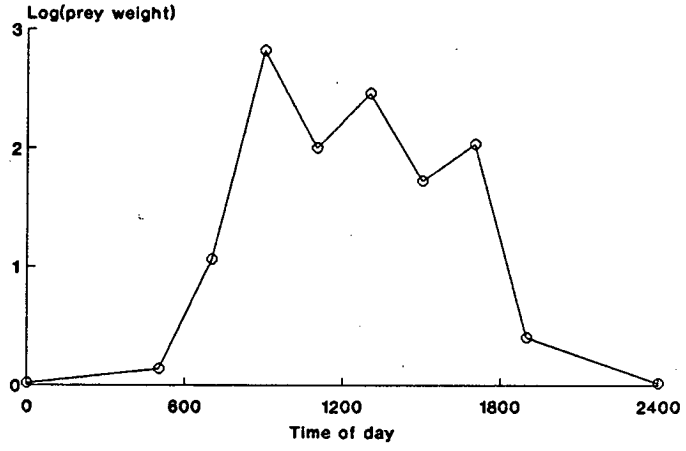


Figure 6.25b. Circadian pattern in prey number collected

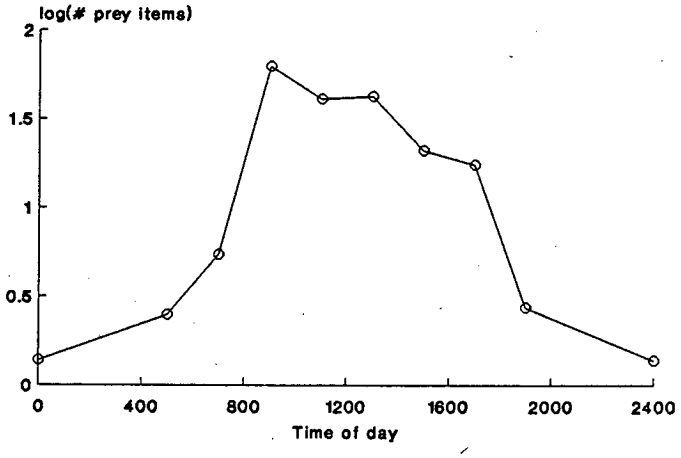
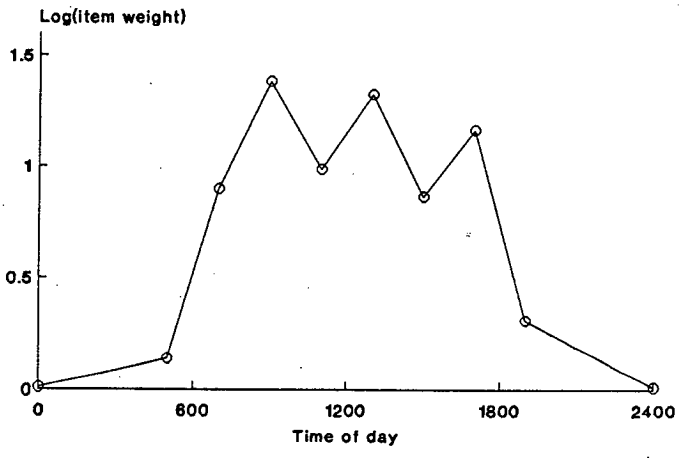


Figure 6.25c. Circadian pattern in average weight of prey items



and to larvae, but some may also be consumed by foragers before leaving the nest.

Unknown quantities of liquid food were also transferred trophallactically from returning workers to leaving workers, both on trails outside the nest, and within the nest. Food exchanged further outside the nest than my monitoring point never reached the nest, and was thus not involved in nest food intake. Exchanges between the monitoring point and the nest were rare, as they caused heavy congestion in the main arterial access routes into the nest. Food transfer from returning to leaving workers inside the nest could not be monitored in these trials. However, in conditions of approximately equal inward and outward flow rates (section 6.3.2), the average weight difference of the two would remain constant, and thus the food entering the non-foraging nest population would be unaffected (discussed more fully in section 6.1.2).

Another source of error was caused by the range of major worker sizes and weights. In March, 1989, the scape lengths of foragers varied from 2.1 to 2.7 mm, and weights from 3.2 to 10.2 mg. The correlation of weight to scape length for major workers inside the nest was 0.54, and for leaving foragers was 0.56. For returning foragers, a much lower correlation of 0.28 was observed, reflecting the variation in crop loads carried by this group.

An analysis of variance indicated that the average scape length of major workers inside the nest was greater than those of foragers leaving and returning to the nest ($F=16.1$, 2x148df, $P=0.0001$; table 6.16; Tukey's HSD test). The forager population at this time was thus smaller than the general nest population. This result supports the important assumption that leaving and returning foragers belong to a

Table 6.16: Analysis of variance for scape length of ants in 3 categories: leaving nest, entering nest, and inside nest.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant category	2	0.4705	0.2353	16.06	0.0001
Error	148	2.1684	0.0146		
Total	150	2.6390			

Table 6.17: Analysis of covariance for weights of ants, adjusted for variation in scape length, in 3 categories: leaving nest, entering nest, and inside nest.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant category	2	21.475	10.737	9.95	0.0001
Scape	1	114.06	114.06	105.73	0.0001
Error	147	158.59	1.0789		
Total	150	368.07			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
SCAPE	7.2527	0.70536

uniform size class. Ideally, comprehensive ant size and weight analyses should be performed for each month of the year to test properly the assumption that the same size classes of ants acted as foragers throughout the day.

An analysis of covariance was used to test for variation between the weights of nest ants, leaving foragers, and returning foragers, after adjusting for differing body size (as measured by antennal scape length). Both factors (ant category and scape length) significantly affected ant weight (table 6.17). Tukey's HSD test showed that ants collected inside nests had a similar average weight to inward bound ants, even after correcting for size differences, while outward bound ants were significantly lighter. This suggests that the crops of nest ants were as full as those of returning foragers, either from tending homopterans inside the nest, or soliciting food from foragers.

6.3.5.2.2. Spatial variation in liquid food collection.

The crop loads collected by foragers varied markedly with the areas foraged. Circadian variation in the average weights of inward and outward bound ants along 2 trails - one leading up into the canopy of the tree, and the other leading down to the ground - were plotted in figure 6.26. The weights of workers returning along a trail from the upper canopy were on average 1.25 mg heavier than those departing, whereas nestward bound workers on the lower trail were 0.21 mg lighter than departing workers. A paired t-test found that upper trail foragers gained significantly larger amounts of weight than lower trail ants ($t=7.1$, 7df, $P=0.0002$).

Figure 6.26. Weight differences between ants moving in and out from 2 trails.

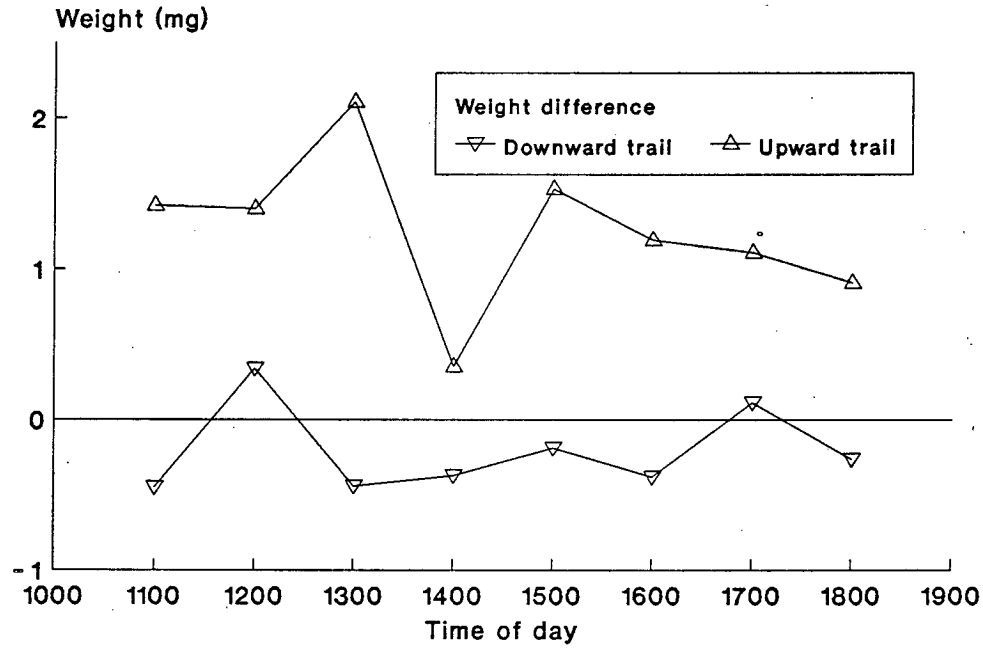
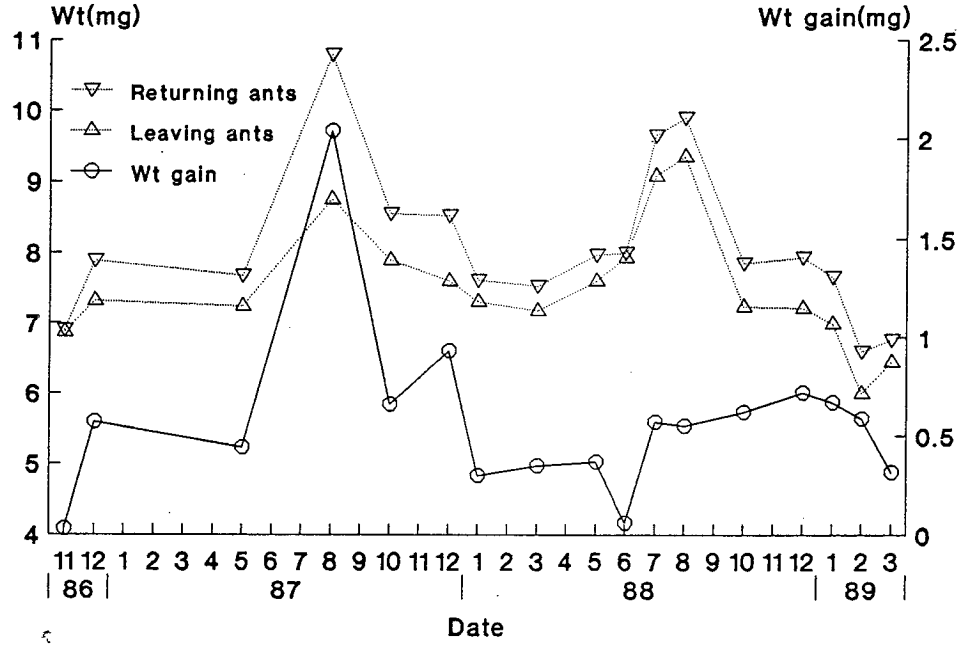


Figure 6.27.Temporal variation in weight differences of ants moving in and out



Foragers leaving via the downward trail thus collected very little honeydew, instead performing other activities, such as prey hunting, patrolling, or inter-nest migration. Unfortunately, without some individual marking technique, the study of these different behaviours was not possible.

6.3.5.2.3. Patterns of liquid food intake.

Liquid food brought into the nest by returning workers did not show any clear seasonal patterns (fig 6.27). Each monthly value displayed in this graph is a measure of the mean weight difference of 500 returning and 500 leaving ants per nest, averaged for all nests monitored in that month. A large peak was observed in August, 1987, but not in the following August, with a relatively uniform level throughout 1988. The reason for this single peak is unknown, but might be associated with the physiological status of occupied trees. The trial nests in August, 1987, inhabited *Pongamia pinnata* trees, which were in relatively poor condition at this time of year, with low sap flow, and thus poor honeydew production by tended homopterans. *Acacia salicina* trees were within foraging distance of both nests, and as this species was observed to flower in August, large quantities of honeydew might have been collected from these trees.

An analysis of covariance was performed on the weight difference data during the period May, 1987 to March, 1989 (table 6.18). Physical variables, and the 3 prey measures were included as covariates, but only prey number was significantly correlated ($F=2.51$, 1x11df, $P=0.029$). High numbers of prey coincided with large differences in the weights of leaving and returning workers. The simplest explanation for

Table 6.18: Analysis of covariance for daily weight difference between leaving and returning ants, adjusted for variation in number of prey collected.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Year	1	0.18107	0.18107	39.34	0.0001
Month	5	1.0997	0.21993	47.78	0.0000
Year*Month	5	0.45324	0.090649	19.69	0.0000
Prey number	1	0.02894	0.02894	6.29	0.0291
Error	11	0.050636	0.0046033		
Total	22	1.7846			

COVARIATE VARIABLES	COEFFICIENT	STD ERROR
Prey number	5.957×10^{-3}	2.376×10^{-3}

Table 6.19: Analysis of variance for circadian in weight difference of leaving and returning ants.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Year	1	2.5542	2.5542	7.68	0.0061
Month	5	12.692	2.5384	7.63	0.0002
Hour	8	9.7910	1.2239	3.68	0.0003
Year*Hour	8	2.2542	0.2818	0.85	0.5638
Year*Month	5	13.451	2.6902	8.09	0.0001
Month*Hour	40	25.067	0.6267	1.88	0.0045
Error	119	39.584	0.3326		
Total	186	114.65			

Figure 6.28. Seasonal patterns in weight differences

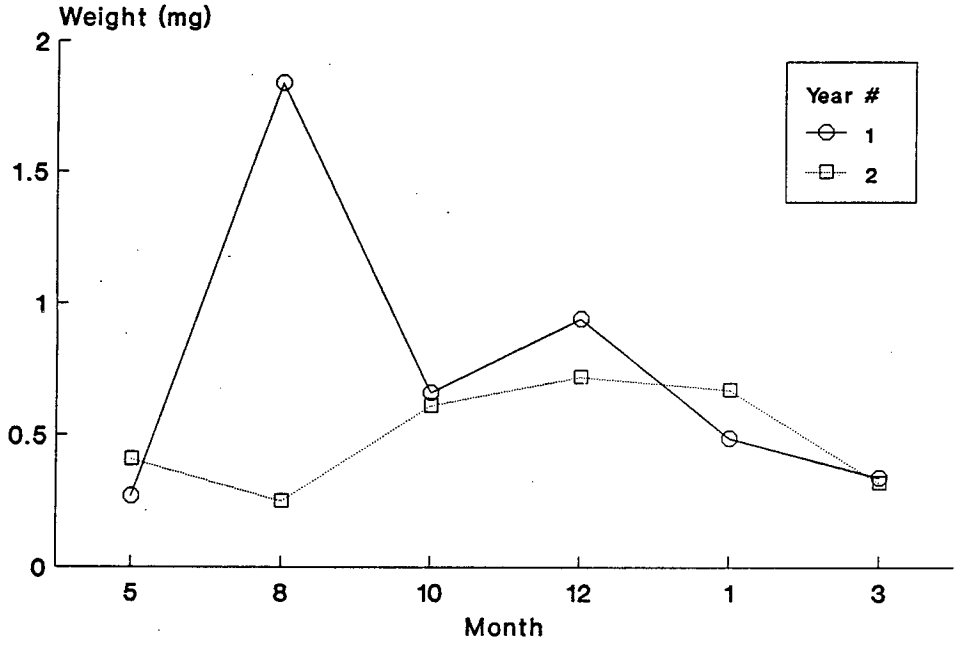
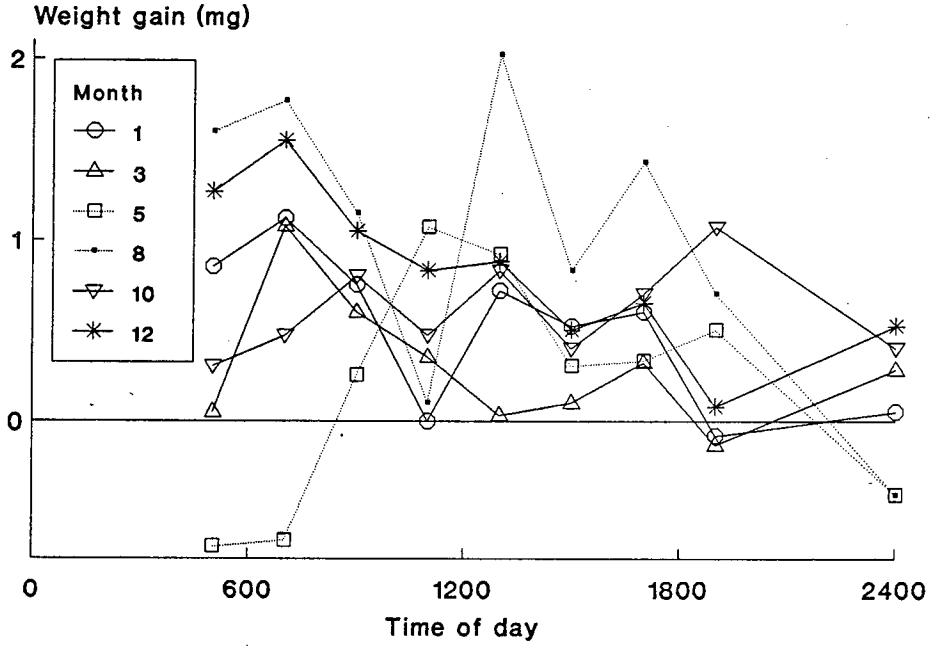


Figure 6.29. Circadian pattern in weight differences of ants moving in and out



this trend is that conditions of high prey availability also favour high honeydew production. Another possibility is that when prey numbers were high, foragers could spend less time searching for prey. Shorter hunting times mean lower consumption of food stores in the body, and possibly more time for honeydew collection, resulting in heavier mean returning weights.

Year, month, and an interaction of year and month all showed significant associations with weight differences (table 6.18). The interactive effect was due mainly to the high levels in August, 1987, described earlier (fig 6.28). Although a peak in weight change was observed in the summer months of the second year, the wide variation in data make such small trends of dubious meaning.

A further analysis of weight differences was performed, to examine circadian variation within each month. The inclusion of the significant year term greatly enlarged the model, so that insufficient computing memory was available for an analysis with covariates. An analysis of variance indicated weight difference varied with all main effects (table 6.19), and with interactions of year by month ($F=8.09$, 5x119df, $P<0.0001$) and month by hour ($F=1.88$, 40x119df, $P=0.004$). The first interactive effect was similar to that seen in the earlier analysis (fig 6.28). The month by hour interactive effect appeared to be due to seasonal variations in circadian patterns of weight differences between leaving and returning ants (fig 6.29). In December, January, and March, peak weight difference occurred at 0700, and slowly dropped throughout the day. In the winter month of May (and in the June data included on this graph), a later peak occurred at 1100, and low levels were observed at night and early morning. August was highly variable, but showed a trend most similar to the summer months. October showed least

variation, with a relatively constant weight difference. The clearest trends were a maximum weight gain by returning workers in the early morning in summer, and a depression in weight gain at night and early morning in mid-winter.

6.3.5.3. Patterns of worker size.

The average weights of both leaving and returning ants displayed clear seasonal trends (fig 6.27). Weights peaked in the winter months of July and August, and were lowest from January to May. As departing ants probably have empty crops, and consequently display a more consistent weight to length relationship than returning ants (section 6.3.5.2.1), only this group was used in further analyses.

The seasonal pattern of scape lengths of ants inside nests (discussed in section 5.3.6) was markedly different to the cycle of seasonal variation in ant weight (fig 6.30a). Maximum scape lengths occurred during periods of low ant weight, and vice versa. The 2 measures displayed a common minimum on 1 occasion, during February, 1989, when both were exceptionally low. Unfortunately, the relationship of the size of ants inside the nest to the size of foraging ants was only recorded in March, 1989, when foragers were significantly smaller than nest ants. The inverse correlation of these 2 measures may thus be caused by seasonal differences in the relationship between size classes of foragers and nest ants, or by variation in food levels stored by foragers.

Figure 6.30a. Temporal patterns in ant scape lengths and leaving ant weights

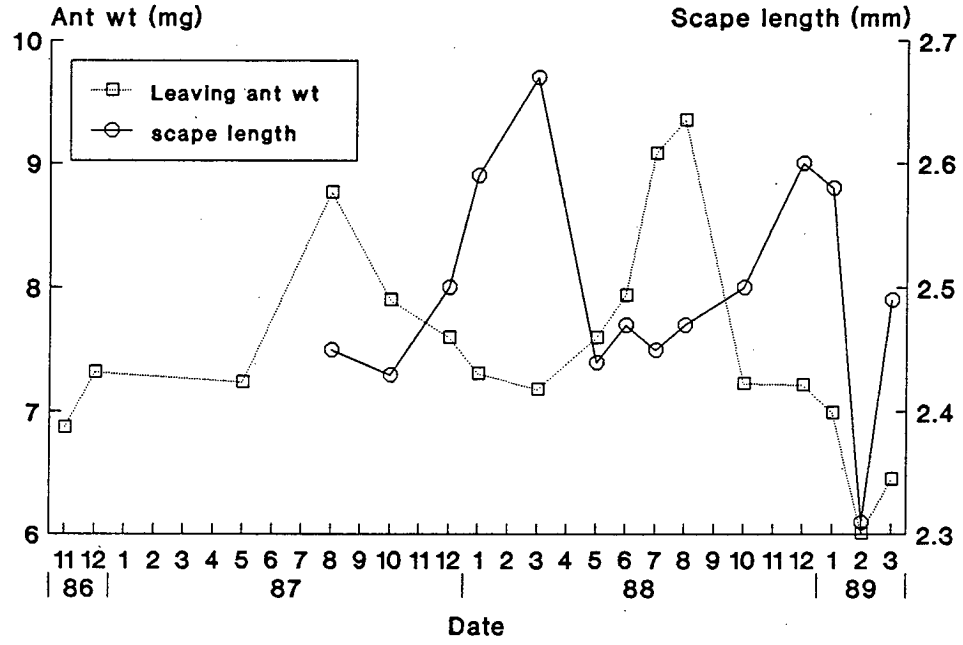
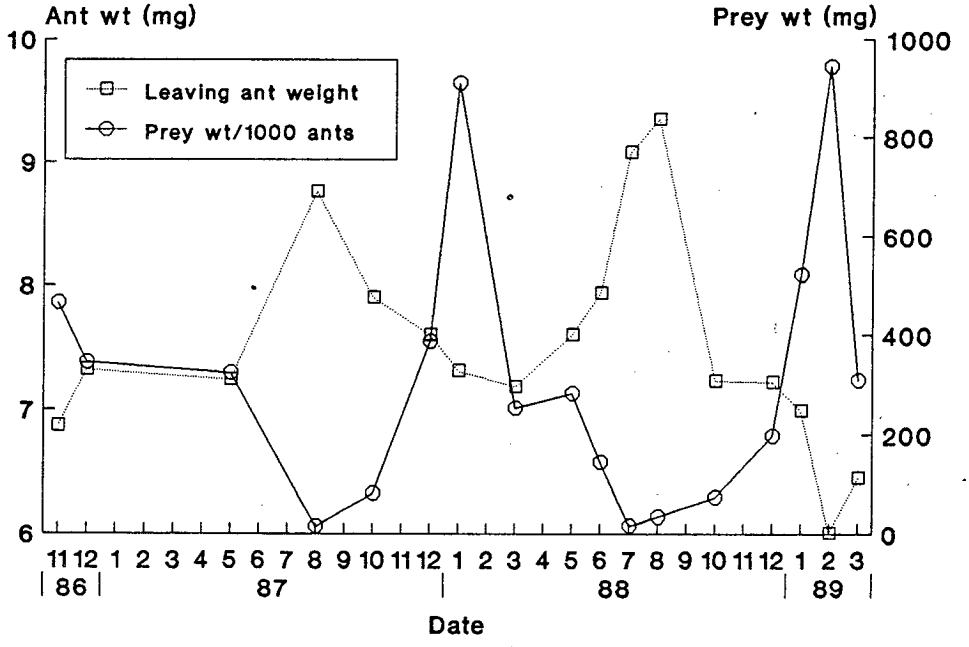


Figure 6.30b. Temporal patterns in prey weight collected and leaving ant weights



Leaving ant weights also showed a distinct inverse relationship with the total prey weight collected (fig 6.30b). The largest quantities of prey were thus collected when departing ants were lightest.

Using an analysis of variance, leaving ant weight was found to vary with month ($F=98.7$, 5x119df, $P<0.0001$; table 6.20), and interactively with year and month ($F=10.36$, 5x119df, $P=0.0001$), and month and hour ($F=1.9$, 40x119df, $P=0.006$). The first interaction term was caused by the more pronounced extremes in weights observed in year 2, with a higher maximum and smaller minimum than in year 1 (fig 6.31). The seasonal trend was nevertheless quite consistent for both years, with highest ant weights in August, and relatively low weights during October, December, January, March, and May.

The month by hour interaction effect was produced primarily by the 2 coldest months - May, and August (fig 6.32). The 4 warmer months displayed minimal circadian variation in departing ant weights. In May, weights were similar to the uniform warmer months from 0900 to 1900, but were higher during the cooler hours from 2400 to 0700. Weights of departing ants in August were consistently higher than any other month recorded, and displayed 2 small peaks in the morning and afternoon. This circadian variation in departing ant weights during May and August might be due either to differences in stored food levels throughout the day, or circadian subdivision of forager populations of varying sizes. Measurements of weight differences during May and August were almost certainly biased by this circadian cycle in departing ant weights.

Table 6.20: Analysis of variance for circadian patterns in weights of ants leaving the nest.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Year	1	0.1101	0.1101	0.68	0.4104
Month	5	79.601	15.920	98.69	0.0001
Hour	8	1.4565	0.1821	1.13	0.3492
Year*Hour	8	0.9437	0.1180	0.73	0.6636
Year*Month	5	8.3578	1.6715	10.36	0.0001
Month*Hour	40	11.943	0.2986	1.85	0.0058
Error	119	19.197	0.1613		
Total	186	148.15			

Figure 6.31. Seasonal patterns in leaving ant weight

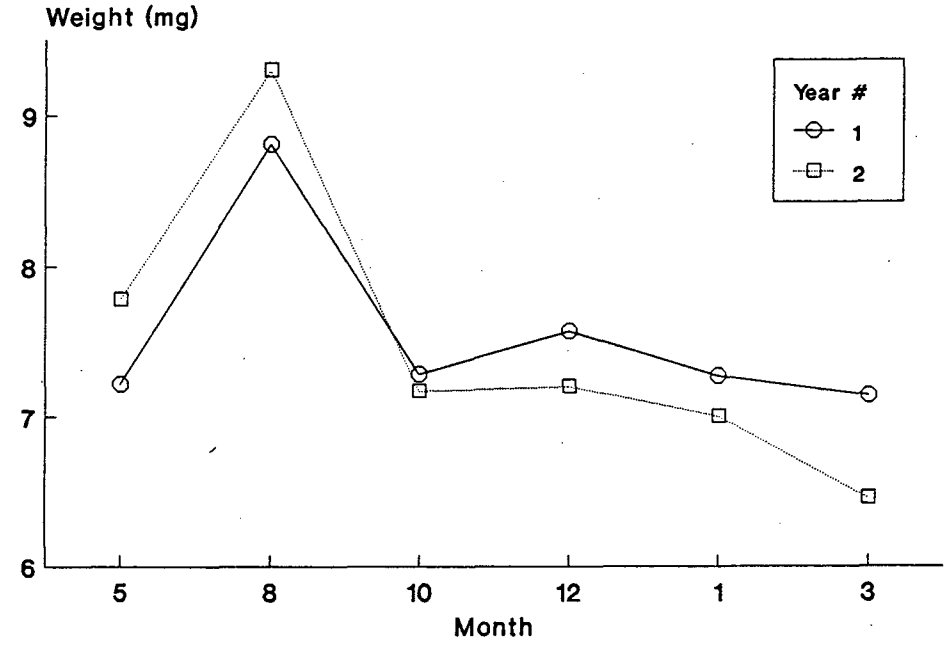
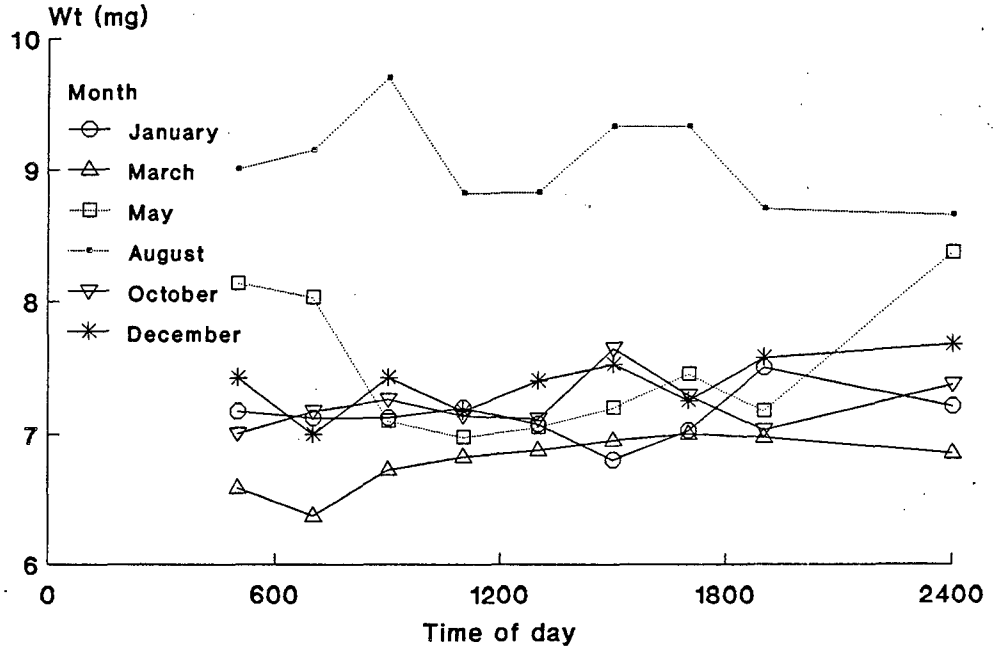


Figure 6.32. Circadian patterns in leaving ant weight



6.3.5.4. Brood transport.

Ants were regularly observed carrying brood (mainly larvae) and other workers. Brood transport is essential for the construction and maintenance of nests, as larval silk is used to bind the leaves of the nest, and the queen is the sole producer of brood in a mature colony. An estimate of brood transportation levels was obtained from the numbers of brood carried by ants collected for liquid food input trials.

Almost all brood transport was observed at night, with maximum levels from 1900 to midnight (fig 6.33). This peak corresponds approximately to the activity peak recorded in the early night during most months (section 6.3.3). A substantial fraction of ants travelling along trails could be engaged in brood transport during this period of the night. In May, 1988, for example, when very high larval proportions were recorded in nests, 21% of the workers collected at 1900 were carrying larvae. Insufficient data was available to analyze the effects of month, year, and physical variables on levels of brood transport.

6.3.6. Dyed food dispersal.

Rhodamine red in a honey solution was the most successful mass marking method developed for ants in the field, and was highly visible through the translucent abdomen wall in quite small amounts. However, ants never fed on honey solutions containing a 0.5% dye concentration for more than 3 days, even when the solutions were changed every day. During the first trials in June and August, the dyed food was consumed for only 1 day, and few ants were consequently marked. In the September

Figure 6.33. Circadian patterns in brood transport and parasite abundance

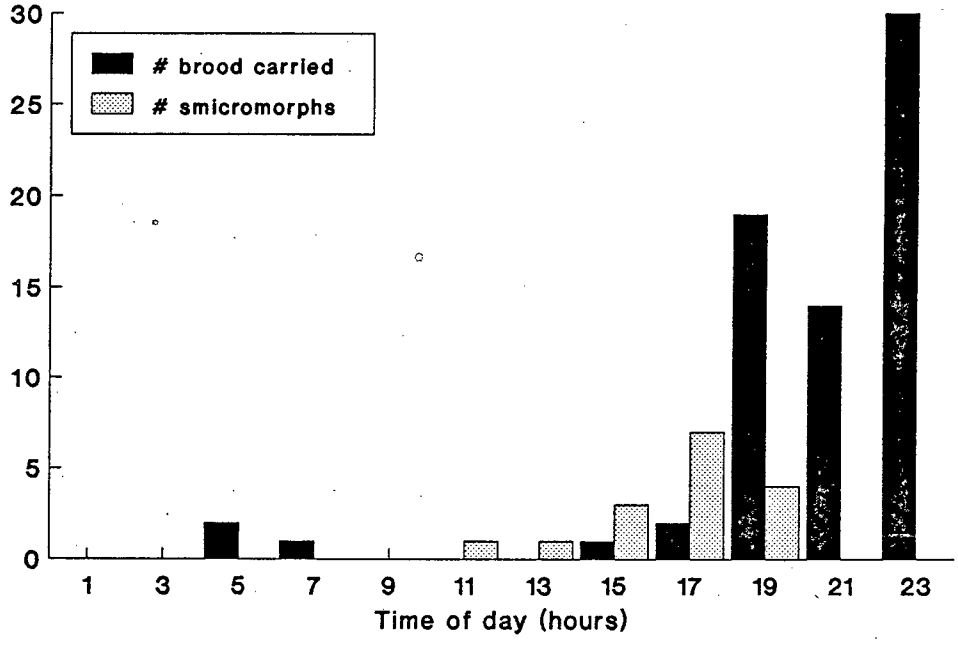
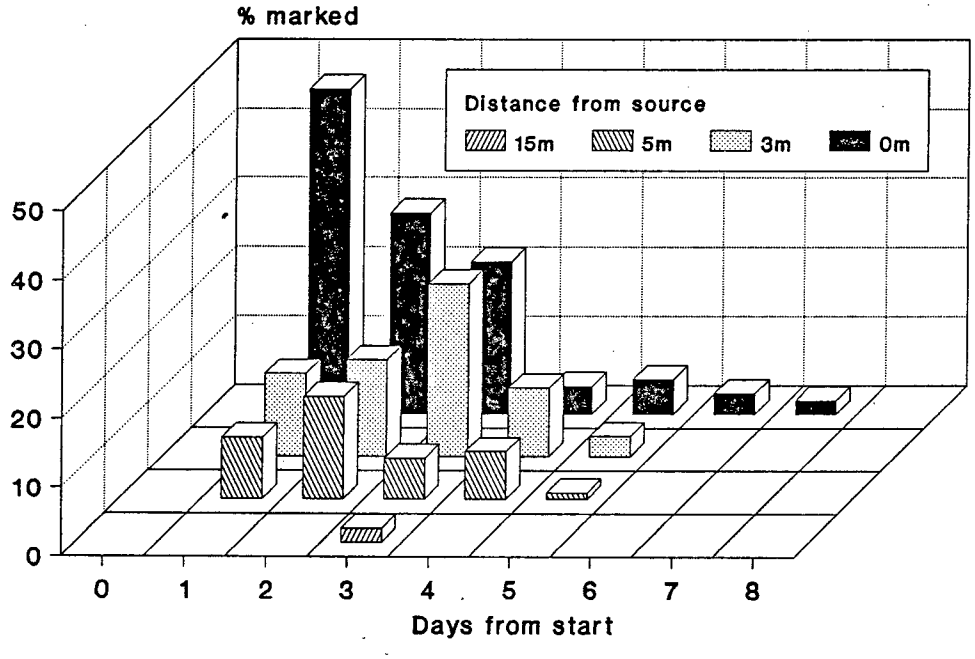


Figure 6.34. Dispersal of dye through ant population



trial, many more ants fed on the dyed food, and over 500 marked ants were recorded during 8 days of monitoring.

Daily changes in the percentage of marked ants observed at 4 monitoring points, at various distances from the food supply, are shown in figure 6.34. No marked ants were observed at a fifth site 30 metres away, and only 2 weakly marked ants were recorded at a distance of 15 metres, after 3 days. Within 1 day of the dyed food introduction, marked ants were observed at sites up to 5 metres away. Marked ants were recorded at the feeder site for 2 days longer than at other sites. This might be due to the smaller quantities of dye in ants further away (although the nearest adjacent site was only 3 metres away), or due to the fidelity of foragers to this particular site, even though no ants were observed feeding on the dyed food from day 4 onwards.

In subsequent trials during October and February, ants were again very reluctant to feed on the dyed food, so further planned dye trials were abandoned.

6.4. Discussion.

6.4.1. Counting by light beam.

The advantages of a light beam counter for monitoring ant activity include:

(1) continuous recording without requiring continuous observation

(2) no disturbance by an observer near the nest

(3) high accuracy, when operating properly.

The accuracy of the present counter system (from 90% to 110% of actual flow rates) was much more consistent than previous field designs. The system of Dibley and Lewis (1972) gave counts ranging from 20% to 120% of observed, with severe underestimates occurring at high flow rates. Skinner (1980a) obtained estimates from 100% to 300% of the actual counts with his counter, although overestimates greater than 150% only occurred during very low flow rates when inaccuracies are less critical. The ground-nesting ants examined in these studies, *Atta spp*, and *Formica rufa*, were detected by a light beam placed just above a wide (up to 20 cm) artificial path, so the alignment of individual ants was much more variable, and a number of ants could pass the beam together. As these species have large colonies, with only one major nest site, maximum flow rates could exceed 300/minute, making wide paths and some inaccuracy inevitable.

Although *O. smaragdina* has very large colonies (up to half a million individuals; Way, 1954a), they are dispersed among many nests, each containing a maximum of around 50000 individuals. Numbers of ants entering and leaving one nest were never observed to exceed 100/minute, allowing a narrow path to be used, to reduce multiple passages. A

shorter beam length, improved electronic hardware, and more effective incident light shielding also probably contributed to improved accuracy.

The major problem encountered while developing this system was maintaining accuracy. Green tree ant bodies block very little infra-red light, so sensitivity must be held as constant as possible. The alignment of the string path between the beam transmitter and the detector was critical, and was occasionally disturbed by birds, or very windy storms. Early problems in slowly declining sensitivity, caused by accumulation of pheromones and dust on the original woven string ant trail, were overcome by using a monofilament nylon trail.

Reliability of the system was limited only by the failure of the power supply, usually the power socket or internal battery of the computer. Use of a dedicated computer or data-logger with a permanently attached power line would reduce this source of failure.

One further problem, inherent in all automated systems, is that possible causes for a change in activity, which might be noticed by a human recorder, will be unobserved. For example, a seemingly inexplicable pulse in activity may be due to alarm/defence recruitment caused by the passage of a large animal, such as a wallaby, or bird. Automated recorders should therefore be supplemented by concurrent human observations at various periods, to detect such unexpected effects.

Automated light-beam counters greatly aid the study of activity cycles in ants, especially those active 24 hours/day. The counter system developed for *O. smaragdina* should be useful for examining activity of arboreal ant species, and any species that will travel along a string path.

6.4.2. Patterns of activity and food intake.

Seasonal patterns.

The numbers of workers moving in and out of nests, relative to the total nest populations, were greatest during the wet season months of December, January, and March. This peak corresponds to the period of maximum larval production, and colony size expansion (chapter 5). The greatest quantity of prey was collected by workers in January. Prey intake was high from December to May, intermediate in October, and lowest in August.

Seasonal trends in weight gains of returning workers were difficult to interpret, due to the very large August, 1987 peak (which was twice that of the next highest weight gain). The very large crop loads in this month may have been caused by intensive honeydew collection on adjacent flowering trees, when the nest trees were in poor physiological condition.

Substantial differences in crop loads could also be collected from different trails, which lead to varying homopteran populations. Crop load differences were recorded between ants using trails leading upwards and downwards from one leaf nest in July; similar differences have been reported between wood ant trails (e.g. Ayre, 1958; Skinner, 1980b). During August, 1987, ants may have been collected from trails to very large honeydew sources. Unfortunately, the fact that these weight gains were unusually large was not appreciated until a complete year's data were collected, so the causes were not investigated. Very small crop loads were recorded in the following August. Foragers in October, December, and January, returned with consistently larger crop

loads than those in March and May.

The amounts of honeydew collec homopterans inside the nest were unknown. Departing ants wer est in August, when scape lengths of workers inside nests wer vely small (section 5.3.6). Assuming the sizes of foragers and cs were similar, foragers in August were thus denser, or, more , had partially full crops from intra-nest honeydew productio r, the assumption of equal-sized foragers and non-foragers was id, at least in March, 1989, when foragers were smaller than a mly sampled from the nest population. More comprehensive stu necessary to quantify such complicating factors as varying s foragers, honeydew intake inside the nest, and the differen ogical conditions of trees in the foraging area.

The factors controlling patt activity and food intake cannot be determined from observ studies. Either laboratory studies or manipulative field exp tion would be required to determine if, for example, more aged when food was more available, or if increased activi oved food collection. The facilities and labour necessary to nusal relations in the very large mature colonies of this speci rohibitively large for the present project.

SEasonal variation in tempera , and light levels did not appear to drive the seasonal patte tivity. Rainfall depressed activity on the few occasions it wa during the present study. This response has been previously weaver ants (Brown, 1959; Greenslade, 1972), and other spe as wood ants (Skinner, 1980a), and leaf-cutter ants (Lev 1974a).

Circadian patterns.

Ant activity displayed obvious circadian variation in some months, but not others. Nests monitored in March, May, and August showed reasonably similar circadian cycles of activity, with minimum ant flows a few hours before dawn, and a maximum at dusk (the "winter pattern"). When adjusted for temperature effects, ant flows in these months were all lowest around midday. The early dawn minimum in unadjusted ant flow was thus probably caused by low temperature inhibition of activity. Peak ant flow was displaced less by temperature adjustment, to the period just after dusk.

Activity in January, October, and December was much less predictable. No circadian pattern could be detected in December (i.e. ants were uniformly active 24 hours/day), but activity was correlated to temperature. Ant activity in October, 1987 and January, 1988 was not related to time of day or any other physical or biological factor measured. In October, 1988 and January, 1989, activity displayed circadian cycles which were similar to, but less distinct than the winter pattern.

These seasonal changes in circadian activity patterns probably explain why some authors have reported weaver ants to be primarily diurnal (Greenslade, 1971b, 1972; Hölldobler, 1979; Hölldobler and Wilson, 1978), while others have observed substantial nocturnal foraging (Leston, 1973; Weber, 1949). The effects of varying climates and levels of inter-specific competition may also influence patterns of activity. For example, *Aphaenogaster rudis*, a generalist ant species, appears to alter its circadian activity cycles from nocturnal to diurnal, when the aggressive nocturnal ant, *Camponotus ferrugineus*, is most abundant (Lynch *et al*, 1980). In the present study, competition

with other ant species was very rare (chapter 5); however, much higher levels have been reported in moister equatorial climates (e.g. Leston, 1973). This topic will be discussed in more detail later.

The only climatic variable which was consistently related to variations in ant activity throughout the day was temperature. Activity patterns were most affected by temperature when trials were conducted in the hottest months (December and January, 1989) and the coldest months (August). Temperature has been correlated to activity in many species (e.g. harvester ants - Bernstein, 1974: wood ants - Ayre, 1958; Holt, 1955; Jensen, 1977; Rosengren, 1977: *Polyrhachis simplex* - Degen and Gersani, 1989), and appears to constrain foraging activity at either extreme (Traniello, 1989). *O. smaragdina* activity was markedly reduced by cold temperatures in the present study, and rose to a maximum level at an optimum temperature of 28 to 33°C. A drop in activity was predicted by the parabolic temperature relationship; however, the maximum temperature during trials was very close to the optimum temperature, so that activity reached a plateau and displayed little variation at high temperatures. Activity was thus constrained by temperature at low extremes only.

Temperature can also have less direct effects on activity. In controlled photoperiod and temperature laboratory trials, Rosengren (1977) found the activity of wood ants increased before temperature began to rise, using an endogenous rhythm entrained by photoperiod and temperature "zeitgebers" (timekeepers). The correspondence of the optimum temperature for green tree ant activity with seasonal temperature patterns may be controlled by an entrained seasonal rhythm. Preliminary laboratory trials suggested the presence of an endogenous circadian activity rhythm in *O. smaragdina*, but experimental work on

temperature and photoperiod effects on circadian rhythms had to be abandoned when laboratory colonies died.

Although seasonal activity and prey intake patterns were correlated, circadian cycles of activity and food intake did not correspond closely. Total prey weight, and prey number collected by foragers were highest during daylight hours (from 0900 to 1700), and were very low at night. This marked lack of nocturnal predation suggests that *O. smaragdina* detects prey visually, rather than by odour (as occurs in the Dacetines; Vowles, 1955). Wood ants also appear to be primarily visual predators (Holt, 1955; Rosengren, 1977). No significant seasonal variation in the circadian pattern of prey intake was detected.

Circadian patterns in crop loads were less distinct, and appeared to vary seasonally. In the warmer months, the weight difference of returning and leaving ants was greatest just after dawn, and lowest around dusk. In cooler months, crop weight peaked later in the day, possibly due to decreased honeydew production by homopterans at low temperatures. Weight differences between leaving and returning workers were very low until dawn in all months, even though ants were observed at populations of tended homopterans continually throughout the day and night. During May and August, results were biased by circadian variations in the weights of leaving workers; either different size classes of workers foraged, or differing amounts of food were carried in the crops of leaving workers throughout the day. However, departing ant weights showed little circadian variation during the 4 warmer months. The small weight differences at night during these months suggest that little honeydew was transported to the nest until after dawn. A number of possibilities come to mind:

(1) The homopterans may be inactive, producing less honeydew at night. Some aphids decrease honeydew excretion at night (Auclair, 1963), and membracid activity in Costa-Rican forest was highest in daytime (Windsor, 1978); unfortunately, very few studies have looked for circadian rhythms in sap-sucking insects. Nocturnally attendant ants in this scenario may be "guarding" their honeydew supply from predators, parasites, and/or other ants.

(2) Returning ants pass collected honeydew to other ants before reaching the sampling point near the nest. This behaviour is possible if a substantial proportion of workers at night are engaged in non-foraging activities, such as brood transport, or inter-nest migration.

(3) Foragers are spending longer outside the nest unsuccessfully searching for prey, so consuming more food reserves.

The high level of activity around dusk, when food intake was very low, suggests that foraging was not the primary activity at this time. Brood transport was most frequent in the early evenings. Many ants also appeared to be travelling along main trunk trails between nests (which are marked with an odour trail from the rectal gland; Hölldobler and Wilson, 1978), and the levels of carried ants seemed to be high (however, numbers were not recorded during the study). Many ants during the evening peak period may thus be dispersing brood and young workers throughout the nests of the colony.

Intermingling of the colony specific odour may also be facilitated (as suggested by Ledoux, 1950). Dye dispersal trials demonstrated that ants (or trophallactically exchanged food) could travel over 15 metres within a few days. Actual ant movements may well be greater than this, but no successful marking technique was developed to observe dispersal rates. Vanderplank (1960) and Majer (1976b) used radioisotope labelled

food to examine colony extents in arboreal ants. This technique is more sensitive than dye; however, I was reluctant to produce "hot" ants in the field.

Territorial patrolling is an important extra-nest behaviour in species which maintain exclusive foraging ranges. Hölldobler (1983) demonstrated the existence of special barracks nests and ants which patrol the outer perimeter of the colony in *O. smaragdina*. Harvester ant colonies also contain discrete worker groups for patrolling and foraging (Gordon, 1983, 1986, 1989). Examination of circadian patterns of task performance was not feasible without a suitable marking technique. Patrolling against alien con-specifics would probably be proportional to the levels of foraging, and thus affect only the magnitude, not the pattern of activity. Patrolling for other species of ants, with different activity cycles, may alter the activity pattern of the defending colony. It would be very interesting to examine activity cycles in *Oecophylla* colonies subjected to intra and inter-specific competition. Only intra-specific competition was observed in the present study, during the colony expansion period from December to May (chapter 5). Much higher levels of competition occur in moister equatorial habitats, where a number of aggressive ant species maintain mutually exclusive territories (Leston, 1973; Majer, 1972; Way, 1953).

The proportions of inward and outward moving ants were relatively similar, ranging from 40 to 60%, except during very cold periods when flow rates were minimal. Ants were therefore present outside the nests at virtually all times (although numbers undoubtedly varied). Even in a small laboratory colony, a persistent ant population was maintained outside the nest throughout the day and night. This pattern has also been observed in wood ant colonies (Skinner, 1980a; Rosengren and

Sundström, 1987). During spring, wood ant foragers returned to the nest mound at night, but continual foraging occurred in summer. Rosengren and Sundström (1987) found the numbers of *Formica polyctena* workers at an aphid population were relatively constant over a 24 hour period in summer.

A continuous forager population may be an advantage for a generalist predator, as different prey insects have different activity periods (Rosengren, 1977). However, the low food intake at night (observed in both my and Rosengren's studies) suggests food availability, or at least its catchability, is markedly variable. A more likely function of nocturnal activity is to maintain continuous patrolling against intrusion by other ant species. The constant presence of workers throughout the foraging range would ensure very effective territorial guarding in highly aggressive green tree ant colonies. The continuous presence of ants at homopteran populations suggests these food sources are also guarded. The reduction in circadian patterns of activity during the wet season months may reflect more continuous patrolling when invasions from intra-specific (and inter-specific in moister habitats) ant colonies are most likely. Predators and parasites of tended homoptera may also be most abundant at this time of year.

Ants probably perform some functions concurrently, for example, prey hunting and patrolling (Rosengren and Sundström, 1987). Other tasks may be performed in circadian sequences, as occurs in *Pogonomyrmex barbatus* (Gordon, 1983). A switch from foraging to brood transport appears to occur in *O. smaragdina* just after dusk, and the frequency of patrolling and homopteran guarding may also vary throughout the day. Further studies are necessary to elucidate the

different types of activity, and their circadian and seasonal variation.

In summary: seasonal patterns of activity and food intake corresponded reasonably well to cycles in colony size and reproduction. Activity, prey intake, and reproduction were all highest during the wet season months from December to March, and colony extents expanded to a peak in May. Seasonal patterns of crop weight suffered from problems of varying forager weights and sizes, and differences in the levels of the 2 food types collected between different trails and trees.

Circadian activity patterns did not correlate to food intake, with nocturnally active ants probably performing tasks other than (or in conjunction with) foraging, such as brood and callow transport, colony scent dispersal, and territorial patrolling. An ant population was always maintained outside nests, possibly to guard against intrusion by alien ants, and to protect homopteran populations. Activity was reduced by low temperatures and rainfall, and also showed an endogenous rhythm.

7. Green tree ants in a mango plantation.

7.1. Introduction.

Interactions between ants and plants have attracted the attentions of researchers for many years (e.g. Bequaert, 1922; Wheeler, 1910), producing a substantial volume of literature on this subject (reviews by Bentley, 1977; Buckley, 1982, 1987; Price et al, 1980; Way, 1963). Ant plant interactions may be mutually beneficial, or ants may benefit at the expense of the plant. Effects may be direct, or indirect, involving additional species. In many cases, an ant plant interaction encompasses a combination of different effects, with a variable net influence dependent on the prevailing conditions. In the following brief summary of interactions between ants and plants, associations are classified by the effect of ants on plants - harmful, beneficial, direct, and indirect.

Ants directly impair plants by consuming seeds or leaves. Seed harvesting ants occur world-wide, and are particularly common in arid environments, where they may consume substantial proportions of the soil seed stocks (Buckley, 1982). Although most seeds are eaten, some are occasionally abandoned in underground granaries, so providing dispersal and protection from other predators and fire. Leaf herbivory is restricted to the tropical American "leaf-cutter" ants, of the tribe Attini (Wilson, 1971). These ants feed on fungus which is cultured on sections of leaves, flowers, or fruits.

Directly beneficial effects include fertilization of seedlings or epiphytes, seed dispersal, and removal of competing vines or intruding

vegetation. Some epiphytic plants have specialized cavities, which are occupied by ants. In exchange, the plant absorbs nutrients from debris deposited by the ants (Janzen, 1974). Some ants also collect epiphyte seeds and place them in carton-covered tunnels, where the seeds germinate.

The seeds of many plant species have ant-attractant food bodies (elaiosomes); ants carry these seeds to their nest, remove the elaiosome, and dump the seed into nutrient-rich refuse chambers or piles. This trait is especially prevalent in Australia and Africa. About 1500 Australian plant species are dispersed to some extent by ants, mainly in arid sclerophyllous vegetation on poor soils (Berg, 1975). In contrast, very few cases of plant pollination by ants have been documented. Beattie (1982) attributes the rarity of ant pollination to the disruptive effects of ants' glandular secretions on the delicate male gametophyte.

Certain ant species protect their host tree from competing vines and other plants, killing intruding branches by chewing growing tips and tendrils. All recorded cases (e.g Janzen, 1966, 1969, 1972; Schupp, 1986) involve well developed or obligate mutualistic associations, with the host tree providing nest sites and food, and the ants deterring herbivores as well as adjacent plants.

The most common effects of ants upon plants are indirect, through influences on other animals which interact with plants, such as herbivores, frugivores, and pollinators. Price *et al* (1980) argue that "theory on insect-plant interactions cannot progress realistically without consideration of the third trophic level". Ants are dominant members of this trophic level.

Many ant species are dualistic feeders, collecting insect prey,

and tending certain homopterans for honeydew. These ants may have a beneficial impact on plants by reducing non-tended herbivores, and a negative effect by encouraging honeydew-producing homopterans which feed on plant sap. Some myrmecophilous homopterans have also been implicated as vectors of plant viral diseases, such as swollen shoot virus in cocoa (Strickland, 1951). Many studies have demonstrated that ants reduce the numbers of leaf-chewing insects (e.g. Jones, 1987; Laine and Niemela, 1980; Majer, 1976c; Tilman, 1978; Way, 1954a), and decrease leaf damage (e.g. Janzen, 1972; Koptur, 1984; Messina, 1981; Room, 1972; Schupp, 1986; Skinner and Whittaker, 1981). Ant-mediated increases in homopteran populations have also been well documented (e.g. Fowler and MacGarvin, 1985; Fritz, 1983; Skinner and Whittaker, 1981; Way, 1954b).

Cost-benefit analyses of three trophic level systems are complex, and are often sensitive to changes in factors such as the physiological status of the interacting species, and the presence of other species in the tree fauna (Buckley, 1987). For example: the prey intake of an ant colony is stimulated during periods of brood production (Robertson, 1988; Sudd, 1987); ants may abandon one homopteran species when another becomes abundant (Skinner, 1980a; Sudd and Sudd, 1985); and different species of herbivore may be variably susceptible to ant predation (Buckley, 1987).

The effects of ant plant interactions on different insect species are generally measured by monitoring their numbers in plants with and without ants. In some studies, ants were experimentally removed from plants and the resultant changes in insect fauna were observed (e.g. Fowler and MacGarvin, 1985; Skinner and Whittaker, 1981).

Effects on the plant are often assessed by measuring areas of leaf

missing. This technique is biassed by the expansion of holes due to subsequent growth of the leaf (Reichle *et al*, 1973; Smith, 1972), and does not evaluate the effect of sap loss from homopterans.

The ultimate measure of a plant's fitness is its reproductive success. A number of studies have examined the seed production of plants with and without ants (e.g. Messina, 1981). However, ant presence may also affect seed dispersal and germination. For example, Thomas (1988) found that the presence of *O.longinoda* ants reduced levels of fruit removal by bats, the primary disperser of the fig, *Ficus capensis*. He also demonstrated that fruits unhandled by frugivores had lower germination success.

Weaver ants can cause substantial indirect effects on inhabited trees. Various studies have reported that weaver ants can reduce insect damage in cocoa (Leston, 1970; Majer, 1976c), coconuts (Way, 1954a, 1958), tea plants (Das, 1959), citrus (Groff and Howard, 1925), and mango trees (Friederichs, 1920). The costs of the large populations of tended homopterans (both inside and outside their nests) have not been quantified. In coconut palms, these costs are outweighed by the benefits of protection from coreid bugs, as demonstrated by the higher nut production in weaver ant inhabited palms (Stapley, 1971; Way, 1954a).

The impact of the green tree ant, *O. smaragdina*, was examined in a plantation of mango trees, *Mangifera indica*, in north Queensland. The insect fauna and levels of leaf damage by chewing insects and homopterans were monitored over 2 years. The quantity of flower production, fruit set, and frugivory were also assessed to examine the effects of ant presence on reproductive output.

7.2 Methods.

The rapid expansion of mango tree (*Mangifera indica* L.) cultivation in north Queensland has provided ideal sites for studying interactions between ants and trees. The "kensington" variety grown in this region has a very distinct reproductive cycle, flowering from July to August, and bearing mature fruit from November to December. The insect fauna of this tree has also been relatively well documented by agricultural entomologists (reviewed by Cunningham, 1986). The chief problem for this study was to locate a farm which was not regularly treated with insecticides. One unsprayed plantation, with 250 trees aged 10 to 12 years, was eventually located at Major Creek, 50 km SSW of Townsville, in early 1987.

To examine the effects of green tree ants on trees, 12 trees with ants were paired with adjacent trees of similar size and condition, but without ants (fig 7.1). Due to unexpected fluctuations in ant colony sizes (see section 5.3.1), only 5 pairs retained their status throughout the study, and 7 pairs for two thirds of the study.

Levels of leaf damage and arthropod fauna were assessed on samples of approximately 400 leaves from each tree. The leaves were collected from 4 zones within the tree - low outer canopy, mid outer canopy, top outer canopy, and inside the canopy. In each zone, leaf clusters were taken from randomly selected compass angles (where 000° is north, and 180° is south), and pruned into a bag. These leaf samples were stored at 4°C, and promptly sorted in the laboratory. The commonest arthropods collected were identified to species, if possible, and other animals were catalogued to class level. Two sources of leaf damage were recorded (shown in plate 7.1) - pale, chlorotic scars due to homopteran

Figure 7.1. Map of Major Creek study site showing locations of tree pairs used in trials.

● - Ant occupied member of tree pair.
o - Ant free member of tree pair.
Members of each tree pair connected by lines.

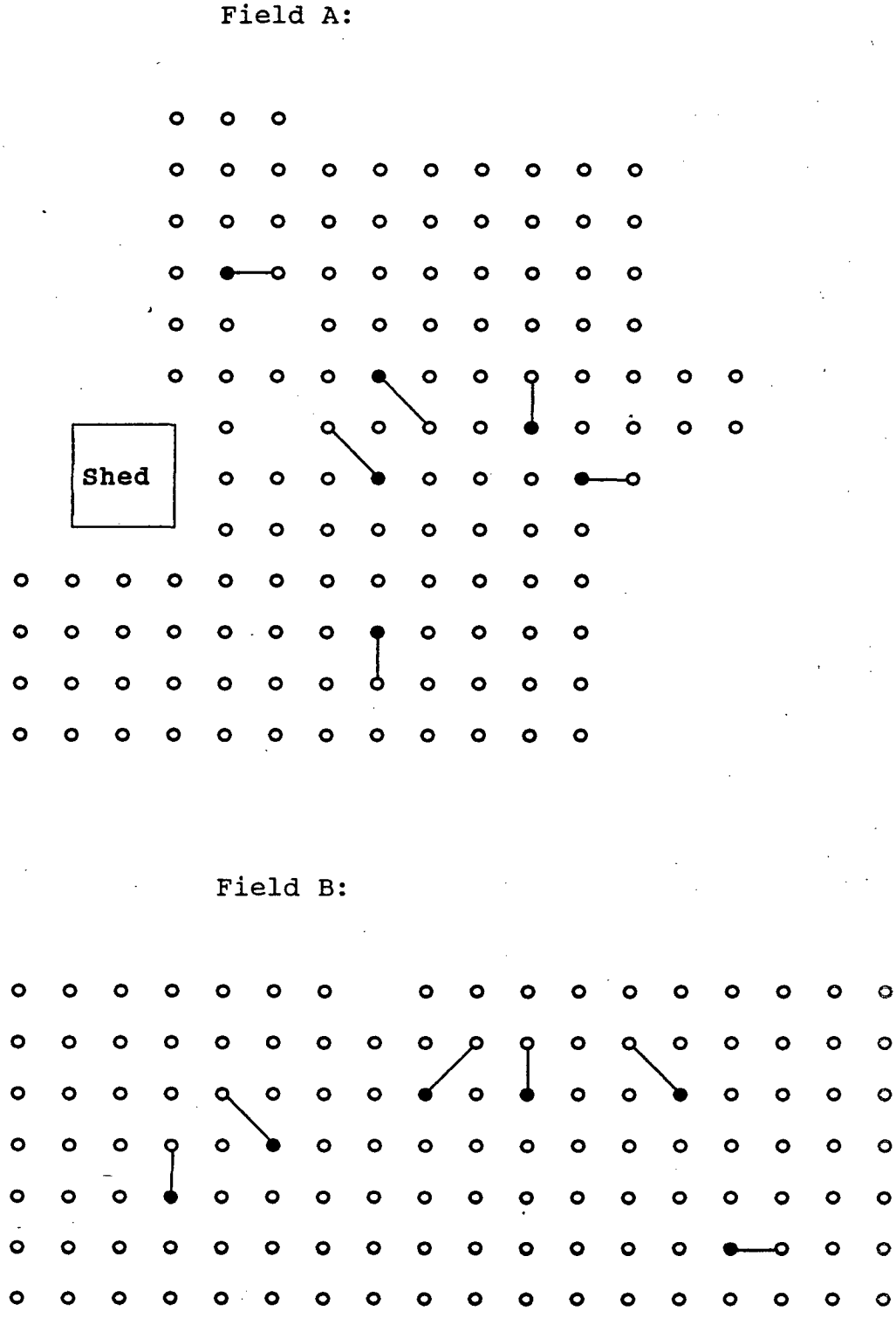
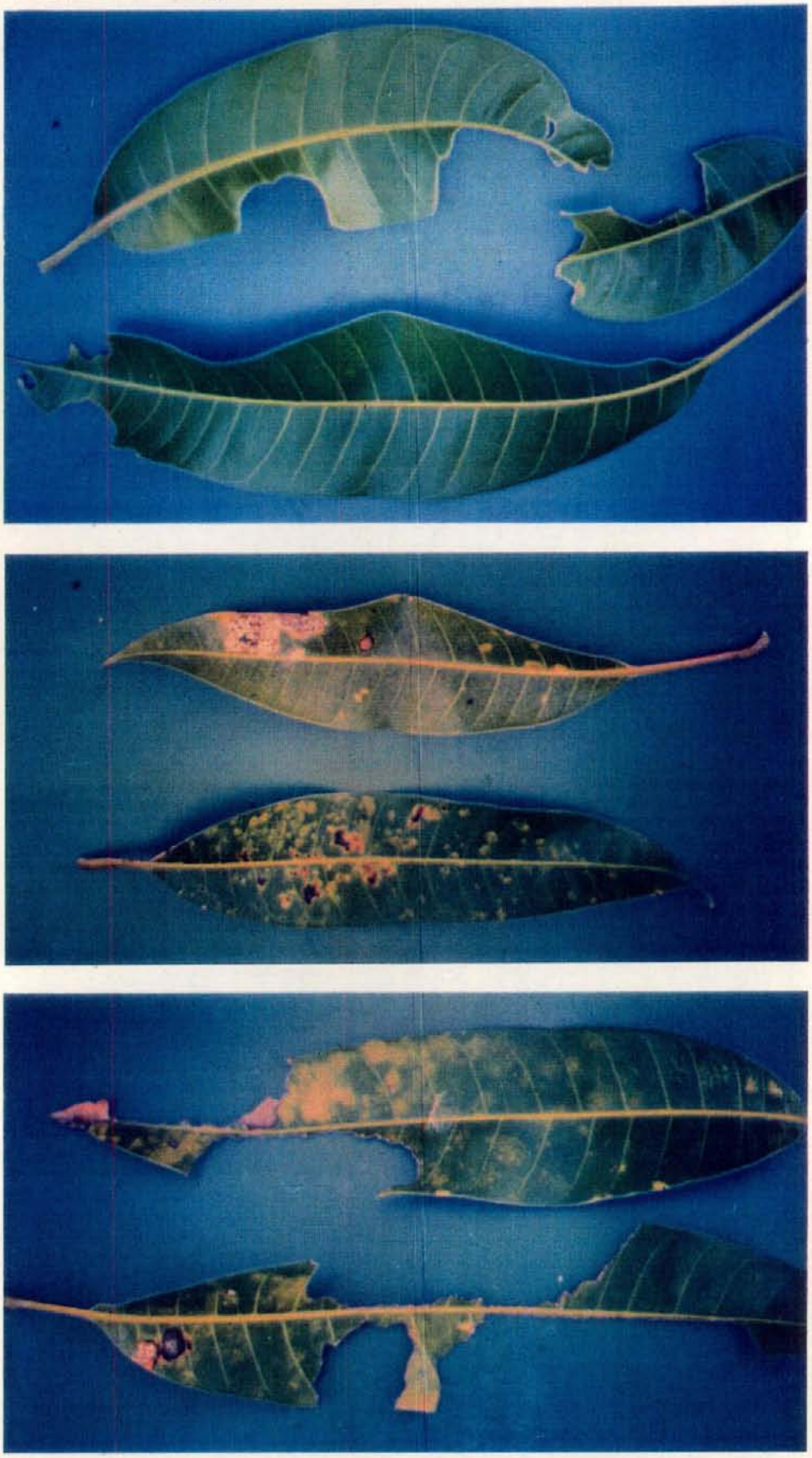


Plate 7. Insect damage of mango leaves.

(a) Eaten.
(b) Homopteran scarred.
(c) Both forms of damage.



feeding, and missing sections of leaf from herbivory. Leaf samples were collected in April, and July, 1987, January, April, and July, 1988, and January, 1989.

For the most numerous arthropod groups, balanced 4 factor analyses of variance were employed to detect differences in abundance between years, months, ant presence and absence, and each tree pair. Numbers were converted to logarithms to reduce the heterogeneity of variances of these count data (Zar, 1984). Each tree pair was effectively a random selection from the total tree population, hence "tree" in this and all subsequent analyses was a random effect. All other factors were fixed effects. When testing the significance of terms without the random tree effect (e.g the ant main effect), the denominator used in the F-test was the next highest order interaction mean square term (MS) including the original factors, plus the tree factor (e.g. the ant by tree interaction term). However, this test could produce spurious significant results when the residual mean square was larger than the "appropriate" interaction mean square; i.e. when the interaction sum of squares was very low. A suitable denominator in this situation was obtained by pooling the interaction term with the residual term, using the formula:

$$\frac{\text{(interaction sums of squares + residual sums of squares)}}{\text{(interaction df + residual df)}}$$

Pooling was performed only when the residual MS was larger than the "appropriate" interaction MS (when the interaction term F value < 1). Arthropod abundances did not vary significantly with location in the tree in preliminary analyses. This term was thus combined into the residual term of each analysis, as available computing memory was insufficient for a 5 factor analysis, including location.

Leaf condition was classified into 4 categories - homopteran marked, eaten, both, or none - from January, 1988, onwards. The proportions of each were transformed using the arcsine square root transformation (Zar, 1984) to produce more normal distributions. The effects of ant presence, month, tree pair, and location within the tree were examined using 4 factor analyses of variance. Leaf condition was not recorded in 1987, so yearly effects could not be analysed. An inverse relationship between proportions of leaves homopteran marked only and proportions of leaves eaten only was observed in leaf samples from all tree pairs, even after correcting for the date effect on these variables. A regression was calculated to describe this correlation.

On one occasion (January, 1989), leaf areas and areas of any missing leaf tissue were measured, using a digitizing tablet attached to an Apple microcomputer. Thirty-eight leaves were recorded from both the upper canopy and lower canopy of each of the paired trees (5 with, 5 without ants). Three measures of leaf loss were calculated: the area of missing leaf tissue, the proportion of missing leaf to total leaf area, and the average hole size. Proportional data were converted using the arcsine square root transformation, and the other statistics were logarithm transformed, to homogenize variances (Zar, 1984). Variation in these transformed values due to ant presence and absence, location within trees, and among tree pairs, was tested using balanced 3 factor analyses of variance. The further effect of leaf size on these leaf consumption measures was examined by adding leaf area as a covariate in 3 factor analyses of covariance.

Mango fruit development was monitored at 3 stages in the 1987 crop season, using the tree pairs selected for leaf sampling. The first observation period was during peak flower production in July, and the

second was in October, when young fruit (from 5 to 40 mm in length) were developing. Flower and young fruit densities were too high to make counts for whole trees (up to 1 million flowers on some trees), so 10 three dimensional quadrats (of 1 m^3 volume) were counted in each tree. Quadrats were placed at 0.5 metre height intervals, and at randomly chosen angles. Each flower spike was classified as young (with less than 10 opened flowers), mature (with 10 or more opened flowers), with young fruit, or empty (with no flowers left). These density data were logarithm transformed, and analyses of variance were used to test for variation in flower density due to ant presence and tree pair number.

During the third monitoring period in late November, fruit were almost ripe, and were few enough to be counted as totals per tree. Numbers of mature fruit appeared to change around each tree, so fruit counts were recorded in 8 sectors of 45 degrees. The logarithm transformed counts were examined for variation in fruit counts between ant presence and absence, among tree pairs, and between the sectors of each tree using an analysis of variance. Ten mangos from each of the 16 paired trees examined in November were inspected for the presence of homopterans, and their distributions on trees with and without ants compared using a Chi-squared test.

The major frugivore of mango fruit in this region is the fruit bat, *Pteropus alecto*. A measure of bat eaten fruit was obtained by counting numbers of fruit with bat feeding marks lying beneath trees. This technique assumes that bats do not carry mangos between trees while feeding, and that subsequent herbivory of fallen fruits occurs randomly through the field. Most bats observed feeding did not carry fruit any distance (possibly because mangos are heavy). Animals feeding on fallen fruit included wallabies and pigs, at night, and some birds

during the day. The effects of birds and wallabies were minimal, but on one occasion, pigs consumed almost all fallen fruit overnight. Numbers under ant occupied and ant free trees were compared using a t-test.

A more comprehensive study of frugivory was planned for 1988, but levels of flowering and fruiting were very low in this season. By tagging 100 fruit per tree with a tree-specific fluorescent mark, rates of fruit loss from different causes could be monitored, and the distance of bat carriage measured (if the marks were not totally eaten off the fruit). The total fruit numbers on 40 trees with, and 40 trees without green tree ants, were counted in October and November, 1988. No trees with 100 fruit were observed, and very few over 50, so marking experiments were abandoned.

7.3. Results.

7.3.1. Insect populations.

Animals recorded in leaf samples included homopterans (coccids, diaspids, and flattids), spiders (mainly salticids), psocopterans, coleopterans (cucujoids and curculionoids), hymenopterans (formicids, ichneumonoideans, chalcidoideans, and apoideans), dipterans, and lepidopteran larvae (table 7.1). No qualitative differences between trees with and without ants were evident, except for one looper caterpillar species (Geometroidea). All 4 specimens of this green tree ant mimicking caterpillar were found on ant occupied trees.

Table 7.1: Frequencies of arthropods collected in leaf samples from 7/87 to 1/89 (24000 leaves).

Arthropod group.	Number collected.	
Homoptera.		
Coccus sp.	2533	
Ceroplastes rubens	568	
Other tended homoptera	530	
Phenacaspis dilata (1 year only)	18817	
Other arthropods.		
Aranae	948	
Colgaroides sp.	347	(+ 847 moults)
Psocoptera	645	
Coleoptera	168	
Diptera	76	
Larval Lepidoptera	56	
Formicidae	216	
Other Hymenoptera	47	
Heteroptera	12	
Blattodae	7	
Other arthropods	65	
Egg cases	719	

Table 7.2: Analysis of variance on coccid abundance.

Ant, Month, Year: fixed factors.
Tree : random factor.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	133.2	133.2	138.0	0.0000
Month	2	4.110	2.055	1.11	0.380
Tree	4	6.263	1.566	0.85	0.537
Year	1	19.22	19.22	12.1	0.025
Ant*Year	1	19.24	19.24	23.0	0.009
Ant*Month	2	7.815	3.907	6.88	0.018
Year*Month	2	13.12	6.561	3.08	0.111
Year*Tree	4	6.335	1.584	0.86	0.533
Ant*Tree	4	3.862	0.965	0.52	0.723
Month*Tree	8	11.19	1.399	0.76	0.650
Ant*Month*Tree	8	4.541	0.568	0.31	0.940
Ant*Year*Tree	4	3.340	0.835	0.45	0.769
Year*Month*Tree	7	14.93	2.133	1.15	0.427
Ant*Year*Month	2	2.821	1.410	0.76	0.501
Error	7	12.94	1.849		
Total	57	281.4			

Significant quantitative differences were present, however, in some groups. The numbers of *Coccus sp*, the main ant attended homopteran, were greatly increased by ant presence ($F=138$, 1x4df, $P<0.0001$; table 7.2), and affected by year ($F=12.1$, 1x4df, $P=0.025$), and interactively by ant with year ($F=23.0$, 1x4df, $P=0.009$), and ant with month ($F=6.88$, 2x8df, $P=0.018$). Trees with green tree ants had 15.6±7.5 coccids/100 leaves, 22 times the level recorded in trees without ants, of 0.70±0.34 coccids/100 leaves. Examination of the ant/year interactive effect (fig 7.2) revealed low coccid levels in both years in ant free trees, and in ant occupied trees during the first year, but much higher levels in ant occupied trees in year 2. Coccid abundance in trees without ants was also consistently low (fig 7.3). In trees with ants, coccids were most frequent in January, and least common in April. A similar pattern emerged for the total numbers of ant-tended homopterans, with significant ant, year, and ant/year effects, but without the interactive effect of month and ant (table 7.3).

The most common insect in mango leaf samples was the diaspid homopteran, *Phenacapsis dilata*, which is not tended by ants. Unfortunately, only 1 year of accurate census data was collected for this species, as samples in the first year were anaesthetized using ethyl acetate, which made these normally translucent white scales transparent and virtually invisible. Nevertheless, abundance of this non-tended scale insect was highest in trees with green tree ants ($F=17.0$, 1x4df, $P=0.015$; table 7.4). Month, tree pair, and an interactive combination of tree and ant also explained significant amounts of variation in *P. dilata* numbers. The interactive effect was mainly caused by a much smaller difference in levels of this diaspid

Table 7.3: Analysis of variance on total ant-attended scale abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	110.2	110.2	80.40	0.0001
Month	2	6.519	3.260	2.82	0.127
Tree	4	5.010	1.253	1.08	0.434
Year	1	26.36	26.36	17.66	0.014
Ant*Year	1	5.878	5.878	30.97	0.005
Ant*Month	2	7.573	3.786	2.42	0.151
Year*Month	2	15.95	7.978	2.18	0.176
Year*Tree	4	6.006	1.501	1.30	0.358
Ant*Tree	4	5.488	1.372	1.18	0.395
Month*Tree	8	9.841	1.230	1.06	0.475
Ant*Month*Tree	8	12.52	1.565	1.35	0.352
Ant*Year*Tree	4	0.759	0.190	0.16	0.950
Year*Month*Tree	7	25.62	3.660	3.16	0.076
Ant*Year*Month	2	2.796	1.398	1.21	0.354
Error	7	8.105	1.158		
Total	57	254.3			

Table 7.4: Analysis of variance on *P. dilata* abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	5.1337	5.1337	17.00	0.015
Month	2	2.1378	1.0689	11.71	0.066
Tree	4	0.9505	0.2376	5.70	0.023
Ant*Month	2	0.0679	0.0340	0.81	0.480
Ant*Tree	4	1.2069	0.3017	7.24	0.012
Month*Tree	7	0.6414	0.0916	2.20	0.160
Error	7	0.2917	0.0417		
Total	27	11.627			

Figure 7.2 - 7.6. Impact of ants on seasonal and inter-tree variation in levels of different arthropod groups.

In graphs showing inter-tree variation, tree pairs have been arranged in ascending order of arthropod abundance for the ant-free member of the pair.

Figure 7.2. Impact of ants on yearly variation in numbers of *Coccus sp*

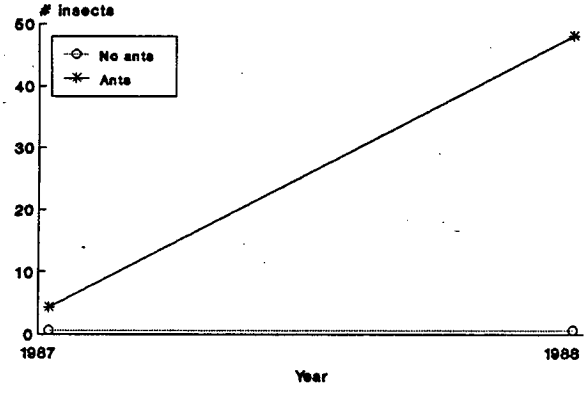


Figure 7.3. Impact of ants on seasonal variation in numbers of *Coccus sp*

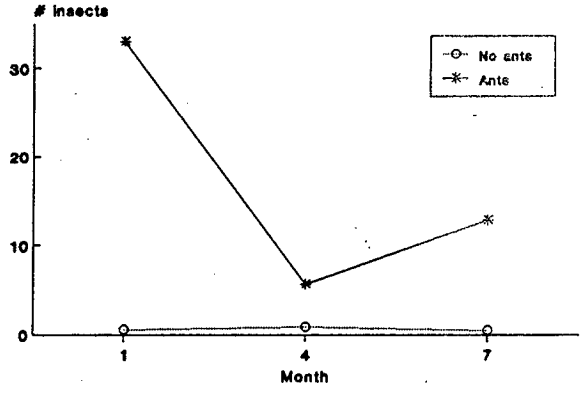


Figure 7.4. Impact of ants on inter-tree variation in *Phenacaspis dilata* numbers

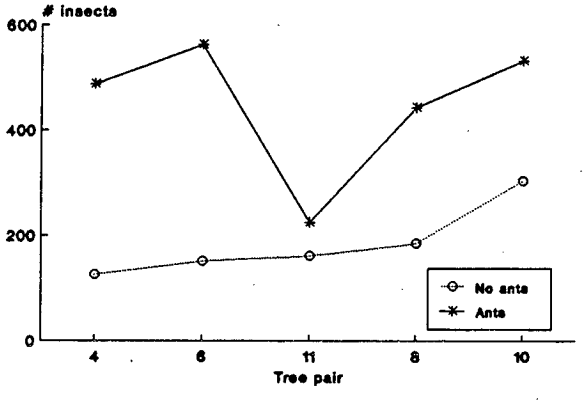


Figure 7.5. Impact of ants on seasonal variation in dipteran numbers

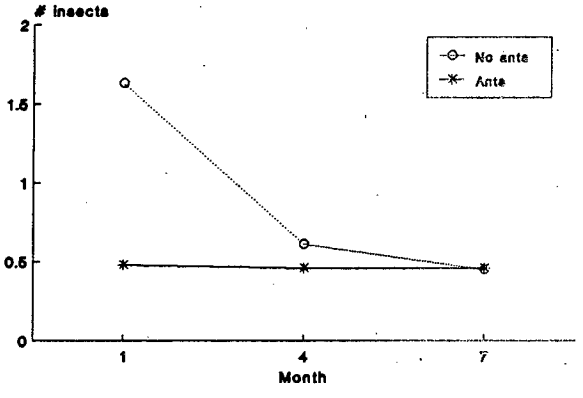
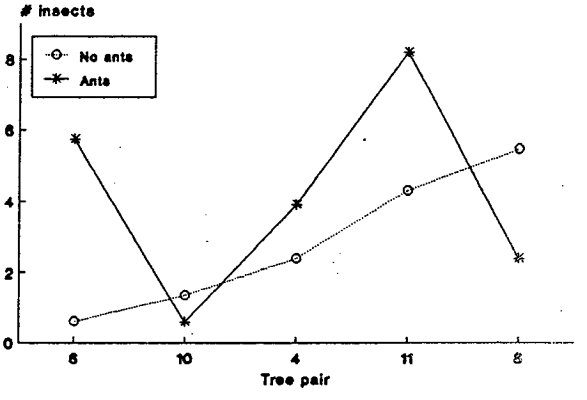


Figure 7.6. Impact of ants on inter-tree variation in psocopteran numbers



in tree pair 11 than in other pairs (fig 7.4).

Other arthropods were affected very differently by the presence of green tree ants. Spider numbers were lower in trees with ants (4.23±1.81 /100leaves) than in trees without (8.35±3.6 /100 leaves; F=8.08, 1x4df, P=0.047; table 7.5), and also increased from year 1 to year 2 (F=21.3, 1x4df, P=0.01). Densities of beetles in trees with ants were 0.66±0.23 /100 leaves, significantly lower than the mean of 1.15±0.41 /100 leaves in ant-free trees (F=11.0, 1x4df, P=0.029; table 7.6). Beetle abundance also varied with month and year. Ant occupied trees had fewer dipterans (0.47±0.11 /100 leaves) than trees without ants (0.82±0.18 /100 leaves), but this effect was not quite significant (F=6.82, 1x4df, P=0.062; table 7.7). The number of dipterans was affected by month, and interactions of year/month and month/ant. Examination of the month/ant interaction suggested that dipteran levels remained consistently low on ant inhabited trees, but rose markedly in January on ant-free trees (fig 7.5). The abundance of arboreal psocopterans in mango trees varied significantly between tree pairs, and interactively with the combination of year/month and tree/ant (F=3.97, 4x7df, P=0.048; table 7.8). Inspection of the tree/ant interaction indicated that some trees had consistently higher psocopteran populations than others, but that the differences were not obviously associated with either tree pair or ant presence (fig 7.6).

An analysis of all non homopteran insects in the leaf samples (table 7.9) showed significantly lower abundance in ant occupied trees (10.6±3.0 /100 leaves) than in trees without ants (19.4±5.5 /100 leaves; F=15.6, 1x4df, P=0.017). This result is consistent with the reduction in leaf herbivory in ant occupied trees indicated by the leaf condition analysis (section 7.3.2). Numbers in the first year were

Table 7.5: Analysis of variance on spider abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	4.7731	4.7731	8.08	0.047
Month	2	1.6031	0.8016	2.10	0.193
Tree	4	5.4425	1.3606	3.56	0.069
Year	1	21.259	21.259	21.3	0.010
Ant*Year	1	1.4422	1.4422	3.78	0.093
Ant*Month	2	2.6226	1.3113	3.43	0.091
Year*Month	2	1.9445	0.9723	2.55	0.148
Year*Tree	4	4.0143	1.0036	2.63	0.125
Ant*Tree	4	2.3884	0.5971	1.56	0.284
Month*Tree	8	6.0305	0.7538	1.97	0.192
Ant*Month*Tree	8	8.0538	1.0067	2.64	0.109
Ant*Year*Tree	4	4.3232	1.0808	2.83	0.109
Year*Month*Tree	7	8.1907	1.1701	3.06	0.081
Ant*Year*Month	2	1.1111	0.5556	1.46	0.296
Error	7	2.6727	0.3818		
Total	57	76.948			

Table 7.6: Analysis of variance on beetle abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	3.4172	3.4172	11.0	0.029
Month	2	16.403	8.2017	12.1	0.004
Tree	4	2.1637	0.5409	0.57	0.690
Year	1	10.094	10.094	21.9	0.009
Ant*Year	1	1.4931	1.4931	1.59	0.248
Ant*Month	2	0.9706	0.4853	0.52	0.618
Year*Month	2	1.4133	0.7066	0.75	0.506
Year*Tree	4	1.8494	0.4623	0.49	0.743
Ant*Tree	4	1.2392	0.3098	0.33	0.850
Month*Tree	8	5.4095	0.6762	0.72	0.675
Ant*Month*Tree	8	4.6563	0.5820	0.62	0.742
Ant*Year*Tree	4	4.0776	1.0194	1.08	0.433
Year*Month*Tree	7	6.6598	0.9514	1.01	0.494
Ant*Year*Month	2	2.5915	1.2958	1.38	0.313
Error	7	6.5891	0.9413		
Total	57	72.267			

Table 7.7: Analysis of variance on dipteran abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	3.5374	3.5374	6.83	0.062
Month	2	3.3775	1.6887	5.19	0.036
Tree	4	1.0329	0.2582	0.70	0.614
Year	1	1.1366	1.1366	3.10	0.122
Ant*Year	1	0.0915	0.0915	0.25	0.633
Ant*Month	2	3.9805	1.9902	6.09	0.025
Year*Month	2	5.1298	2.5649	4.87	0.047
Year*Tree	4	1.8724	0.4681	1.28	0.364
Ant*Tree	4	2.0741	0.5185	1.41	0.323
Month*Tree	8	2.6036	0.3255	0.89	0.570
Ant*Month*Tree	8	2.6193	0.3274	0.89	0.567
Ant*Year*Tree	4	1.8398	0.4600	1.25	0.372
Year*Month*Tree	7	3.6872	0.5267	1.44	0.323
Ant*Year*Month	2	3.0360	1.5180	4.14	0.065
Error	7	2.5693	0.3670		
Total	57	39.458			

Table 7.8: Analysis of variance on psocopteran abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	2.4478	2.4478	2.60	0.151
Month	2	6.3129	3.1564	3.55	0.095
Tree	4	17.055	4.2637	4.53	0.040
Year	1	7.1915	7.1915	3.87	0.121
Ant*Year	1	0.0336	0.0336	0.04	0.856
Ant*Month	2	0.1846	0.0923	0.10	0.908
Year*Month	2	19.207	9.6034	7.90	0.008
Year*Tree	4	7.4405	1.8601	1.97	0.203
Ant*Tree	4	15.879	3.9697	4.21	0.048
Month*Tree	8	9.4055	1.1757	1.25	0.392
Ant*Month*Tree	8	5.6180	0.7022	0.75	0.657
Ant*Year*Tree	4	5.7222	1.4305	1.52	0.295
Year*Month*Tree	7	8.5122	1.2160	1.29	0.372
Ant*Year*Month	2	0.0124	0.0062	0.01	0.993
Error	7	6.5936	0.9419		
Total	57	120.61			

Table 7.9: Analysis of variance on non-homopteran insect abundance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	3.1158	3.1158	15.6	0.017
Month	2	0.8189	0.4094	0.72	0.520
Tree	4	2.7779	0.6945	1.22	0.383
Year	1	15.980	15.980	10.0	0.034
Ant*Year	1	0.4068	0.4068	0.71	0.426
Ant*Month	2	0.7132	0.3566	0.63	0.562
Year*Month	2	3.1379	1.5689	2.75	0.131
Year*Tree	4	6.3866	1.5966	2.80	0.111
Ant*Tree	4	0.8032	0.2008	0.35	0.835
Month*Tree	8	5.2782	0.6598	1.16	0.431
Ant*Month*Tree	8	5.6166	0.7021	1.23	0.398
Ant*Year*Tree	4	3.9940	0.9985	1.75	0.243
Year*Month*Tree	7	4.2966	0.6138	1.08	0.463
Ant*Year*Month	2	0.0860	0.0430	0.08	0.928
Error	7	3.9938	0.5704		
Total	57	57.306			

Table 7.10: Analysis of variance on egg abundance.

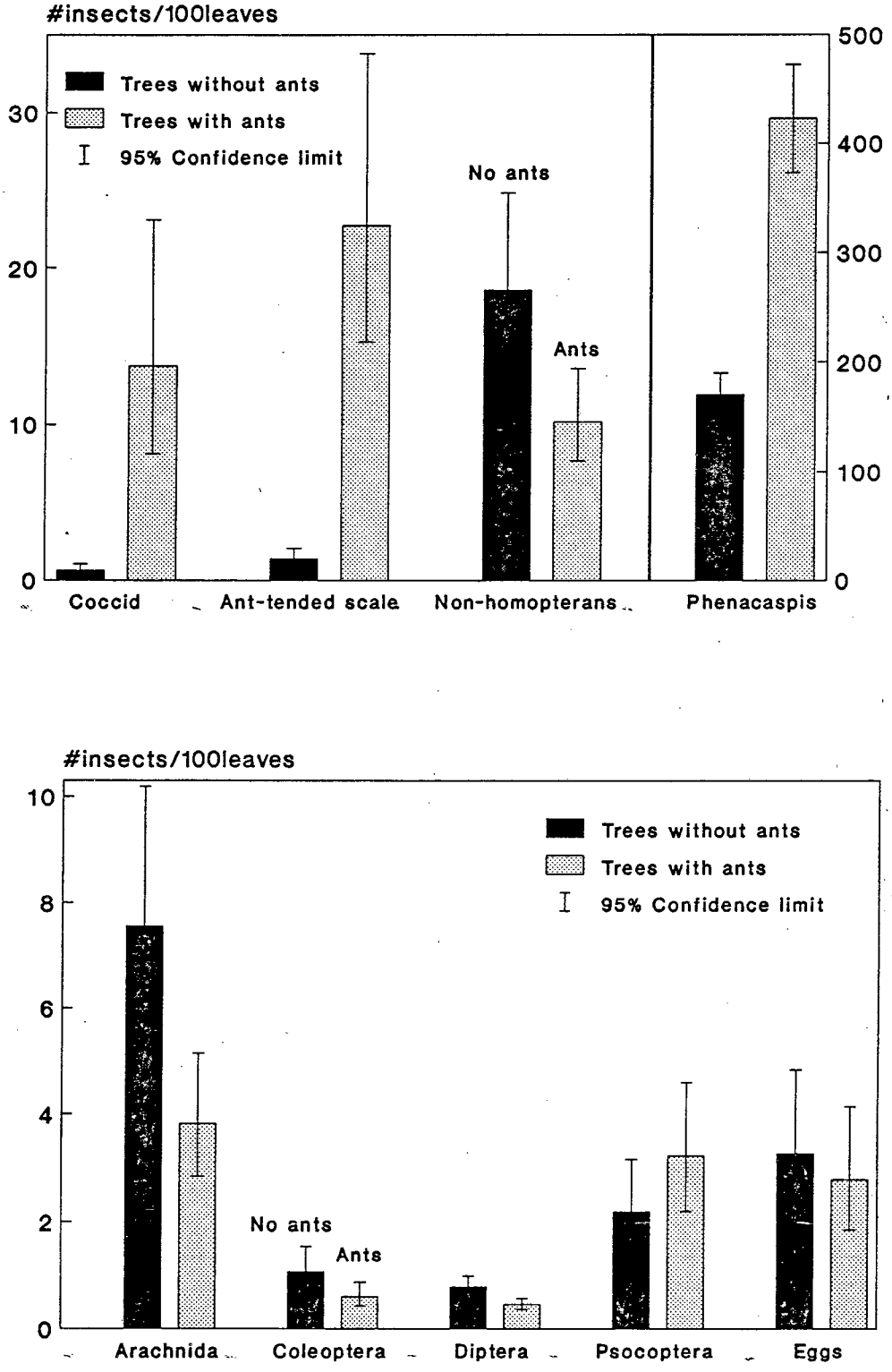
Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	0.1159	0.1159	0.20	0.680
Month	2	29.600	14.800	15.5	0.002
Tree	4	2.8668	0.7167	0.65	0.645
Year	1	5.7922	5.7992	16.3	0.002
Ant*Year	1	0.1834	0.1834	0.17	0.696
Ant*Month	2	0.5035	0.2518	0.23	0.802
Year*Month	2	19.292	9.6460	8.77	0.012
Year*Tree	4	1.4204	0.3551	0.32	0.855
Ant*Tree	4	2.3016	0.5754	0.52	0.724
Month*Tree	8	7.6466	0.9558	0.87	0.582
Ant*Month*Tree	8	7.5492	0.9434	0.86	0.588
Ant*Year*Tree	4	1.8795	0.4699	0.43	0.786
Year*Month*Tree	7	7.7195	1.1028	1.00	0.500
Ant*Year*Month	2	4.3615	2.1808	1.98	0.209
Error	7	7.7207	1.1030		
Total	57	106.52			

higher than those in the second year (F=10.0, 1x4df, P=0.034).

Numbers of insect eggs found on leaves were also recorded and analyzed. The commonest eggs were, in order of abundance, hemipteran, coleopteran, and blattodean eggs. Ants had no effect on egg numbers (F=0.20, 1x4df, P=0.68; table 7.10), suggesting that ants were not influencing oviposition rates or preying on insects at the egg stage. Egg abundance varied significantly with month (F=15.5, 2x8df, P=0.002), with most eggs present in April, and fewest in the dry season month, July. Year also affected egg density, both on its own, and interactively with month.

To summarize the important results of these analyses, average abundances (and 95% confidence intervals) of observed animal groups per 100 leaves were plotted for ant occupied and ant free trees (fig 7.7). Numbers of Coccus sp, total ant tended homoptera, and *Phenacaspis dilata*, were significantly higher on trees with ants. Spider and beetle levels were significantly lower on ant inhabited trees. Dipteran abundances were higher in trees without ants in January, but dropped to levels similar to those in trees with ants in April and July. Densities of psocopterans and insect eggs showed no significant variation due to ant presence or absence.

Figure 7.7. Impact of ants on levels of various arthropod groups in leaf samples.



7.3.2. Leaf condition.

Most chlorotic scars on mango leaves were produced by the diaspid, *Phenacaspis dilata*. As levels of this homopteran were higher in trees with ants, proportions of scarred leaves were also expected to be greater in ant inhabited trees. An analysis of variance confirmed this expectation ($F=17.0$, 1x4df, $P=0.015$; table 7.11). The average percentage of homopteran marked leaves in trees without ants was 38.6±5.1%, and 52.2±6.5% in trees with ants. Scarred leaf fractions also varied significantly with month on its own, and interactively with ant ($F=6.8$, 3x12df, $P=0.0063$). Position within the tree did not significantly affect the proportions of this, or any other leaf category tested. The average percentage of scarred leaves steadily declined during the study, from early 1988 till early 1989. Examination of the month/ant interaction effect (fig 7.8) showed that ant occupied trees had distinctly higher scarred leaf fractions in all but the first month sampled, January, 1988.

The proportion of leaves with missing pieces was affected by ant presence ($F=85.8$, 1x16df, $P<0.0001$; table 7.12), month, and a combination of both ($F=8.2$, 3x24df, $P=0.001$). Although the analyses of scarred and eaten levels gave similar significant effects, the trends of each effect were opposite. Thus, the average percentage of eaten leaves was lower in trees with ants (18.5±5%) than in trees without ants (35.6±4.4%). The eaten leaf fraction steadily rose during the study, and was markedly lower in ant inhabited trees in all months except January, 1988 (fig 7.9).

Table 7.11: Analysis of variance on proportion of leaves with homopteran damage.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Position	1	0.0002	0.0002	0.01	0.914
Ant	2	0.5611	0.5611	17.04	0.015
Tree	4	0.1313	0.0328	1.87	0.180
Month	1	1.6729	0.5576	31.8	0.000
Ant*Tree	1	0.1317	0.0329	1.88	0.179
Ant*Pos.	2	0.0188	0.0188	1.07	0.321
Ant*Month	2	0.1949	0.0650	6.79	0.006
Tree*Pos.	4	0.0308	0.0077	0.44	0.777
Tree*Month	4	0.4632	0.0386	2.20	0.093
Month*Pos.	8	0.0200	0.0067	0.38	0.769
Ant*Tree*Pos.	8	0.0432	0.0108	0.62	0.660
Ant*Tree*Month	4	0.1149	0.0096	0.55	0.846
Ant*Month*Pos.	7	0.0211	0.0070	0.40	0.754
Tree*Month*Pos.	2	0.1670	0.0139	0.79	0.652
Error	7	0.2102	0.0175		
Total	57	3.7813			

Table 7.12: Analysis of variance on proportion of leaves with holes.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Position	1	0.00927	0.00927	1.11	0.3122
Ant	1	0.63096	0.63096	85.79	0.0001
Tree	4	0.08436	0.02109	2.53	0.0952
Month	3	0.87104	0.29035	14.34	0.0003
Ant*Tree	4	0.01778	0.00444	0.53	0.7136
Ant*Pos.	1	0.00544	0.00544	0.65	0.4347
Ant*Month	3	0.15160	0.05053	8.19	0.0011
Tree*Pos.	4	0.08028	0.02007	2.41	0.1068
Tree*Month	12	0.24294	0.02025	2.43	0.0689
Month*Pos.	3	0.01265	0.00422	0.51	0.6852
Ant*Tree*Pos.	4	0.04078	0.01020	1.22	0.3513
Ant*Tree*Month	12	0.04820	0.00402	0.48	0.8895
Ant*Month*Pos.	3	0.01008	0.00336	0.40	0.7530
Tree*Month*Pos.	12	0.16911	0.01409	1.69	0.1874
Error	12	0.09992	0.00833		
Total	79	2.47443			

Figure 7.8. Temporal variation in % homopteran scarred leaves

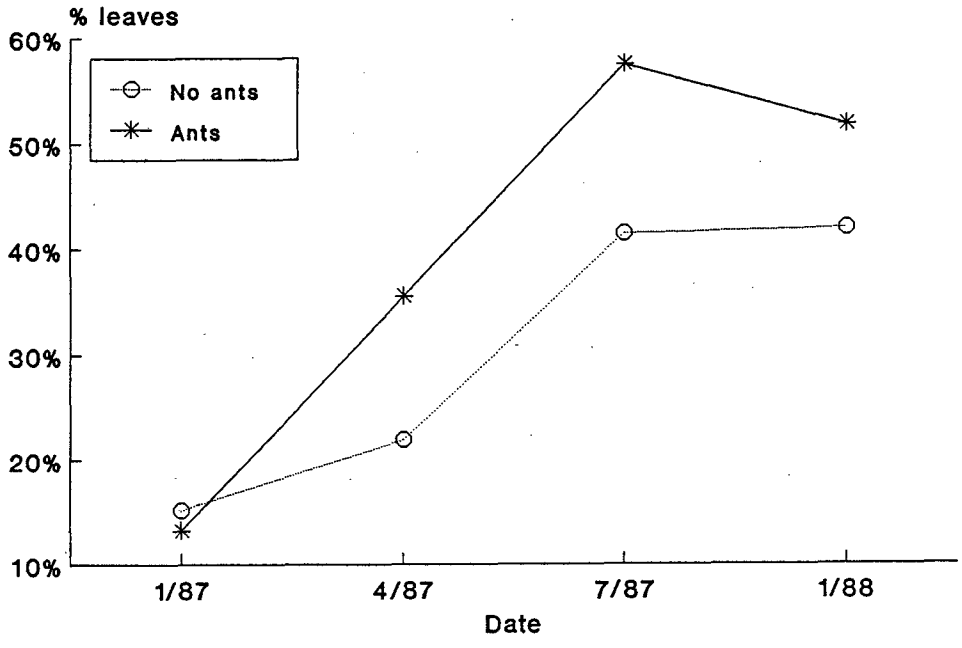
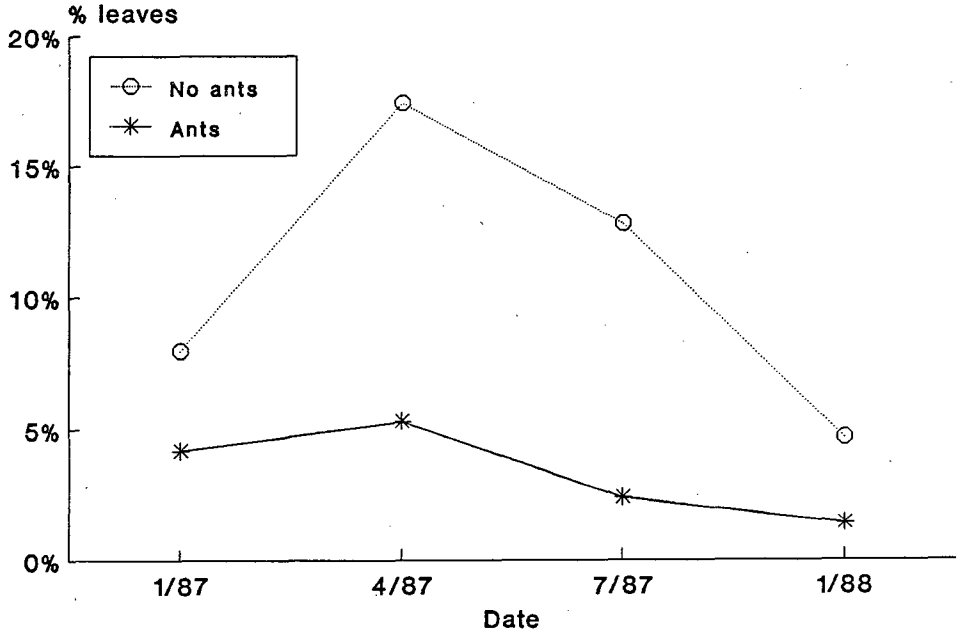


Figure 7.9. Temporal variation in % eaten leaves



These results suggested an inverse relationship between the levels of homopteran marked and eaten leaves. The confounding effect of monthly trends was removed by adding a correction factor to proportions recorded for each month, so that average proportions for each month were equal to the grand mean for all records. A plot of these month corrected proportions of eaten leaves and scarred leaves for all trees showed a significant inverse relationship ($r=-0.82$, 78df, $P<0.001$; fig 7.10a). A regression predicting the fraction scarred from the fraction eaten (an arbitrary choice not implying any causal effects) for trees with ants was:

$S = 0.60 - 1.23\ E$ ($r=0.81$, 38df, $P<0.001$)

where S is proportion of leaves with homopteran scars,

and E is proportion of leaves eaten.

For trees without ants, the derived equation was:

$S = 0.52 - 0.84\ E$ ($r=0.82$, 38df, $P<0.001$)

The regression coefficients of these equations were significantly different ($t=2.41$, 76df, $P=0.018$). The steeper slope for trees with ants was mainly due to the low percentage of eaten, but very high percentage of scarred leaves in some ant inhabited trees during July, 1988, and January, 1989 (fig 7.10b). However, no particular trees or months displayed consistently higher scarred and lower eaten proportions than predicted by the regression.

The proportion of leaves with neither form of damage varied with month, and interactively with ant presence and tree ($F=4.8$, 4x12df, $P=0.015$; table 7.13). However, no obvious trends were observed in this interactive effect (fig 7.11). Levels of leaves with both homopteran damage and holes appeared to be lower in ant inhabited trees (11.4±2.2%) than ant free trees (17.2±3.5%), but this effect was not

Fig 7.10a. Impact of ants on correlation of eaten and scarred leaf proportions

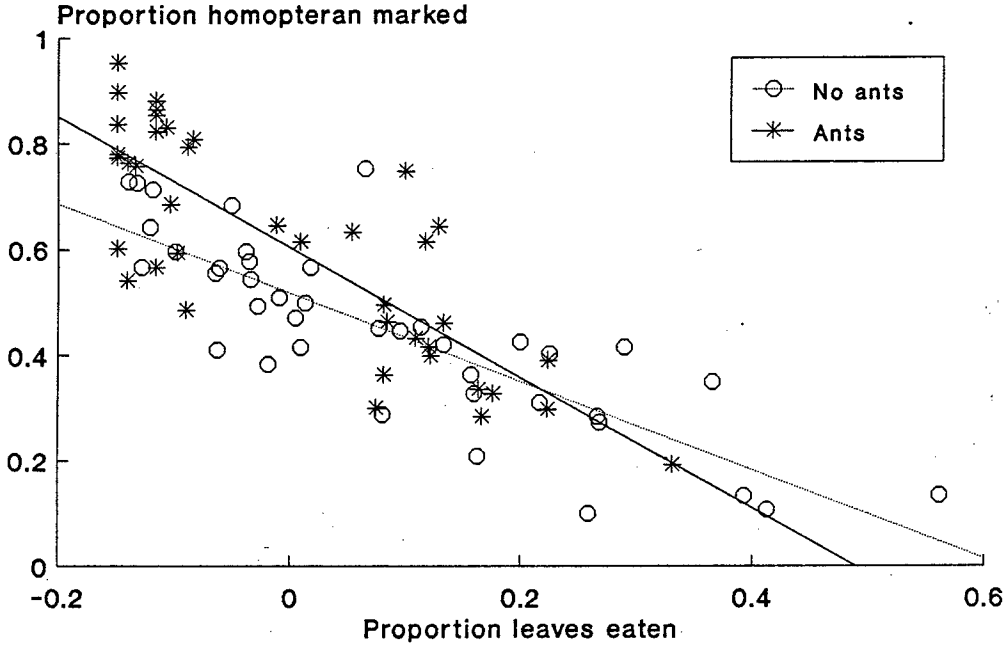


Fig 7.10b. Seasonal breakdown for correlation of eaten and scarred leaf proportions in ant-occupied trees

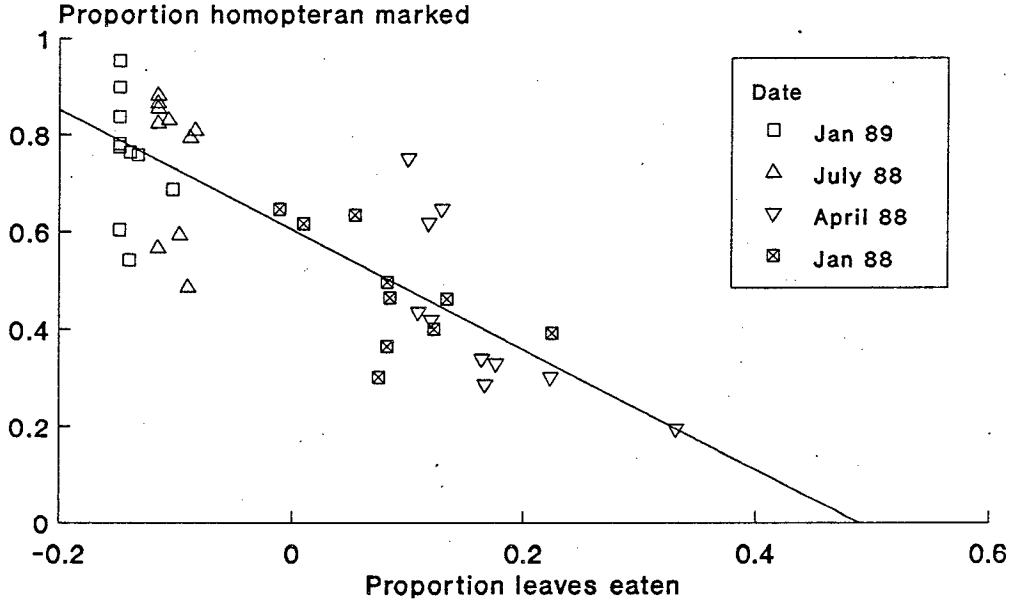


Table 7.13: Analysis of variance on proportion of leaves with no damage.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Position	1	0.00963	0.00963	0.69	0.4219
Ant	1	0.00807	0.00807	0.12	0.7460
Tree	4	0.04448	0.01112	0.80	0.5489
Month	3	1.39049	0.46350	12.63	0.0005
Ant*Tree	4	0.26770	0.06692	4.80	0.0151
Ant*Pos.	1	0.00017	0.00017	0.01	0.9131
Ant*Month	3	0.06810	0.02270	1.91	0.1815
Tree*Pos.	4	0.03670	0.00917	0.66	0.6324
Tree*Month	12	0.44050	0.03671	2.64	0.0533
Month*Pos.	3	0.01880	0.00627	0.45	0.7220
Ant*Tree*Pos.	4	0.07670	0.01918	1.38	0.2995
Ant*Tree*Month	12	0.14244	0.01187	0.85	0.6069
Ant*Month*Pos.	3	0.02412	0.00803	0.58	0.6410
Tree*Month*Pos.	12	0.26404	0.02200	1.58	0.2200
Error	12	0.16716	0.01393		
Total	79	2.95909			

Table 7.14: Analysis of variance on proportion of leaves with holes and homopteran damage.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Position	1	0.01517	0.01517	1.24	0.2876
Ant	1	0.13947	0.13947	7.10	0.0561
Tree	4	0.10952	0.02738	2.23	0.1262
Month	3	0.27128	0.09043	5.81	0.0109
Ant*Tree	4	0.07857	0.01964	1.60	0.2367
Ant*Pos.	1	0.02942	0.02942	2.40	0.1472
Ant*Month	3	0.01851	0.00617	0.50	0.6870
Tree*Pos.	4	0.02251	0.00563	0.46	0.7643
Tree*Month	12	0.18689	0.01557	1.27	0.3421
Month*Pos.	3	0.04295	0.01432	1.17	0.3622
Ant*Tree*Pos.	4	0.05025	0.01256	1.03	0.4332
Ant*Tree*Month	12	0.14704	0.01225	1.00	0.4999
Ant*Month*Pos.	3	0.00698	0.00233	0.19	0.9012
Tree*Month*Pos.	12	0.09834	0.00820	0.67	0.7517
Error	12	0.14702	0.01225		
Total	79	1.36393			

Figure 7.11. Inter-tree variation in % undamaged leaves

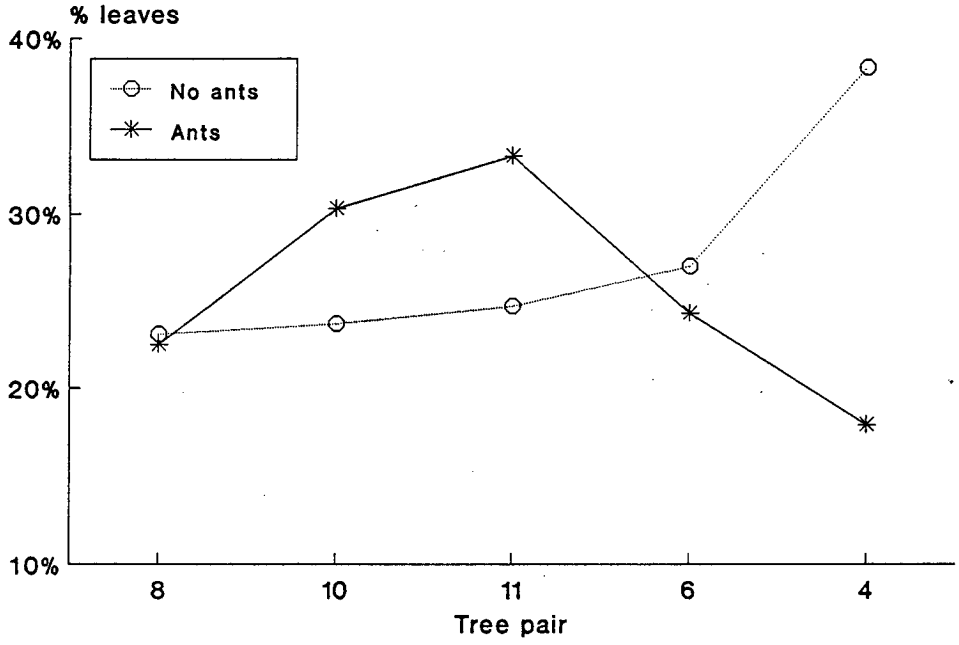
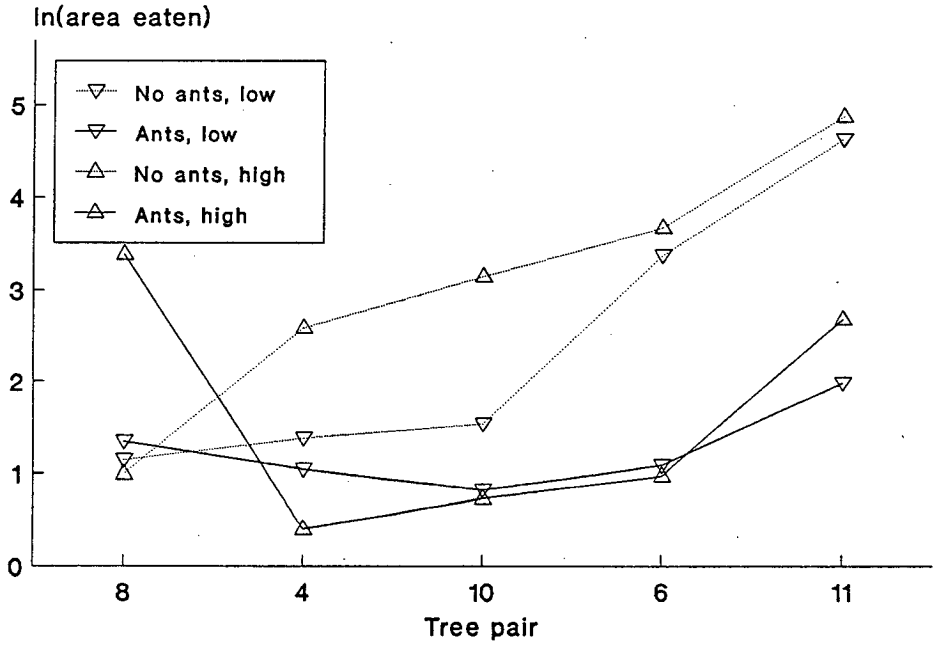


Figure 7.12. Effects of tree,leaf height and ant presence on leaf area eaten



quite significant (F=7.1, 1x4df, P=0.056; table 7.14). A significant monthly effect was observed.

Analyses of variance for the total leaf area eaten, the proportion of leaf area eaten, and the average hole size in leaves gave very similar results, so only the conclusions for the area of leaf eaten are tabulated. All 3 measures were significantly larger in the upper canopy of trees than in the lower canopy, and varied among tree pairs (table 7.15). The presence of ants affected eaten leaf area interactively with tree (F=20.9, 4x740df, P=0.0001), and also in interaction with both tree and position within tree (F=6.2, 4x740df, P=0.0001). The highest order interaction was plotted in figure 7.12. Trees without ants had larger areas of missing leaf than trees with ants in all tree pairs but one (causing the lower order interaction). The area of eaten leaf was generally more uniform in ant occupied trees, except for the markedly higher area missing in the upper canopy sample of tree number 8. The significance of the highest order interaction is attributable to this anomalous data point.

The inclusion of total leaf area of each leaf into this analysis indicated that this variable significantly affected all 3 measures of leaf damage (for area eaten, F=7.5, 1x739df, P=0.006; table 7.15b). As leaf size increased, area eaten, proportion of leaf eaten, and average hole size also rose. However, the effects of the other variables in the analysis were unaltered.

Table 7.15: Analyses on area of leaf eaten.

(a) Analysis of variance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
ANT	1	315.27	315.27	3.51	0.1344
TREE	4	470.01	117.50	27.27	0.0001
POS	1	49.798	49.798	10.89	0.0299
TREE*ANT	4	359.49	89.873	20.86	0.0001
TREE*POS	4	18.289	4.5722	1.06	0.3748
ANT*POS	1	3.3202	3.3202	0.125	0.7415
TREE*ANT*POS	4	106.22	26.554	6.16	0.0001
Error	740	3188.7	4.3089		
Total	759	4511.0			

(b) Analysis of covariance.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
ANT	1	336.06	336.06	3.69	0.1271
TREE	4	491.15	122.79	28.75	0.0001
POS	1	53.512	53.512	12.53	0.0004
TREE*ANT	4	363.93	90.983	21.30	0.0001
TREE*POS	4	20.469	5.1174	1.20	0.3103
ANT*POS	1	1.2577	1.2577	0.29	0.5876
TREE*ANT*POS	4	105.65	26.414	6.18	0.0001
LEAF	1	31.954	31.954	7.48	0.0064
Error	739	3156.7	4.2716		
Total	759	4511.0			

6.3.3. Fruit production.

In July, 1987, trees had an average of 20.6 spikes/m^3. Most spikes had over 10 opened flowers, with a mean of 26.5 per spike. As most trees in the study site were roughly 90 cubic metres in volume, the average number of opened flowers per tree was estimated to be 49000, borne on 1850 spikes. No fruit were present at this time. The effects of ant presence and tree pair on numbers of young (<10 open flowers), mature (>10 open flowers), and total spikes were examined using 2 way analyses of variance. All three spike counts varied substantially between tree pairs (for total number, F=4.9, 5x108df, P=0.0004; table 7.16c). An interaction between ant and tree was found to influence young and mature spike numbers, but not total numbers. These interactive effects showed no consistent trends (fig 7.13), and were probably an artifact of the highly variable onset and density of flowering seen in mango trees (e.g. Scholefield and Oag, 1986). This interpretation is supported by the highly significant tree effect for all spike measures, and the non-significant influence of ant and tree on total spike number.

By October, flowers had all senesced, and the surviving spikes had from 0 to 9 young fruit. Spike density had dropped to 10.2 spikes/m^3, with only 3.8 spikes/m^3 bearing fruit. Thus, the average number of fruit-bearing spikes per tree was 340, giving an 18% fruit set. Mean fruit density was 4.5/m^3, or 405 fruit/tree, so spikes bore, on average, only 1.2 fruit each. Fruit numbers, and 3 measures of spike density were analysed: number of dead spikes (with no fruit), spikes with fruit, and total spikes (table 7.17). Spike and fruit numbers did not vary between trees with and without ants (e.g. for fruit number,

Table 7.16: Analyses of variance fornumbers of flower spikes per m^3 in mango trees during July.

(a) Young spikes (<10 opened flowers).

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	4.0333	4.0333	0.10	0.7657
Tree	5	718.57	143.71	8.77	0.0001
Tree*Ant	5	201.77	40.353	2.46	0.0373
Error	108	1768.8	16.378		
Corrected	119	2693.2			

(b) Mature spikes (>10 opened flowers).

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	45.633	45.633	0.36	0.5773
Tree	5	994.17	198.83	3.77	0.0035
Tree*Ant	5	640.57	128.11	2.43	0.0396
Error	108	5693.6	52.719		
Corrected	119	7374.0			

(c) Total spikes.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	76.800	76.800	1.60	0.2625
Tree	5	795.87	159.17	4.92	0.0004
Tree*Ant	5	240.00	48.000	1.48	0.2015
Error	108	3496.8	32.378		
Corrected	119	4609.5			

Figure 7.13. Inter-tree variation in number of mature spikes in July

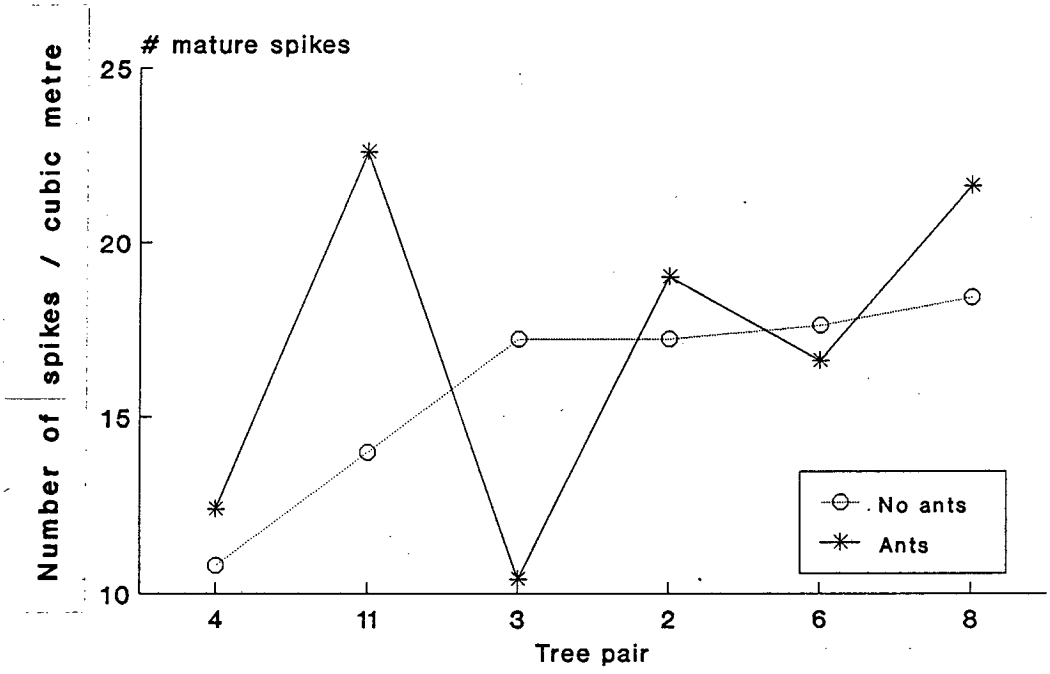


Figure 7.15. Inter-tree variation in number of mature fruit in November

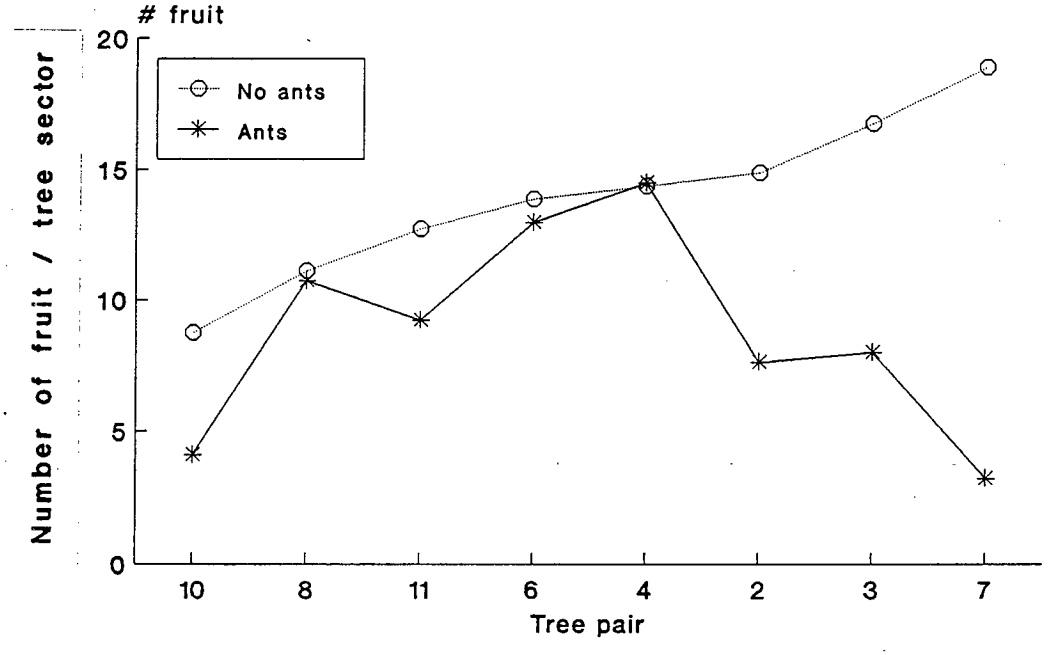


Table 7.17: Analyses of variance for numbers of flower spikes and fruit per m^3 in mango trees during October.

(a) Dead spikes

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	1.9600	1.9600	0.30	0.5835
Tree	4	73.360	18.340	2.73	0.0340
Tree*Ant	4	4.2400	1.0600	0.16	0.9590
Error	90	604.80	6.7200		
Corrected	99	684.36			

(b) Fruiting spikes.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	10.240	10.240	3.48	0.0659
Tree	4	75.040	18.760	6.17	0.0002
Tree*Ant	4	3.3600	0.8400	0.28	0.8926
Error	90	273.60	3.0400		
Corrected	99	362.24			

(c) Total spikes.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	3.2400	3.2400	0.41	0.5243
Tree	4	139.76	34.940	4.26	0.0033
Tree*Ant	4	9.3600	2.3400	0.29	0.8869
Error	90	738.40	8.2044		
Corrected	99	890.76			

Table 7.17 (d) Fruit.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	2.5600	2.5600	0.24	0.6503
Tree	4	152.56	38.140	5.72	0.0004
Tree*Ant	4	41.840	10.460	1.57	0.1894
Error	90	600.00	6.6667		
Corrected	99	796.96			

Table 7.18: Analyses of variance for abundance of fruit in mango trees during November.

Source	DF	Sum of Squares	Mean Square	F ratio	Pr>F
Ant	1	835.38	835.38	7.35	0.0619
Tree	7	631.30	90.186	7.43	0.0001
Angle	7	1119.2	159.88	9.78	0.0001
Ant*Tree	7	795.93	113.70	9.32	0.0001
Ant*Angle	7	196.30	28.044	2.30	0.0418
Tree*Angle	49	800.76	16.342	1.34	0.1544
Error	49	596.88	12.181		
Corrected	127	4975.7			

F=.38, 1x90df, P=0.54), but tree pair was again significant (F=5.7, 4x90df, P=0.0004). Spike density in July was not, however, a good predictor of fruit-bearing spike or fruit numbers in October, with no consistent relationships within tree pairs from July to October.

Numbers of fruit had dropped in November, to an average of 91 per tree, just before harvesting. Only 4.9% of spikes in July thus bore fruit to maturity, a very low success rate.

Numbers of fruit in November varied significantly between tree pairs (F=7.4, 7x49df, P<0.0001; table 7.18) and among sectors around the trees (F=9.8, 7x49df, P<.0001), and was also affected by an interaction between tree pair and ant presence (F=9.3, 7x49df, P<0.0001). The eastern side of the trees produced the highest numbers of mature fruit (figure 7.14). Examination of the interactive effect (fig 7.15) suggested that fruit yields were lower in ant occupied trees in some tree pairs, but not others. Separate analyses for each tree pair indicated that fruit numbers were significantly lower in the ant inhabited tree of tree pairs 6, 3, and 2. However, no difference between the members of these pairs was observed in October, thus the presence of ants appeared to cause fruit loss in the last month of development. Green tree ants also reduced fruit yield most substantially in those pairs where the ant free member had highest yields.

Some correlation was found between young fruit numbers in October and mature fruit in November, but the small common pool of 5 trees gave a not quite significant result (figure 7.16, F=7.67, 1x3df, P=0.069). Obtaining a good predictor of mature fruit number for a stage before ant effects have occurred would be very useful for examining the interaction between tree pair and ant presence. For example, the

Figure 7.14. Rose diagram of numbers of mature fruit in 45° sectors around trees in November, 1987. 1 cm = 2 fruit.

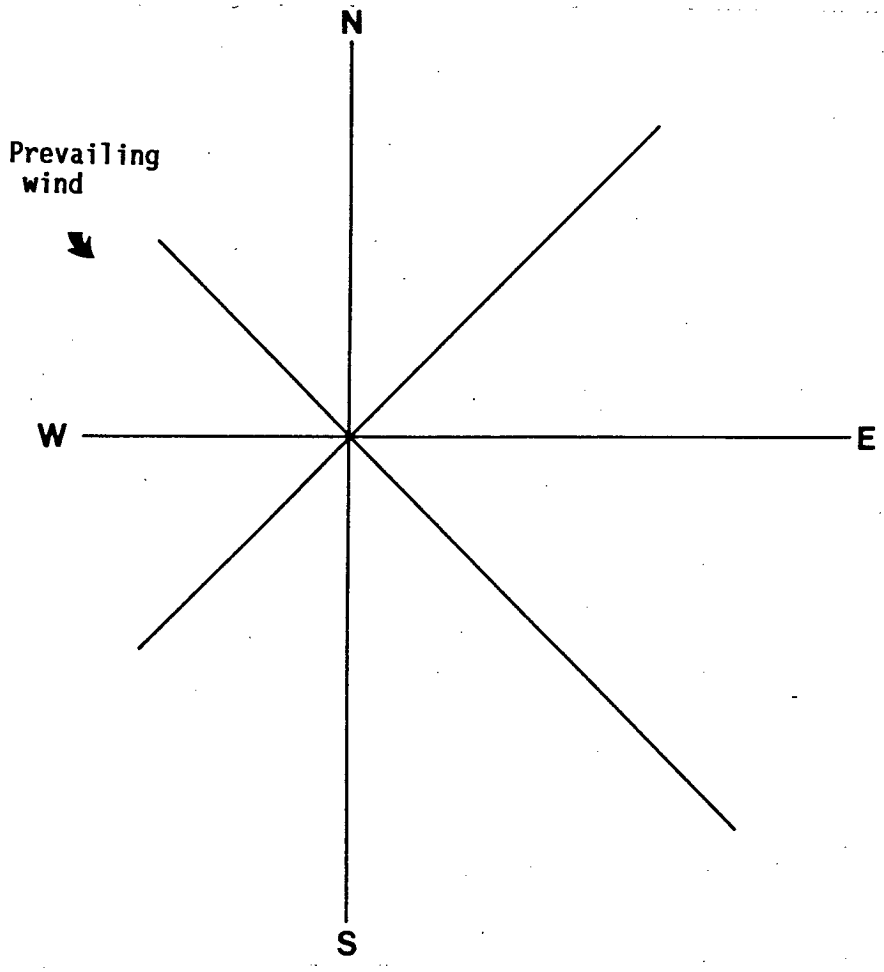
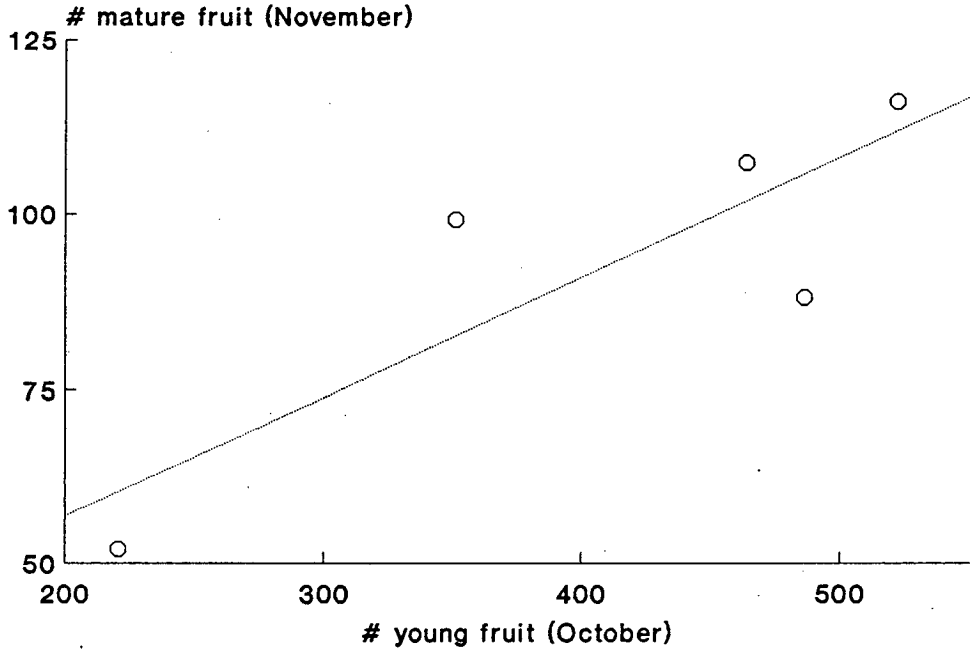


Figure 7.16. Correlation of fruit numbers in October and November, 1987.



hypothesis that ants only reduce fruit yield on trees with large crops of young fruit could be tested.

Mature fruit supported populations of homopterans, ranging from 0 to over 50. The rates of occurrence of these bugs on fruit of trees with and without ants were significantly different, with homopterans on 38 of 80 mature mangos examined on ant occupied trees, and only 5 out of 80 on ant free trees (χ^2=32.6, 1df, P<0.0001). This would increase the sap loss of those trees with green tree ants, and so encourage fruit drop. Ants were also found tending these homopteran populations on 51 of the 80 mangos in ant inhabited trees, in numbers from 1 to over 100.

The mean number of bat marked fruit under ant occupied trees was 4.0, significantly lower than the average of 7.2 fruit found under ant free trees (using a paired t-test, t=3.2, 7df, P<.02). Bats thus appeared to be deterred from taking fruit on trees with green tree ants.

6.4. Discussion.

Leaf samples from mango trees occupied by *O. smaragdina* had more ant tended homopterans and fewer non-tended insects than trees without ants. Interestingly, they also had higher numbers of the untended diaspid, *Phenacaspis dilata*. This species does not produce honeydew; it was the commonest scale recorded on mango leaves, and the chief cause of chlorotic scars on leaves. Way (1954b) recorded similar increased abundances of the diaspids *Aspidiotus destructor*, *Hemiberlesia latinae*, and *Phenacaspis inday* in coconut trees inhabited

by *O. longinoda*, presumably due to incidental protection from predators or parasites. Fowler and MacGarvin (1985) attributed increased numbers of leaf-miners in ant-occupied birch trees to removal of competitors or predators by ants. Ants can thus cause detrimental effects to trees by incidentally protecting untended insects, as well as by encouraging and protecting honeydew-producing homopterans.

Green tree ants reduced numbers of both herbivores (e.g. beetles) and predators (e.g. spiders). Laine and Niemela (1980) observed reduced spider densities in birch trees near *Formica aquilona* nests. They offered 2 plausible processes for this effect: competitive exclusion by the reduction of available prey, and direct predation of spiders by ants. Risch and Carroll (1982a) gave a third explanation for the reduction of mobile predators in vegetable crops by *Solenopsis geminata*: ant disturbance may cause emigration from the site. In these 2 studies, ants appeared to produce a net benefit to the plants, as leaf damage was less in plants frequented by ants. However, Fritz (1983) demonstrated that ant exclusion of the hemipteran predator of a leaf-mining beetle allowed increased beetle survival, and thus more leaf damage, on black locust plants (although the observed differences were small). The impact of ants on plant herbivory thus depends on the relative effects on herbivore and predator populations.

Unfortunately, leaf clipping samples do not collect very active and flying insects effectively (Fenton and Howell, 1972), so important insect groups such as large orthopterans and predatory hemipterans were unmonitored in the present study. The numbers of dipterans collected may also have been biassed by this sampling technique. However, the reduction in area missing from leaves and in frequencies of leaves with holes indicates that leaf-chewing herbivory was reduced by the presence

of green tree ants, regardless of the effect of ants on other predators.

In many tropical tree crops, the dominant ants (including *Oecophylla spp.*) often form a patchwork of mutually exclusive territories - the ant mosaic - each with a characteristic insect fauna (Leston, 1973; Majer, 1976c; Room, 1971). These dominants are keystone species, to use the terminology of Paine (1974, 1976), controlling the species composition of their territory through predation, competitive monopolisation of food resources, and aggressive territorial behaviour. Majer (1976c) found that *O. longinoda* had the smallest associated insect fauna of any dominant ant species in cocoa trees, and especially reduced orthopterans and heteropterans.

The densities of flower and fruit in the Major Creek mango plantation were highly variable from year to year, and between trees. Information on factors influencing initiation and quantity of flowering in mango trees is surprisingly scarce (Chacko, 1986), but large environmental and genetic variation in flowering has been observed in other studies (e.g. Scholefield and Oag, 1986).

The eastern side of the trees produced the highest numbers of mature fruit, probably due to either light or wind differences. Other workers have suggested quantitative differences in flowering and fruiting were caused by longer periods of direct sunlight on the eastern side of trees (e.g. Chacko, 1986). Fruit were also dislodged in strong winds, which, from my limited observations and discussions with local farmers, blew mainly from the west, and north-west, during storms. The eastern aspect of the farm was protected from wind by the Mt Elliot range.

The presence of ants did not appear to affect the numbers of

flowers or young fruit in 1987. However, in trees with large crops of young fruit, ant occupation may result in high fruit losses during the last stage of fruit development. Crop yields during this study were very small, so these trends require further substantiation in a year with better crops.

The mechanism by which ants could augment fruit loss may be by increasing numbers of sap-feeding homopterans. The developing fruits on mango trees have nutrient requirements far outstripping the photosynthetic output of the leaves (Chacko, 1986). "Reserve" food materials from roots, trunk, and branches must be mobilised to meet supply, and may limit the maximum number of fruit which can be produced. Any drain on nutient flow by sap-feeding insects during the fruiting season (from July to December) could thus cause fruit drop, especially in trees with large crops. Densities of the diaspid, *P. dilata*, were highest in ant inhabited trees during July and January, and numbers of the ant-tended *Coccus sp* increased from July to a peak in January. Most fruit on trees with ants also supported populations of homopterans, which were tended by ants. Ant occupied trees thus experienced a much higher sap loss from these insects during the fruiting season.

Seasonal variation in colony size was previously correlated to the physiological status of inhabited trees, with colonies expanding when trees flowered or produced new flushes of leaf growth (section 5.3.1). This colony expansion may be triggered by the increasing numbers of honeydew-producing homopterans observed during this period. Increased honeydew levels alone may account for the rapid spread of ant colonies, as this sugary food is the major souce of energy for adult workers (Brian and Abbott, 1977; Sudd, 1987).

The numbers of bat marked fruit lying beneath trees with ants were lower than beneath trees without ants. Benzie (1985) found that the African weaver ant, *O. longinoda*, similarly deterred bats from fig fruit. Further trials were planned to confirm the 1987 results on bat frugivory and fruit production in mango trees, but these were abandoned due to very poor crop yields in 1988.

This study did not consider the germination success of the mango seed. The mango seed weevil, *Cryptorhynchus mangiferae*, can destroy large proportions of seeds without any outward evidence of attack (Simpson, 1984). Friederichs (1920) reported that *O. smaragdina* reduced weevil damage in mango fruit in Java. These ants might deter adult weevils from depositing eggs on the young fruit. Unfortunately, too few weevils were collected in leaf samples to test whether ant presence reduced weevil numbers.

From a commercial viewpoint, these results suggest that removal of *O. smaragdina* from mango trees may improve mango crop yields, but may increase frugivory by fruit bats. Ants might become more beneficial if levels of herbivory rose. An outbreak of a herbivorous insect, for example, could be reduced by green tree ants. However, the increased homopteran abundance (both tended and untended) in trees occupied by *O. smaragdina* is a disadvantage which needs to be carefully weighed against possible benefits to any commercial crops.

These results are difficult to interpret from the ecological viewpoint of the mango tree, as the short term effects observed in this study may be unimportant for a species with such a long lifespan. Also, the mango tree is an introduced species, which is thought to originate from the tropical rainforests of the Indo-Burman region (Mukherjee, 1972). Interactions between the mango tree, ants, and other insects may

thus be substantially different in its native habitat. Interestingly, the reproductive output of mango trees in their native environment is lower than in drier climates (Chacko, 1986; Singh, 1977). Factors other than seed production appear to have been important in controlling the distribution of this species. The major effect of green tree ants for the mango tree in its native habitat may well be reduced seed dispersal if disperser species like fruit bats are discouraged from visiting the tree. More information on the reproductive strategies of tropical rainforest trees, and the genus *Mangifera* in particular, is needed before the associations between mango trees and their insect fauna can be understood.

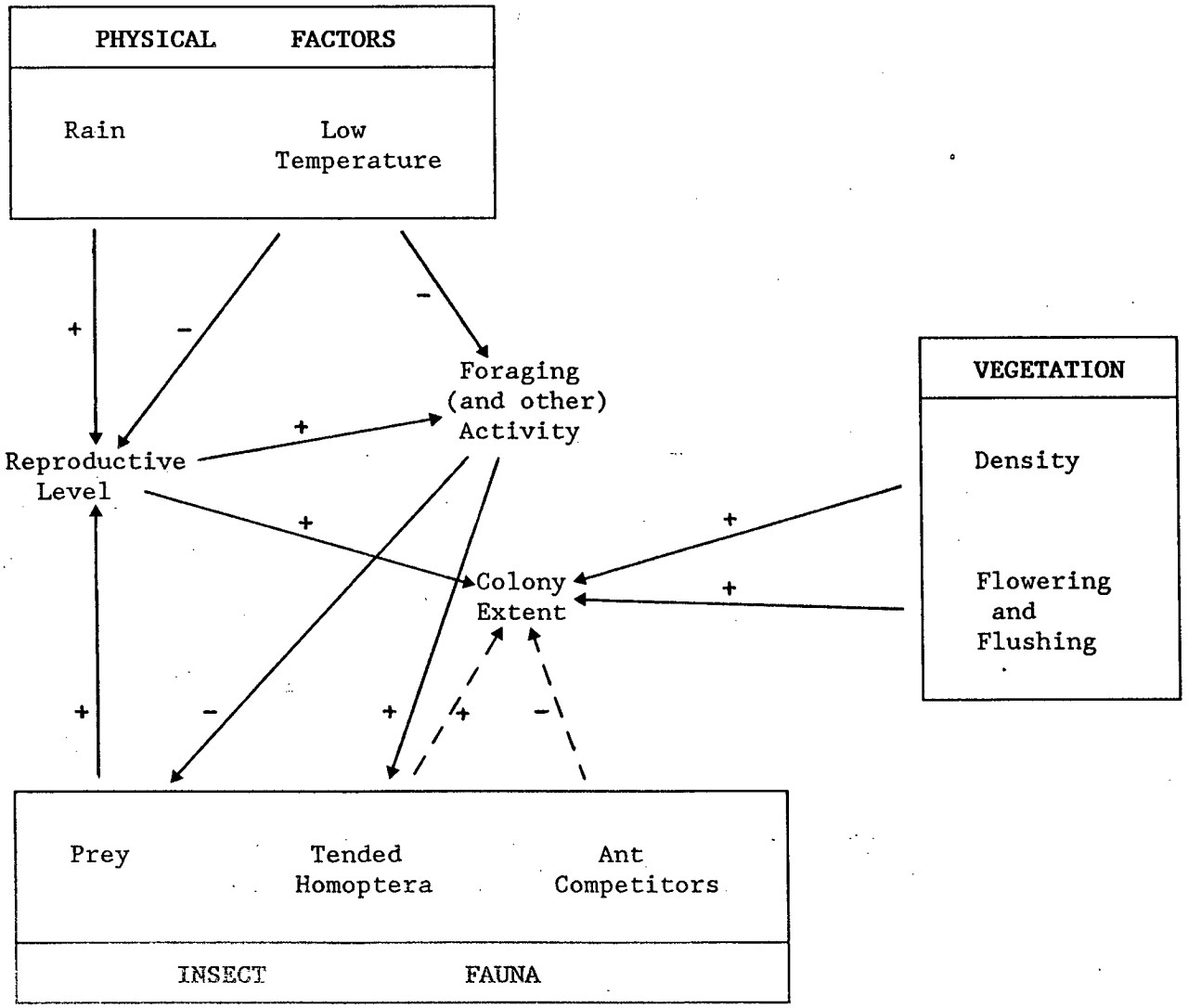
8. Final conclusions.

8.1. Factors influencing ant colonies.

Substantial seasonal variation in colony structure and function has been demonstrated in *O. smaragdina* populations inhabiting the seasonally dry tropical climate of the Townsville region. Most previous investigations of the weaver ant genus (e.g. Greenslade, 1971a,b; Vanderplank, 1960; Way, 1954a) have been conducted in wet equatorial habitats with minimal seasonality; much less colony variation was reported in these climates. The interactions observed between green tree ant colony dynamics and their physical and biotic environment in the present study have been summarised in figure 8.1.

Temperature is a major factor limiting the distribution of ectothermic organisms, since it directly influences their development and survival. *O. smaragdina* was recorded only from sites above the tropic of Capricorn (23° 30'S) and with average minimum temperatures above 17°C. Brown (1973) suggested low temperatures may limit ant distribution by inhibiting brood development or foraging efficiency; both of these effects were observed in the present study. The larval stage of *O. smaragdina* was particularly sensitive to low temperatures, with a threshold of 16.8±0.7°C. During winter, larvae develop more slowly than eggs or pupae, and this may allow the maintenance of a substantial larval population (needed for nest-binding silk supplies) when egg production is low. A more equatorial population of the African weaver ant, *O. longinoda*, showed little seasonality in brood production and no differences in developmental rate thresholds between the immature stages (Vanderplank, 1960; Way, 1954a).

Figure 8.1: Schematic representation of interactions between colony dynamics and the physical and biotic environment.



In most months, ant activity was reduced by low temperatures, and all ant movement halted below 12°C. Activity may also drop slightly at very high temperatures. However, this effect was very small, and may actually reflect uniformly high activity levels throughout the warmer temperature range.

Rainfall patterns had a major impact on green tree ant populations, both alone and in combination with temperature. The Australian distribution of *O. smaragdina* was delimited successfully by a curvilinear combination of rainfall and temperature. Brood production was also strongly correlated to rainfall. Sexual forms were produced only during the wet season, and proportions of both larvae and pupae rose with increasing moisture up to rainfall levels of 300 mm/month. However, pupal numbers declined at higher rainfalls, possibly due to the high investment in sexual production in these conditions (Greenslade, 1971a). Heavy rains reduced ant movements, presumably due to the physical hazard of being struck by raindrops, but this effect was minor in the relatively dry Townsville climate.

Temperature is generally considered to be less important than rainfall in determining seasonality in the tropics (e.g. Gibbs and Leston, 1970; Janzen and Schoener, 1968; Jones, 1987; Wolda, 1978). Although this may be true of weaver ant populations in equatorial climates, both temperature and rainfall exert substantial effects on populations in the Townsville environment. The present study could not fully elucidate the mechanisms underlying the correlations of climate with colony dynamics. Climatic factors can directly affect colonies; for example, low temperature inhibition of larval development, but they may also influence weaver ant colonies indirectly by affecting vegetation or insect populations.

Vegetation patterns have a strong influence on arboreal ants (e.g. Majer, 1976a; Brown, 1959). The distributional limits of *O. smaragdina* (above the directly development-inhibiting temperature of 17°C) are probably indirectly controlled by temperature and rainfall through their effect on vegetation density. In Townsville, green tree ants only inhabited areas of high tree density, with interconnecting canopies (as previously reported by Taylor and Adedoyin, 1978). Colony extents varied with seasonal changes in the physiological status of trees. Maximum extents coincided with peak flowering levels, and lagged the peak in new leaf growth by two months. Although a plentiful supply of leaves may encourage colony expansion by providing abundant nest sites, the primary influence of flowering and flushing on colony extent is probably indirect, acting through increased food levels.

Prey intake was highest during the period of maximum reproduction, when protein needs were highest (e.g. Brian *et al*, 1981; Sudd, 1987). The results of trials monitoring liquid food collected from homopterans were rather ambiguous, but appeared to peak during periods of tree flowering and flushing. Tended homopteran numbers in mango trees incresed during the flowering and fruiting season, when colonies were expanding. Substantial migration between the nests of a green ant colony is necessary to disseminate brood from the central egg-producing queenright nest, and to maintain a uniform colony scent. Larger colony extents thus incur higher energy costs, and may therefore be limited to periods of high honeydew input when homopterans are abundant. Other studies have linked similar changes in wood ant territories to fluctuations in honeydew supplies (Rosengren *et al*, 1987; Skinner, 1980b). These ants may increase territory areas during periods of high honeydew availability in order to locate and protect the largest

possible homopteran population, and hence collect most honeydew.

Sudd (1987) has suggested that during periods of plentiful honeydew supply, ants have extra energy to devote to prey hunting, which would otherwise be energetically unprofitable. High honeydew input does appear to coincide with increased activity, prey intake, and reproduction in colonies inhabiting native vegetation. However, homopteran levels and colony extent were not synchronised with ant reproduction in the mango farm habitat, suggesting that increased colony extent was not necessarily linked to prey collection for brood nutrition.

Competing ant species have a major impact on weaver ant colonies in moist equatorial habitats (e.g. Leston, 1973; Room, 1971; Vanderplank, 1960), but little interspecific competition was observed in the present study. Intra-specific competition between colonies was recorded during periods of colony expansion, but only within small portions of the total colony boundaries.

Although seasonal cycles in colony structure and behaviour were correlated with various physical and biotic factors, they may be maintained to some extent by endogenous rhythms. Many temperate ant species, for example, have an internally controlled seasonal reproductive pattern which is entrained by temperature and photoperiod cues at certain times of year (Brian, 1987). Endogenous circadian rhythms have also been detected in ants (McCluskey, 1958; Rosengren, 1977; Rosengren and Fortelius, 1986). The present study produced strong evidence for internal rhythms, at least on a circadian level, in green tree ant activity and food intake.

8.2. The impact of ants on the environment.

O. smaragdina has a major effect on the arboreal arthropod fauna, increasing tended (and some untended) homopteran levels, and reducing the numbers of many other arthropods. Leston (1973) coined the term "dominant" for aggressive ant species which maintain large populations, and exclude other dominants from their territories. Most dominant ants substantially alter their associated arboreal fauna, often in a pattern characteristic of each dominant (Majer, 1976c; Way, 1953).

Marine animal species which have similar important influences on community structure and diversity have been called "keystone" species (Paine, 1974, 1976, 1980). The removal of a keystone species usually causes dramatic changes in the community. For example, the removal of the predatory starfish, *Pisaster ochraceus*, can result in the competitive exclusion of many species by the mussel, *Mytilus californianus*, and hence reduced diversity (Paine, 1966, 1980). However, the removal of a dominant ant often leads to increased arthropod abundance and diversity (e.g. Majer, 1976c; Risch and Carroll, 1982a). This discrepancy may be the explained by a number of factors. Firstly, ants are generalist predators, whereas *P. ochraceus* is a specialist (Risch and Carroll, 1982a). Also, ants often attack other predators which may influence community structure (Laine and Niemela, 1980; Fritz, 1983). Thirdly, differing interaction strengths between the members of different herbivore assemblages may affect the levels of competitive exclusion which occur when a keystone predator is removed (Paine, 1980).

The effectiveness of some ant species in controlling arthropod communities has led to numerous studies of their potential as

biological control agents (e.g. Brown, 1959; Risch and Carroll, 1982b; Stapley, 1971; Way, 1953, 1954a), and development of strategies for the implementation of control by ants (Leston, 1973; Room, 1973). For example, Stapley (1971) used a selective herbicide and insecticide treatment in coconut plantations to replace populations of *Pheidole megacephala* with *O. smaragdina*, which can control the coreid bug, *Amblypelta cocophaga*.

Most studies have ignored temporal variation in the effectiveness of ants in controlling arthropod fauna. The activity and prey intake of green tree ant colonies in the present study were highly seasonal, peaking in the wet season when their level of reproduction was highest. Seasonal patterns of foraging activity and reproduction have been correlated to food availability in other species, such as wood ants (Skinner, 1980a,b) and desert seed harvester ants (Bernstein, 1979). This synchronization maximises the reproductive potential of colonies (Brian and Abbott, 1977, Robertson, 1988), and may also enable colonies to develop sexual forms at the same time (Bernstein, 1979).

The greatest impact of green tree ants on herbivore populations would thus be expected during the wet season reproductive period (December to April). This trend was observed for dipteran abundances in mango tree leaf samples (with maximum reduction by ants during January), but not in other insect groups. The major mango defoliaters (orthopterans, mainly from the genus *Valanga*; Cunningham, 1986) were too active to be collected by leaf clipping samples. However, the reduction in leaf damage from chewing insects by ants was most pronounced in April, indicating that ants controlled this form of herbivory most effectively during the wet season (reproductive) months.

Robertson (1988) correlated varying levels of *Cactoblastis cactorum* egg predation by ants to seasonality in the ants' larval production. To date, few studies have addressed this aspect. A number of researchers have demonstrated that herbivore control by ants improved when ant activity on plants increased due to the presence of extra-floral nectaries (e.g. Bentley, 1977; Smiley, 1985; Tilman, 1978), or ant-tended homopterans (e.g. Messina, 1981; Strauss, 1987). The abundance of tended homopterans in mango leaf samples peaked in January. Casual observations suggested that highest levels of homopteran tending may actually occur during the fruiting season; however, leaf samples were not collected to confirm this trend. Temporal variation in defoliator protection by ants could be influenced by seasonal differences, both in tended homopteran numbers and the reproductive level of the ant colony. In many cases, these two parameters probably vary synchronously, so their effects on plant protection would be difficult to separate.

Green tree ant colonies dispersed into larger numbers of nests, each with smaller populations, during the wet season. This decentralization of nests may improve territorial defence and foraging efficiency, by producing a more even distribution of ants throughout the territory (Hölldobler and Lumsden, 1980), and probably enhances the protective capability of colonies.

Circadian activity patterns may also influence the impact of ants on arthropod fauna. Green tree ants returned with prey mainly during daylight hours; this trend has also been observed in wood ants (e.g. Skinner, 1980b; Rosengren, 1977, Rosengren and Sundström, 1987), and is probably due to these species' reliance on vision for hunting. Many leaf-chewing insects in forests are active at night (Windsor, 1978),

and would thus be less susceptible to predation by diurnal predators such as *O. smaragdina*.

However, green tree ants were continuously active, even if not successfully foraging for 24 hours/day (except during very cold weather). Various studies have shown that ants can deter herbivores from feeding through disturbance, without causing mortality (e.g. Fritz, 1983; Messina, 1981), thus low prey intake may not necessarily indicate poor plant protection. Activities such as territorial patrolling and homopteran/extra-floral nectary guarding might provide consistently high protection, whereas brood transport and inter-nest migration along trunk trails would probably confer little control.

As well as offering beneficial effects, ants can harm the fitness of plants by encouraging homopterans, attacking predators or seed dispersers, and consuming seeds or seed elaiosomes (Horvitz and Schemske, 1984). The fruit production of mango trees was reduced by green tree ants, probably due to increased sap loss from homopterans. Buckley (1983) also reported reduced seed set by a plant bearing extra-floral nectaries when ants had access to homopteran honeydew.

Several studies have shown that reduction of predator numbers by ants can increase the populations of certain herbivores, especially those with some protection against ants, such as leaf-miners and leaf-rollers (Fowler and MacGarvin, 1985; Fritz, 1983). *O. smaragdina* reduced numbers of both predators (e.g. spiders) and leaf-chewing herbivores, but the net result to the tree was a decrease in leaf area eaten.

Green tree ants did not eat mango fruit, but may discourage fruit bats, an important disperser. A similar effect was demonstrated by Thomas (1988) for the African weaver ant, which deterred bats from

fruit in fig trees. However, Benzie (1985) reported that *O. smaragdina* vacated nests around fruit of *Syzygium cumini* when they neared maturity, possibly in response to reduced nutrient flows for homopteran honeydew production. These fruit obtained protection from herbivores (other than homoptera) during development, and unhindered dispersal when mature; this association suggests some level of co-evolutionary development between ant and plant.

The formation of such associations will depend on the relative magnitudes of beneficial and detrimental interactions, and their temporal and spatial variation (Horvitz and Schemske, 1984; Louda, 1982; Price *et al*, 1980). In general, the benefits of plant protection from folivores and frugivores must outweigh harmful effects such as homopteran sap-feeding, predator reduction, seed predation, and seed disperser interference. These effects will be strongly influenced by seasonal timing, with greatest levels of predation by ants when they are reproducing. In the Townsville environment, mango trees flower when green tree ants exhibit lowest reproductive activity, and thus probably recieve minimal protection. Plants fruiting in the wet season are most likely to benefit from the presence of *O. smaragdina* in the Townsville region (and to develop co-evolutionary mutualisms).

In studies examining ant plant interactions in seasonal climates, the temporal dynamics of ant populations will influence the beneficial and/or detrimental effects of the association. The incorporation of seasonal variation into future studies may greatly aid the understanding of the often complex interactions and co-evolutionary development between ants and plants.

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Appendix A. Activity counts for nests monitored from May 1987 to March 1989.

1.a. May 1987

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (μe)	Nest Pop.
1	1	9	23.10	24.76	2.62	0.00	825.54	9600
1	1	11	60.00	29.41	5.34	0.00	1396.24	9600
1	1	13	35.50	31.04	4.54	0.00	1455.29	9600
1	1	15	17.75	29.90	4.14	0.00	850.55	9600
1	1	17	22.75	26.79	1.48	0.00	180.48	9600
1	1	19	49.33	23.93	0.47	0.00	0.21	9600
1	1	21	17.33	22.12	0.29	0.00	0.01	9600
1	1	23	5.69	20.82	0.18	0.00	0.01	9600
1	1	1	1.91	20.22	0.12	0.00	0.01	9600
1	1	3	0.67	19.66	0.06	0.00	0.01	9600
1	1	5	0.50	19.11	0.01	0.00	0.08	9600
1	1	7	3.08	19.66	0.00	0.00	40.71	9600
1	2	9	27.40	23.47	1.45	0.00	578.90	9600
1	2	11	52.67	29.07	5.47	0.00	1393.39	9600
1	2	13	39.75	30.99	4.56	0.00	1469.21	9600
1	2	15	15.58	30.08	4.28	0.00	921.02	9600
1	2	17	13.17	27.06	1.71	0.00	223.78	9600
1	2	19	22.17	23.56	0.44	0.00	0.26	9600
1	2	21	15.17	22.03	0.28	0.00	0.01	9600
1	2	23	6.31	20.89	0.19	0.00	0.01	9600
1	2	1	3.36	20.29	0.13	0.00	0.01	9600
1	2	3	0.50	19.74	0.08	0.00	0.01	9600
1	2	5	0.08	19.18	0.02	0.00	0.08	9600
1	2	7	4.33	19.57	0.00	0.00	33.07	9600
2	1	11	190.85	28.69	0.60	0.00	1559.62	27104
2	1	13	186.20	29.84	1.79	0.00	1616.99	27104
2	1	15	250.97	29.10	1.02	0.00	1046.15	27104
2	1	17	246.49	26.07	1.76	0.00	354.68	27104
2	1	19	253.77	21.91	0.75	0.00	1.68	27104
2	1	21	190.96	19.38	0.00	0.00	0.01	27104
2	1	23	102.70	18.65	0.00	0.00	0.01	27104
2	1	1	107.93	18.13	0.00	0.00	0.01	27104
2	1	3	119.19	17.63	0.00	0.00	0.01	27104
2	1	5	186.67	17.13	0.00	0.00	0.01	27104
2	1	7	178.45	17.57	0.02	0.00	118.56	27104
2	1	9	120.49	23.74	0.39	0.00	865.61	27104
2	2	11	135.80	28.26	0.57	0.00	1578.79	27104
2	2	13	169.59	29.82	1.71	0.00	1625.38	27104
2	2	15	196.84	29.10	1.02	0.00	1046.15	27104
2	2	17	327.51	26.07	1.76	0.00	354.68	27104
2	2	19	339.64	21.91	0.75	0.00	1.68	27104
2	2	21	345.43	19.38	0.00	0.04	0.01	27104
2	2	23	276.21	18.65	0.00	0.22	0.01	27104
2	2	1	120.45	18.13	0.00	0.22	0.01	27104
2	2	3	19.41	17.63	0.00	0.22	0.01	27104
2	2	5	3.92	17.13	0.00	0.21	0.01	27104
2	2	7	105.47	17.53	0.02	0.02	110.48	27104
2	2	9	182.90	22.66	0.30	0.00	673.93	27104
3	1	11	139.29	29.50	0.40	0.00	1800.00	21607
3	1	13	123.51	29.79	1.59	0.00	1637.50	21607
3	1	15	159.00	29.10	1.02	0.00	1046.15	21607
3	1	17	184.97	26.07	1.76	0.00	354.68	21607
3	1	19	149.63	21.91	0.75	0.00	1.68	21607
3	1	21	99.70	19.38	0.00	0.00	0.01	21607
3	1	23	88.87	18.65	0.00	0.00	0.01	21607
3	1	1	70.21	18.13	0.00	0.00	0.01	21607
3	1	3	45.24	17.63	0.00	0.00	0.01	21607
3	1	5	26.12	17.13	0.00	0.00	0.01	21607
3	1	7	75.82	17.57	0.02	0.00	118.56	21607
3	1	9	146.76	22.61	0.34	0.00	735.91	21607
3	2	9	104.02	23.65	0.44	0.00	849.97	21607
3	2	11	98.59	28.57	0.57	0.00	1594.55	21607
3	2	13	106.62	29.82	1.77	0.00	1593.81	21607
3	2	15	122.40	28.94	0.97	0.00	988.03	21607
3	2	17	159.60	25.76	1.83	0.00	299.74	21607
3	2	19	186.61	21.56	0.58	0.00	0.84	21607
3	2	21	124.70	19.30	0.00	0.00	0.01	21607
3	2	23	62.64	18.61	0.00	0.00	0.01	21607
3	2	1	33.52	18.09	0.00	0.00	0.01	21607
3	2	3	27.08	17.59	0.00	0.00	0.01	21607
3	2	5	18.68	17.10	0.00	0.00	0.01	21607
3	2	7	58.56	17.79	0.04	0.00	152.64	21607

1.b. May 1988

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	49.46	24.50	14.05	0.00	1412.50	15112
1	1	13	36.29	25.46	15.96	0.00	1198.96	15112
1	1	15	106.72	25.39	13.59	0.00	665.63	15112
1	1	17	126.95	22.90	8.91	0.00	230.76	15112
1	1	19	113.31	20.12	3.50	0.00	0.29	15112
1	1	21	65.99	18.82	2.13	0.00	0.01	15112
1	1	23	16.25	15.84	1.30	0.00	0.01	15112
1	1	1	11.73	14.22	1.00	0.00	0.01	15112
1	1	3	13.84	13.77	1.00	0.00	0.01	15112
1	1	5	10.82	13.30	1.00	0.00	0.01	15112
1	1	7	32.59	16.20	3.68	0.00	76.89	15112
1	1	9	98.39	19.04	5.95	0.00	330.77	15112
1	2	11	150.54	23.66	3.11	0.00	712.50	15112
1	2	13	115.32	25.37	4.53	0.00	560.21	15112
1	2	15	93.08	25.51	3.95	0.00	208.47	15112
1	2	17	156.25	23.18	2.56	0.00	72.19	15112
1	2	19	219.29	20.25	0.80	0.00	0.84	15112
1	2	21	223.72	18.99	0.14	0.00	0.01	15112
1	2	23	129.53	16.09	0.00	0.00	0.01	15112
1	2	1	99.12	14.26	0.00	0.00	0.01	15112
1	2	3	94.56	13.81	0.00	0.00	0.01	15112
1	2	5	85.75	13.34	0.00	0.00	0.01	15112
1	2	7	125.81	15.75	2.95	0.00	57.79	15112
1	2	9	159.14	18.94	5.92	0.00	313.85	15112
2	1	9	137.78	19.71	5.87	0.00	438.03	23237
2	1	11	195.92	23.83	3.15	0.00	697.50	23237
2	1	13	201.60	25.46	4.46	0.00	523.96	23237
2	1	15	237.98	25.39	3.90	0.00	197.35	23237
2	1	17	298.74	22.90	2.38	0.00	60.95	23237
2	1	19	395.66	20.12	0.74	0.00	0.29	23237
2	1	21	352.88	18.82	0.10	0.00	0.01	23237
2	1	23	250.10	15.84	0.00	0.00	0.01	23237
2	1	1	145.64	14.22	0.00	0.00	0.01	23237
2	1	3	160.89	13.75	0.00	0.00	0.01	23237
2	1	5	107.36	13.26	0.00	0.00	0.01	23237
2	1	7	166.99	16.49	3.74	0.00	79.81	23237
2	2	11	120.28	23.75	2.99	0.00	696.36	23237
2	2	13	128.44	25.37	4.53	0.00	560.21	23237
2	2	15	187.14	25.51	3.95	0.00	208.47	23237
2	2	17	291.71	23.18	2.56	0.00	72.19	23237
2	2	19	231.67	20.25	0.80	0.00	0.84	23237
2	2	21	205.74	18.99	0.14	0.00	0.01	23237
2	2	23	197.54	16.09	0.00	0.00	0.01	23237
2	2	1	161.31	14.26	0.00	0.00	0.01	23237
2	2	3	138.26	13.81	0.00	0.00	0.01	23237
2	2	5	131.44	13.34	0.00	0.00	0.01	23237
2	2	7	199.74	15.74	2.95	0.00	55.78	23237
2	2	9	98.21	19.20	6.01	0.00	358.57	23237

2.a. August 1987.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	9	147.62	19.64	0.89	0.00	143.91	45592
1	1	11	148.12	23.41	3.64	0.00	374.24	45592
1	1	13	174.34	28.07	5.09	0.00	438.54	45592
1	1	15	191.08	24.23	4.18	0.00	217.71	45592
1	1	17	195.01	22.85	5.08	0.00	58.83	45592
1	1	19	238.77	20.87	1.31	0.00	1.34	45592
1	1	21	255.11	19.65	0.46	0.00	0.01	45592
1	1	23	183.55	18.54	0.15	0.00	0.01	45592
1	1	1	173.03	17.84	0.00	0.00	0.01	45592
1	1	3	131.59	17.53	0.00	0.00	0.01	45592
1	1	5	99.32	17.20	0.00	0.00	0.01	45592
1	1	7	107.19	17.47	0.18	0.01	32.67	45592
1	2	9	163.95	18.92	1.57	0.00	515.00	45592
1	2	11	113.64	21.81	2.84	0.00	362.50	45592
1	2	13	132.70	22.68	3.72	0.10	565.60	45592
1	2	15	133.40	23.53	5.01	0.00	706.91	45592
1	2	17	192.59	22.01	3.14	0.00	247.92	45592
1	2	19	227.18	19.87	1.14	0.00	1.68	45592
1	2	21	194.61	18.65	0.46	0.00	0.01	45592
1	2	23	144.08	17.54	0.15	0.00	0.01	45592
1	2	1	124.63	16.68	0.00	0.00	0.01	45592
1	2	3	56.67	16.05	0.00	0.00	0.01	45592
1	2	5	30.25	15.41	0.00	0.00	0.01	45592
1	2	7	50.01	15.87	0.21	0.00	103.34	45592
2	1	11	181.21	22.83	4.55	0.00	1481.67	35796
2	1	13	179.31	26.25	5.45	0.00	1666.17	35796
2	1	15	166.01	25.28	4.03	0.00	1148.56	35796
2	1	17	209.00	23.40	5.44	0.00	361.11	35796
2	1	19	231.64	20.84	1.31	0.00	1.68	35796
2	1	21	230.61	18.97	0.46	0.00	0.01	35796
2	1	23	173.05	16.96	0.15	0.00	0.01	35796
2	1	1	165.04	15.68	0.00	0.00	0.01	35796
2	1	3	134.90	15.05	0.00	0.00	0.01	35796
2	1	5	79.88	14.41	0.00	0.00	0.01	35796
2	1	7	82.33	14.38	0.18	0.00	131.39	35796
2	1	9	144.13	18.50	0.73	0.00	643.33	35796
2	2	9	145.35	19.00	0.77	0.00	313.43	35796
2	2	11	166.96	27.05	5.16	0.00	1100.00	35796
2	2	13	144.64	28.73	5.66	0.00	1676.17	35796
2	2	15	146.06	26.33	5.18	0.00	1191.67	35796
2	2	17	197.13	23.65	5.43	0.00	426.00	35796
2	2	19	255.39	21.02	1.61	0.00	5.67	35796
2	2	21	212.64	19.13	0.49	0.00	0.01	35796
2	2	23	141.40	17.13	0.17	0.00	0.01	35796
2	2	1	47.15	15.73	0.00	0.00	0.01	35796
2	2	3	13.54	15.11	0.00	0.00	0.01	35796
2	2	5	3.17	14.46	0.00	0.00	0.01	35796
2	2	7	7.60	14.24	0.14	0.00	27.23	35796
3	1	11	179.13	26.38	5.10	0.00	1437.09	30897
3	1	13	146.23	29.44	5.66	0.00	1588.50	30897
3	1	15	149.45	26.42	5.18	0.00	1191.67	30897
3	1	17	153.14	23.44	5.43	0.00	426.00	30897
3	1	19	95.05	20.81	1.61	0.00	5.67	30897
3	1	21	43.87	18.48	0.49	0.00	0.01	30897
3	1	23	21.82	16.25	0.17	0.00	0.01	30897
3	1	1	10.36	14.46	0.00	0.00	0.01	30897
3	1	3	2.80	13.22	0.00	0.00	0.01	30897
3	1	5	0.07	11.92	0.00	0.00	0.01	30897
3	1	7	4.72	12.58	0.14	0.00	65.00	30897
3	1	9	173.24	19.14	1.09	0.00	626.82	30897
3	2	11	193.87	28.29	4.24	0.00	1624.29	30897
3	2	13	181.49	28.25	4.73	0.00	1664.17	30897
3	2	15	161.75	26.10	4.67	0.00	1137.22	30897
3	2	17	195.64	23.15	5.44	0.00	361.11	30897
3	2	19	172.34	19.83	1.31	0.00	1.68	30897
3	2	21	95.26	17.30	0.46	0.00	0.01	30897
3	2	23	60.62	15.07	0.15	0.00	0.01	30897
3	2	1	32.58	13.51	0.00	0.00	0.01	30897
3	2	3	13.60	12.58	0.00	0.00	0.01	30897
3	2	5	3.49	11.61	0.00	0.00	0.01	30897
3	2	7	48.72	12.78	0.18	0.00	89.72	30897
3	2	9	153.00	19.56	0.89	0.00	719.03	30897

2.b. August 1988.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light ($\mu\epsilon$)	Nest Pop.
1	1	11	92.13	25.36	9.08	0.00	634.22	25245
1	1	13	119.93	26.77	8.50	0.00	640.93	25245
1	1	15	135.51	25.82	7.96	0.00	539.55	25245
1	1	17	171.19	22.99	5.02	0.00	274.58	25245
1	1	19	177.66	20.63	2.80	0.00	1.68	25245
1	1	21	129.20	19.81	1.94	0.00	0.01	25245
1	1	23	100.71	19.10	0.31	0.00	0.01	25245
1	1	1	83.14	18.73	0.00	0.00	0.01	25245
1	1	3	74.04	18.44	0.00	0.00	0.01	25245
1	1	5	61.36	18.14	0.00	0.00	0.01	25245
1	1	7	80.29	18.85	1.99	0.00	71.97	25245
1	1	9	99.72	22.72	8.70	0.00	353.36	25245
1	2	11	77.39	26.95	5.23	0.00	1010.72	25245
1	2	13	94.30	26.86	5.73	0.00	541.43	25245
1	2	15	115.58	23.42	4.79	0.00	306.39	25245
1	2	17	129.81	20.73	2.87	0.00	6.54	25245
1	2	19	152.65	19.87	2.09	0.00	0.01	25245
1	2	21	149.19	19.16	0.43	0.00	0.01	25245
1	2	23	101.58	18.50	0.00	0.00	0.01	25245
1	2	1	85.03	17.90	0.00	0.00	0.01	25245
1	2	3	72.30	17.33	0.00	0.00	0.01	25245
1	2	5	63.43	17.63	0.79	0.00	93.75	25245
1	2	7	95.92	21.52	5.04	0.00	632.62	25245
1	2	9	90.79	25.48	4.33	0.00	1319.05	25245
2	1	13	239.85	27.86	6.30	0.00	528.57	50868
2	1	15	259.65	26.64	5.65	0.00	532.86	50868
2	1	17	339.08	23.11	4.67	0.00	274.58	50868
2	1	19	284.06	20.63	2.80	0.00	1.68	50868
2	1	21	290.81	19.81	1.94	0.00	0.01	50868
2	1	23	216.73	19.07	0.31	0.00	0.01	50868
2	1	1	193.66	18.45	0.00	0.00	0.01	50868
2	1	3	164.14	17.88	0.00	0.00	0.01	50868
2	1	5	123.98	17.28	0.00	0.00	0.01	50868
2	1	7	143.10	17.83	1.05	0.00	123.34	50868
2	1	9	228.15	21.91	5.19	0.00	685.18	50868
2	1	11	247.05	27.25	5.20	0.00	1545.00	50868
2	2	11	247.05	27.25	5.20	0.00	1545.00	50868
2	2	13	262.01	28.48	7.34	0.00	1582.83	50868
2	2	15	228.38	25.79	11.87	0.00	1147.17	50868
2	2	17	271.01	23.06	6.31	0.00	403.33	50868
2	2	19	294.75	20.32	1.40	0.00	1.68	50868
2	2	21	262.69	19.21	0.53	0.00	0.01	50868
2	2	23	162.93	18.14	0.09	0.00	0.01	50868
2	2	1	147.52	17.45	0.00	0.00	0.01	50868
2	2	3	115.99	16.88	0.00	0.00	0.01	50868
2	2	5	64.13	16.28	0.00	0.00	0.01	50868
2	2	7	81.45	17.27	0.09	0.00	71.97	50868
2	2	9	225.96	22.22	0.89	0.00	338.30	50868
3	1	13	180.71	29.79	8.38	0.00	1460.57	37680
3	1	15	173.50	26.03	9.08	0.00	1147.17	37680
3	1	17	196.92	23.06	5.53	0.00	403.33	37680
3	1	19	184.08	20.21	1.40	0.00	1.68	37680
3	1	21	155.42	18.69	0.53	0.00	0.01	37680
3	1	23	106.85	17.18	0.09	0.00	0.01	37680
3	1	1	82.27	16.18	0.00	0.00	0.01	37680
3	1	3	12.17	15.31	0.00	0.00	0.01	37680
3	1	5	1.42	14.41	0.00	0.00	0.01	37680
3	1	7	21.08	15.10	0.74	0.00	131.86	37680
3	1	9	126.86	19.18	3.49	0.00	592.35	37680
3	1	11	201.70	27.38	5.41	0.00	1468.00	37680
3	2	11	201.70	27.38	5.41	0.00	1468.00	37680
3	2	13	199.67	28.20	7.34	0.00	1582.83	37680
3	2	15	195.67	25.36	11.87	0.00	1147.17	37680
3	2	17	258.42	23.38	6.31	0.00	403.33	37680
3	2	19	251.67	20.66	2.80	0.00	1.68	37680
3	2	21	184.50	20.04	1.94	0.00	0.01	37680
3	2	23	158.62	19.57	0.31	0.00	0.01	37680
3	2	1	167.55	19.36	0.00	0.00	0.01	37680
3	2	3	152.17	19.22	0.00	0.00	0.01	37680
3	2	5	139.25	19.07	0.00	0.00	0.01	37680
3	2	7	133.58	19.64	0.09	0.00	71.97	37680
3	2	9	224.36	23.44	1.68	0.00	355.58	37680

3.a. October 1987.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	24.52	29.68	4.82	0.00	1618.18	8726
1	1	13	19.43	30.82	8.20	0.00	1690.98	8726
1	1	15	22.57	30.84	7.44	0.00	980.88	8726
1	1	17	55.04	29.44	2.94	0.00	206.25	8726
1	1	19	27.38	27.83	0.52	0.00	2.51	8726
1	1	21	76.13	26.71	0.05	0.00	0.01	8726
1	1	23	85.13	25.69	0.00	0.00	0.01	8726
1	1	1	0.30	25.08	0.00	0.00	0.01	8726
1	1	3	0.18	25.00	0.00	0.00	0.84	8726
1	1	5	0.00	25.23	0.05	0.00	65.92	8726
1	1	7	35.43	26.63	0.38	0.00	423.43	8726
1	1	9	27.93	27.67	1.48	0.00	903.57	8726
1	2	11	28.86	28.82	3.41	0.00	1414.29	8726
1	2	13	37.55	32.32	7.79	0.00	1731.25	8726
1	2	15	24.14	32.52	6.93	0.00	963.54	8726
1	2	17	50.97	31.93	3.73	0.00	311.46	8726
1	2	19	32.00	30.72	1.21	0.00	20.00	8726
1	2	21	62.81	29.08	0.21	0.00	0.01	8726
1	2	23	88.20	27.25	0.05	0.00	0.01	8726
1	2	1	84.56	26.50	0.00	0.00	0.01	8726
1	2	3	6.29	25.58	0.00	0.00	0.01	8726
1	2	5	33.67	24.25	0.00	0.00	5.00	8726
1	2	7	48.84	24.47	0.19	0.00	187.29	8726
1	2	9	18.78	26.41	1.21	0.00	740.63	8726
2	1	17	43.89	28.85	4.30	0.00	143.00	7082
2	1	19	52.25	28.15	1.37	0.00	17.00	7082
2	1	21	54.95	26.94	0.20	0.00	0.43	7082
2	1	23	21.69	26.09	0.01	0.00	0.01	7082
2	1	1	14.66	24.90	0.00	0.00	0.01	7082
2	1	3	10.36	24.43	0.00	0.00	0.01	7082
2	1	5	10.29	24.07	0.02	0.00	2.09	7082
2	1	7	10.81	24.88	0.17	0.00	193.19	7082
2	1	9	9.08	27.19	0.50	0.00	819.44	7082
2	1	11	45.57	29.51	3.66	0.00	1544.44	7082
2	1	13	26.20	30.03	4.67	0.00	1637.50	7082
2	1	15	24.47	30.31	6.19	0.00	919.44	7082
2	2	11	9.25	26.71	0.66	0.28	433.27	7082
2	2	13	8.93	30.23	2.55	0.00	1133.33	7082
2	2	15	18.69	30.21	4.54	0.00	503.61	7082
2	2	17	58.03	29.18	5.94	0.00	311.53	7082
2	2	19	21.62	27.03	4.97	0.00	7.28	7082
2	2	21	29.35	26.05	5.44	0.00	0.01	7082
2	2	23	77.41	25.43	3.10	0.00	0.01	7082
2	2	1	49.63	24.81	1.03	0.00	0.01	7082
2	2	3	16.89	24.08	0.00	0.42	0.01	7082
2	2	5	0.00	24.01	0.00	0.00	3.16	7082
2	2	7	29.35	24.91	0.42	0.00	91.69	7082
2	2	9	8.22	26.77	4.25	0.00	377.79	7082

3.b. October 1988.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	230.13	31.83	6.07	0.00	1763.64	17603
1	1	13	232.30	32.97	9.88	0.00	1697.71	17603
1	1	15	254.96	30.70	9.14	0.00	1331.43	17603
1	1	17	383.88	28.28	8.89	0.00	416.95	17603
1	1	19	480.03	26.02	3.26	0.00	5.01	17603
1	1	21	336.23	25.14	1.23	0.00	0.01	17603
1	1	23	271.27	24.73	0.00	0.00	0.01	17603
1	1	1	240.95	24.33	0.00	0.00	0.01	17603
1	1	3	227.55	23.95	0.00	0.00	0.01	17603
1	1	5	234.30	23.60	0.31	0.00	2.63	17603
1	1	7	274.31	25.53	2.78	0.00	64.03	17603
1	1	9	313.33	28.27	2.56	0.00	155.64	17603
1	2	11	265.56	33.10	6.36	0.00	1796.00	17603
1	2	13	256.96	33.10	9.73	0.00	1715.79	17603
1	2	15	308.40	30.70	9.14	0.00	1331.43	17603
1	2	17	429.75	28.28	8.89	0.00	416.95	17603
1	2	19	490.56	26.02	3.26	0.00	5.01	17603
1	2	21	420.73	25.14	1.23	0.00	0.01	17603
1	2	23	369.04	24.73	0.00	0.00	0.01	17603
1	2	1	299.40	24.33	0.00	0.00	0.01	17603
1	2	3	251.31	23.95	0.00	0.00	0.01	17603
1	2	5	291.94	23.60	0.31	0.00	2.63	17603
1	2	7	268.80	25.53	2.78	0.00	64.03	17603
1	2	9	277.93	28.57	2.97	0.00	338.52	17603
2	1	11	502.76	32.04	6.30	0.00	1071.00	25773
2	1	13	372.98	32.91	10.02	0.00	1580.63	25773
2	1	15	461.31	30.48	9.12	0.00	1273.00	25773
2	1	17	595.62	28.09	8.31	0.00	346.96	25773
2	1	19	732.55	25.88	3.28	0.00	3.01	25773
2	1	21	600.56	25.11	1.01	0.00	0.01	25773
2	1	23	515.09	24.70	0.00	0.00	0.01	25773
2	1	1	453.97	24.30	0.00	0.00	0.01	25773
2	1	3	474.62	23.92	0.00	0.00	0.01	25773
2	1	5	502.55	23.62	0.55	0.00	3.71	25773
2	1	7	523.83	25.81	2.76	0.00	73.31	25773
2	1	9	510.07	29.08	3.10	0.00	535.53	25773
2	2	13	436.94	32.33	9.96	0.00	1635.78	25773
2	2	15	541.58	30.55	9.07	0.00	1321.22	25773
2	2	17	591.69	28.28	8.89	0.00	416.95	25773
2	2	19	930.29	26.02	3.26	0.00	5.01	25773
2	2	21	933.01	25.14	1.23	0.00	0.01	25773
2	2	23	801.58	24.73	0.00	0.00	0.01	25773
2	2	1	698.06	24.33	0.00	0.00	0.01	25773
2	2	3	567.79	23.95	0.00	0.00	0.01	25773
2	2	5	531.39	23.60	0.31	0.00	2.63	25773
2	2	7	485.41	25.53	2.78	0.00	64.03	25773
2	2	9	666.71	28.78	3.29	0.00	481.62	25773
2	2	11	675.89	31.86	5.87	0.00	1494.06	25773

4.a. December 1987.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	91.38	27.65	4.97	0.01	726.96	1260
1	1	13	34.00	29.15	9.97	0.00	1161.35	1260
1	1	15	64.75	29.36	8.73	0.00	898.28	1260
1	1	17	129.50	26.65	6.56	0.00	195.03	1260
1	1	19	78.08	24.78	5.43	0.00	19.05	1260
1	1	21	5.33	22.84	2.04	0.04	0.01	1260
1	1	23	19.69	22.00	2.69	0.00	0.01	1260
1	1	1	53.00	22.00	3.52	0.00	0.01	1260
1	1	3	56.17	22.00	3.49	0.00	0.01	1260
1	1	5	68.17	22.15	2.14	0.00	3.99	1260
1	1	7	50.42	24.42	2.15	0.00	376.85	1260
1	1	9	67.58	25.91	4.84	0.01	654.73	1260
1	2	9	59.45	32.23	2.18	0.00	997.17	1260
1	2	11	45.17	34.38	6.12	0.00	2539.18	1260
1	2	13	35.75	34.56	7.19	0.00	2325.63	1260
1	2	15	67.08	33.92	6.33	0.00	2058.75	1260
1	2	17	47.42	31.71	3.94	0.00	798.25	1260
1	2	19	7.83	28.99	3.03	0.00	108.11	1260
1	2	21	59.58	27.39	1.76	0.00	0.01	1260
1	2	23	130.38	26.60	1.14	0.00	0.01	1260
1	2	1	127.27	26.12	0.95	0.00	0.01	1260
1	2	3	110.92	25.53	0.90	0.00	0.01	1260
1	2	5	78.25	25.12	0.95	0.00	10.54	1260
1	2	7	56.82	27.90	3.29	0.00	158.89	1260
2	1	9	174.22	28.45	6.83	0.00	1309.09	2000
2	1	11	156.33	32.08	1.50	0.31	897.52	2000
2	1	13	118.17	30.64	2.05	0.63	787.50	2000
2	1	15	172.75	31.50	4.44	0.00	1494.84	2000
2	1	17	75.50	28.01	10.44	1.53	357.11	2000
2	1	19	16.08	23.40	0.22	0.31	0.75	2000
2	1	21	10.58	22.78	0.00	0.00	0.01	2000
2	1	23	1.85	22.53	0.00	0.00	0.01	2000
2	1	1	0.64	22.33	0.00	0.00	0.01	2000
2	1	3	0.00	22.16	0.00	0.00	0.01	2000
2	1	5	0.50	22.04	0.07	0.00	9.56	2000
2	1	7	92.67	24.31	6.69	0.00	483.37	2000
2	2	9	73.33	28.46	4.17	0.00	1322.73	2000
2	2	11	83.67	33.01	2.03	0.00	1828.67	2000
2	2	13	121.33	33.75	4.54	0.00	1697.62	2000
2	2	15	160.92	32.86	3.97	0.00	1455.37	2000
2	2	17	175.75	30.63	5.02	0.00	803.33	2000
2	2	19	214.33	27.84	5.67	0.00	67.97	2000
2	2	21	229.58	25.97	2.81	0.00	0.01	2000
2	2	23	212.00	24.28	0.45	0.00	0.01	2000
2	2	1	181.09	23.67	0.00	0.00	0.01	2000
2	2	3	122.00	23.32	0.00	0.00	0.01	2000
2	2	5	111.75	23.03	0.06	0.00	0.29	2000
2	2	7	73.67	24.38	3.59	0.00	383.26	2000

4.b. December 1988.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	32.32	30.43	3.47	0.00	411.67	2733
1	1	13	33.43	31.70	2.41	0.00	533.40	2733
1	1	15	35.88	30.70	3.32	0.00	495.74	2733
1	1	17	29.76	27.02	2.62	0.00	644.60	2733
1	1	19	44.73	25.13	0.35	0.00	108.62	2733
1	1	21	34.94	24.84	0.00	0.00	0.01	2733
1	1	23	22.86	24.63	0.00	0.00	0.01	2733
1	1	1	30.51	24.42	0.00	0.00	0.01	2733
1	1	3	21.19	24.23	0.00	0.00	0.01	2733
1	1	5	30.23	24.14	0.00	0.00	2.09	2733
1	1	7	28.53	26.04	0.05	0.00	399.55	2733
1	1	9	19.30	30.13	1.18	0.00	1020.46	2733
1	2	11	71.19	32.06	3.67	0.00	428.89	2733
1	2	13	42.28	32.25	2.41	0.00	533.40	2733
1	2	15	39.93	30.77	3.32	0.00	495.74	2733
1	2	17	53.49	27.02	2.62	0.00	644.60	2733
1	2	19	61.96	25.13	0.35	0.00	108.62	2733
1	2	21	69.87	24.84	0.00	0.00	0.01	2733
1	2	23	68.32	24.63	0.00	0.00	0.01	2733
1	2	1	52.90	24.42	0.00	0.00	0.01	2733
1	2	3	45.95	24.23	0.00	0.00	0.01	2733
1	2	5	52.92	24.14	0.00	0.00	2.09	2733
1	2	7	59.14	26.04	0.05	0.00	399.55	2733
1	2	9	38.42	29.57	0.75	0.00	993.18	2733
2	1	9	56.02	29.05	1.01	0.00	313.64	2140
2	1	11	42.18	32.85	3.09	0.00	830.00	2140
2	1	13	39.97	34.33	1.94	0.00	1467.08	2140
2	1	15	46.09	31.78	2.02	0.24	401.67	2140
2	1	17	39.97	27.22	5.07	1.18	40.50	2140
2	1	19	29.20	25.19	0.97	0.00	13.50	2140
2	1	21	14.75	24.86	0.00	0.00	0.01	2140
2	1	23	30.70	24.64	0.00	0.00	0.01	2140
2	1	1	30.25	24.44	0.00	0.00	0.01	2140
2	1	3	21.98	24.25	0.00	0.00	0.01	2140
2	1	5	16.96	24.11	0.00	0.00	1.26	2140
2	1	7	32.37	25.75	0.03	0.00	92.80	2140
2	2	11	29.71	32.47	3.82	0.00	832.14	2140
2	2	13	44.84	32.22	2.835	0.5	420.625	2140
2	2	15	85.47	30.77	1.25	0.00	495.74	2140
2	2	17	42.92	27.02	3.80	0.00	644.60	2140
2	2	19	43.36	25.13	0.70	0.00	108.62	2140
2	2	21	48.30	24.84	0.00	0.00	0.01	2140
2	2	23	28.25	24.63	0.00	0.00	0.01	2140
2	2	1	36.69	24.42	0.00	0.00	0.01	2140
2	2	3	43.14	24.23	0.00	0.00	0.01	2140
2	2	5	37.98	24.14	0.00	0.00	2.09	2140
2	2	7	35.99	25.99	0.05	0.00	399.55	2140
2	2	9	36.21	29.76	1.54	0.00	1137.12	2140

5.a. January 1988.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	35.18	30.43	3.47	0.00	411.67	2975
1	1	13	36.39	31.70	2.41	0.00	533.40	2975
1	1	15	39.05	30.70	3.32	0.00	495.74	2975
1	1	17	32.39	27.02	2.62	0.00	644.60	2975
1	1	19	48.69	25.13	0.35	0.00	108.62	2975
1	1	21	38.03	24.84	0.00	0.00	0.01	2975
1	1	23	24.88	24.63	0.00	0.00	0.01	2975
1	1	1	33.21	24.42	0.00	0.00	0.01	2975
1	1	3	23.06	24.23	0.00	0.00	0.01	2975
1	1	5	32.90	24.14	0.00	0.00	2.09	2975
1	1	7	31.06	26.04	0.05	0.00	399.55	2975
1	1	9	21.01	30.13	1.18	0.00	1020.46	2975
1	2	11	77.49	32.06	3.67	0.00	428.89	2975
1	2	13	46.02	32.25	2.41	0.00	533.40	2975
1	2	15	43.46	30.77	3.32	0.00	495.74	2975
1	2	17	58.22	27.02	2.62	0.00	644.60	2975
1	2	19	67.44	25.13	0.35	0.00	108.62	2975
1	2	21	76.05	24.84	0.00	0.00	0.01	2975
1	2	23	74.37	24.63	0.00	0.00	0.01	2975
1	2	1	57.59	24.42	0.00	0.00	0.01	2975
1	2	3	50.02	24.23	0.00	0.00	0.01	2975
1	2	5	57.60	24.14	0.00	0.00	2.09	2975
1	2	7	64.37	26.04	0.05	0.00	399.55	2975
1	2	9	41.82	29.57	0.75	0.00	993.18	2975
2	1	9	51.46	29.05	1.01	0.00	313.64	1966
2	1	11	38.75	32.85	3.09	0.00	830.00	1966
2	1	13	36.72	34.33	1.94	0.00	1467.08	1966
2	1	15	42.34	31.78	2.02	0.24	401.67	1966
2	1	17	36.72	27.22	5.07	1.18	40.50	1966
2	1	19	26.83	25.19	0.97	0.00	13.50	1966
2	1	21	13.55	24.86	0.00	0.00	0.01	1966
2	1	23	28.21	24.64	0.00	0.00	0.01	1966
2	1	1	27.79	24.44	0.00	0.00	0.01	1966
2	1	3	20.19	24.25	0.00	0.00	0.01	1966
2	1	5	15.58	24.11	0.00	0.00	1.26	1966
2	1	7	29.74	25.75	0.03	0.00	92.80	1966

5.b. January 1989.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (με)	Nest Pop.
1	1	11	138.08	30.82	1.36	0.00	1154.17	4875
1	1	13	153.82	31.64	2.53	0.00	722.22	4875
1	1	15	101.09	31.15	1.46	0.03	429.80	4875
1	1	17	120.72	30.13	1.76	0.00	226.51	4875
1	1	19	249.14	28.88	0.63	0.00	29.13	4875
1	1	21	158.88	27.82	0.00	0.00	0.01	4875
1	1	23	110.14	27.06	0.00	0.02	0.01	4875
1	1	1	79.69	26.73	0.00	0.00	0.01	4875
1	1	3	51.32	26.42	0.00	0.00	0.01	4875
1	1	5	78.50	26.10	0.00	0.00	0.84	4875
1	1	7	167.99	26.49	2.81	0.00	496.06	4875
1	1	9	184.89	28.25	2.41	0.00	1145.05	4875
1	2	11	138.08	30.82	1.36	0.00	1154.17	4875
1	2	13	135.75	31.30	3.57	0.00	1110.12	4875
1	2	15	136.29	30.49	1.90	0.03	560.71	4875
1	2	17	157.32	28.79	1.66	0.00	425.75	4875
1	2	19	193.15	27.83	0.63	0.00	66.63	4875
1	2	21	199.30	27.11	0.00	0.74	0.01	4875
1	2	23	24.95	26.02	0.00	0.24	0.01	4875
1	2	1	9.43	25.64	0.00	0.00	0.01	4875
1	2	3	2.10	25.37	0.00	0.00	0.01	4875
1	2	5	9.66	25.09	0.00	0.00	0.84	4875
1	2	7	96.03	25.85	0.21	0.00	132.69	4875
1	2	9	196.42	27.76	0.85	0.02	897.31	4875
2	1	13	159.11	29.00	1.26	0.02	425.00	5582
2	1	15	148.91	29.46	1.26	0.15	411.57	5582
2	1	17	182.79	29.50	1.64	0.03	288.85	5582
2	1	19	210.43	28.38	0.77	0.00	51.67	5582
2	1	21	258.41	27.28	0.00	0.00	0.01	5582
2	1	23	33.91	26.63	0.00	0.00	0.01	5582
2	1	1	11.67	26.13	0.00	0.00	0.01	5582
2	1	3	3.57	25.65	0.00	0.00	0.01	5582
2	1	5	3.66	25.16	0.00	0.02	0.84	5582
2	1	7	82.57	26.07	0.34	0.00	281.94	5582
2	1	9	221.76	28.32	1.06	0.00	875.97	5582
2	1	11	227.38	29.32	1.43	0.00	1225.00	5582
2	2	13	169.77	31.69	3.11	0.00	1627.78	5582
2	2	15	162.28	31.13	2.98	0.00	1388.89	5582
2	2	17	181.01	30.11	2.27	0.00	561.94	5582
2	2	19	200.45	28.90	0.52	0.00	54.59	5582
2	2	21	279.18	28.11	0.00	0.00	0.01	5582
2	2	23	220.34	27.60	0.00	0.00	0.01	5582
2	2	1	170.91	27.11	0.00	0.00	0.01	5582
2	2	3	129.11	26.64	0.00	0.00	0.01	5582
2	2	5	159.88	26.15	0.00	0.00	0.84	5582
2	2	7	142.04	26.87	2.76	0.00	561.25	5582
2	2	9	201.87	28.40	3.37	0.00	1242.19	5582
2	2	11	192.33	29.57	3.02	0.00	1571.15	5582

6.a. March 1988.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (μe)	Nest Pop.
1	1	11	49.56	29.39	0.92	0.00	1390.91	1944
1	1	13	58.50	30.65	2.27	0.00	941.54	1944
1	1	15	61.00	29.71	0.79	0.00	656.69	1944
1	1	17	52.50	28.10	0.12	0.00	195.67	1944
1	1	19	20.67	25.94	0.00	0.00	1.68	1944
1	1	21	4.50	25.32	0.00	0.00	0.01	1944
1	1	23	0.38	24.73	0.00	0.00	0.01	1944
1	1	1	0.00	23.63	0.00	0.00	0.01	1944
1	1	3	0.67	22.19	0.00	0.00	0.01	1944
1	1	5	2.17	20.69	0.00	0.00	0.01	1944
1	1	7	11.29	20.07	0.09	0.00	44.49	1944
1	1	9	46.88	25.51	0.50	0.00	368.04	1944
1	2	9	46.88	25.51	0.50	0.00	368.04	1944
1	2	11	53.92	29.08	0.92	0.00	1336.52	1944
1	2	13	62.08	30.65	2.27	0.00	941.54	1944
1	2	15	68.08	29.71	0.79	0.00	656.69	1944
1	2	17	77.25	28.10	0.12	0.00	195.67	1944
1	2	19	82.42	25.94	0.00	0.00	1.68	1944
1	2	21	73.50	25.32	0.00	0.00	0.01	1944
1	2	23	63.00	24.73	0.00	0.00	0.01	1944
1	2	1	43.64	23.63	0.00	0.00	0.01	1944
1	2	3	35.75	22.19	0.00	0.00	0.01	1944
1	2	5	27.67	20.69	0.00	0.00	0.01	1944
1	2	7	34.67	20.88	0.22	0.00	82.50	1944
2	1	11	130.02	30.82	1.36	0.00	1154.17	4590
2	1	13	144.83	31.64	2.53	0.00	722.22	4590
2	1	15	95.19	31.15	1.46	0.03	429.80	4590
2	1	17	113.67	30.13	1.76	0.00	226.51	4590
2	1	19	234.59	28.88	0.63	0.00	29.13	4590
2	1	21	149.60	27.82	0.00	0.00	0.01	4590
2	1	23	103.70	27.06	0.00	0.02	0.01	4590
2	1	1	75.04	26.73	0.00	0.00	0.01	4590
2	1	3	48.33	26.42	0.00	0.00	0.01	4590
2	1	5	73.92	26.10	0.00	0.00	0.84	4590
2	1	7	158.18	26.49	2.81	0.00	496.06	4590
2	1	9	174.09	28.25	2.41	0.00	1145.05	4590
2	2	11	130.02	30.82	1.36	0.00	1154.17	4590
2	2	13	127.82	31.30	3.57	0.00	1110.12	4590
2	2	15	128.33	30.49	1.90	0.03	560.71	4590
2	2	17	148.13	28.79	1.66	0.00	425.75	4590
2	2	19	181.87	27.83	0.63	0.00	66.63	4590
2	2	21	187.66	27.11	0.00	0.74	0.01	4590
2	2	23	23.49	26.02	0.00	0.24	0.01	4590
2	2	1	8.88	25.64	0.00	0.00	0.01	4590
2	2	3	1.98	25.37	0.00	0.00	0.01	4590
2	2	5	9.09	25.09	0.00	0.00	0.84	4590
2	2	7	90.42	25.85	0.21	0.00	132.69	4590
2	2	9	184.95	27.76	0.85	0.02	897.31	4590
3	1	13	168.98	29.00	1.26	0.02	425.00	5928
3	1	15	158.14	29.46	1.26	0.15	411.57	5928
3	1	17	194.13	29.50	1.64	0.03	288.85	5928
3	1	19	223.48	28.38	0.77	0.00	51.67	5928
3	1	21	274.43	27.28	0.00	0.00	0.01	5928
3	1	23	36.01	26.63	0.00	0.00	0.01	5928
3	1	1	12.40	26.13	0.00	0.00	0.01	5928
3	1	3	3.79	25.65	0.00	0.00	0.01	5928
3	1	5	3.88	25.16	0.00	0.02	0.84	5928
3	1	7	87.69	26.07	0.34	0.00	281.94	5928
3	1	9	235.51	28.32	1.06	0.00	875.97	5928
3	1	11	241.48	29.32	1.43	0.00	1225.00	5928
3	2	13	180.30	31.69	3.11	0.00	1627.78	5928
3	2	15	172.35	31.13	2.98	0.00	1388.89	5928
3	2	17	192.23	30.11	2.27	0.00	561.94	5928
3	2	19	212.88	28.90	0.52	0.00	54.59	5928
3	2	21	296.50	28.11	0.00	0.00	0.01	5928
3	2	23	234.00	27.60	0.00	0.00	0.01	5928
3	2	1	181.51	27.11	0.00	0.00	0.01	5928
3	2	3	137.12	26.64	0.00	0.00	0.01	5928
3	2	5	169.79	26.15	0.00	0.00	0.84	5928
3	2	7	150.85	26.87	2.76	0.00	561.25	5928
3	2	9	214.39	28.40	3.37	0.00	1242.19	5928
3	2	11	204.26	29.57	3.02	0.00	1571.15	5928

6.b. March 1989.

Nest #	Day #	Time of day	#ants /10min	Temp. (°C)	Wind km/hr	Rain (mm)	Light (μe)	Nest Pop.
1	1	11	200.00	26.14	1.71	0.00	442.86	5413
1	1	13	228.40	28.50	2.62	0.00	630.21	5413
1	1	15	202.37	28.85	1.80	0.00	1261.46	5413
1	1	17	219.55	27.54	2.17	0.00	583.15	5413
1	1	19	258.13	24.91	0.25	0.00	25.23	5413
1	1	21	151.03	24.22	0.00	0.00	0.01	5413
1	1	23	118.04	23.91	0.00	0.00	0.01	5413
1	1	1	93.60	23.63	0.00	0.00	0.01	5413
1	1	3	48.05	23.36	0.00	0.00	0.01	5413
1	1	5	59.88	23.12	0.00	0.00	0.51	5413
1	1	7	50.51	23.88	0.00	0.02	119.56	5413
1	1	9	196.02	25.48	0.00	0.00	298.15	5413
1	2	11	300.21	28.71	1.19	0.00	803.13	5413
1	2	13	283.33	30.60	2.83	0.00	714.58	5413
1	2	15	263.07	29.99	1.41	0.00	1261.46	5413
1	2	17	291.05	28.53	2.14	0.00	583.17	5413
1	2	19	340.33	25.45	0.27	0.00	25.59	5413
1	2	21	221.19	24.64	0.00	0.00	0.01	5413
1	2	23	138.94	24.21	0.00	0.00	0.01	5413
1	2	1	121.77	23.82	0.00	0.00	0.01	5413
1	2	3	100.41	23.47	0.00	0.00	0.01	5413
1	2	5	129.94	23.11	0.00	0.00	0.64	5413
1	2	7	216.36	23.92	0.00	0.00	316.88	5413
1	2	9	280.93	27.11	0.33	0.00	1082.22	5413
2	1	11	83.34	27.85	0.97	0.47	425.19	3551
2	1	13	126.09	29.30	2.18	0.02	467.49	3551
2	1	15	129.40	28.19	1.68	0.00	270.39	3551
2	1	17	157.95	26.69	0.74	0.00	122.27	3551
2	1	19	209.65	25.24	0.04	0.00	8.47	3551
2	1	21	249.34	24.38	0.00	0.00	0.01	3551
2	1	23	19.44	23.79	0.00	0.54	0.01	3551
2	1	1	7.36	23.29	0.00	0.00	0.01	3551
2	1	3	2.90	22.75	0.00	0.48	0.01	3551
2	1	5	2.90	22.02	0.00	0.32	0.32	3551
2	1	7	19.51	22.57	0.01	0.35	76.35	3551
2	1	9	31.19	25.06	0.39	0.22	210.42	3551
2	2	13	87.39	28.62	1.40	0.31	550.70	3551
2	2	15	131.76	29.35	2.05	0.00	743.75	3551
2	2	17	161.86	27.85	1.51	0.02	272.32	3551
2	2	19	163.35	25.32	0.28	0.00	18.52	3551
2	2	21	175.23	24.61	0.00	0.00	0.01	3551
2	2	23	161.69	24.15	0.00	0.00	0.01	3551
2	2	1	121.28	23.70	0.00	0.00	0.01	3551
2	2	3	79.58	23.28	0.00	0.00	0.01	3551
2	2	5	23.35	22.82	0.00	0.12	0.64	3551
2	2	7	51.37	23.23	0.13	0.00	80.63	3551
2	2	9	118.19	25.13	0.45	0.02	265.00	3551
2	2	11	122.78	27.20	0.81	0.00	470.32	3551

Appendix B. BASIC program used in section 6.3.2 to simulate foraging dynamics using observed inward and outward flow rates from a nest in December 1988.

```
 5 rem Outward ant flow/10 minutes recorded each hour from 0100 to 2400
10 DATA 208,167,126,121,116,169,222,220,218,182,146,118
20 DATA 90,158,226,194,162,168,174,205,236,201,166,187
15 rem Outward ant flow/10 minutes recorded each hour from 0100 to 2400
30 DATA 232,194,156,156,156,178,200,195,190,143,96,81
40 DATA 66,126,186,164,142,154,166,190,214,207,200,216
50 rem Initialize arrays: A contains 500 foragers
60 DIM A(500), LEAVE(23), RET(23), T(500), D(500):OPTION BASE 0
65 rem Start all foragers inside nest
70 FOR I=1 TO 500
80 A(I)=1:NEXT I
85 rem Input observed inward and outward flow rates
90 FOR I=0 TO 23
100 READ LEAVE(I):NEXT I
110 FOR I=0 TO 23
120 READ RET(I):NEXT I
130 PRINT"     HR     P(out)   P(in)    nest  forager   in flow  out
flow   trip length",
140 rem Run simulation for J hours
145 FOR J=1 TO 150
150 TRIP=0:R=0:L=0:IN=0:OUTS=0
160 HR=HR+1:H=HR-(INT(HR/24)*24)
165 rem Calculate probabilities of leaving (PL) and returning (PR)
170 PL=0.67*LEAVE(H)/RET(H)
180 PR=0.67*RET(H)/LEAVE(H)
185 rem Check status of each ant, and branch to appropriate subroutine
186 rem Ant inside nest = 1, ant outside nest = 0
190 FOR I=1 TO 500
200 IF A(I)=1 THEN GOSUB 290 ELSE GOSUB 340
210 NEXT I
215 rem Calculate average trip length (AVTRIP)
220 IF R>0 THEN AVTRIP=TRIP/R
225 rem Count numbers of ants inside (IN) and outside (OUT) nest
230 FOR I=1 TO 500
240 IF A(I)=0 THEN OUTS=OUTS+1 ELSE IN=IN+1
250 NEXT I
260 PRINT USING "######.##"; HR,PL,PR,IN,OUTS,L,R,AVTRIP
280 NEXT J
282 END
285 rem Test if ant A(I) leaves nest
290 IF RND>PL THEN GOTO 320
300 D(I)=HR:L=L+1
310 A(I)=0
320 RETURN
330 rem Test if ant A(I) returns to nest
340 IF RND>PR THEN GOTO 390
350 T(I)=HR-D(I)
360 A(I)=1
370 TRIP=TRIP+T(I)
380 R=R+1
390 RETURN
```