Ant Research 1954 – 1976

Institute of Terrestrial Ecology

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The Institute of Terrestrial Ecology (*ITE*) was established in 1973, from the former Nature Conservancy's research stations and staff, joined later by the Institute of Tree Biology and the Culture Centre of Algae and Protozoa. ITE contributes to and draws upon the collective knowledge of the fourteen sister institutes which make up the *Natural Environment Research Council*, spanning all the environmental sciences.

The Institute studies the factors determining the structure, composition and processes of land and freshwater systems, and of individual plant and animal species. It is developing a sounder scientific basis for predicting and modelling environmental trends arising from natural or man-made change. The results of this research are available to those responsible for the protection, management and wise use of our natural resources.

Nearly half of ITE's work is research commissioned by customers, such as the Nature Conservancy Council who require information for wildlife conservation, the Forestry Commission and the Department of the Environment. The remainder is fundamental research supported by NERC.

ITE'S expertise is widely used by international organisations in overseas projects and programmes of research.

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This leaflet is one of a series describing research which is currently being done by the Institute of Terrestrial Ecology (ITE), a component body of the Natural Environment Research Council. Each leaflet describes a particular aspect of ITE's research and indicates the nature of the problem, the methods used in the research, and possible practical applications of the results.

Introduction

Social insects, as representatives of a highly evolved and successful terrestrial group of animals, can be expected to offer interesting answers to a number of ecological problems. Ants as soil insects are widely and densely distributed even in temperate regions of the globe, especially where human interference is light, and there is no doubt at all that they play an important part in maintaining soil fertility (Plates 1 & 2). Heath in southern England has always been highly prized for its amenity value, its aesthetic properties and, not least, by naturalists, for its rich variety of plants and animals. Hence the establishment of the Furzebrook Research Station by the Nature Conservancy in 1954 and the initiation of a programme of research on ant populations which continues today under the Institute of Terrestrial Ecology of the Natural Environment Research Council. Apart from the obvious contribution that this work has made to heathland management, there have been a number of less expected applications. Two can be mentioned: first, that the basic knowledge of the colony of *Myrmica* has proved of great value to research on the life cycle and conservation of the large blue butterfly, and, second, that the same basic knowledge has contributed greatly to the study of ant populations in the tropics where they affect agricultural practice in many ways. In these warm parts of the world, whether wet or dry, ants (and termites) occur in amazing density and complexity and members of our project group have contributed to production studies culminating in an International Biological Programme Synthesis Volume (IBP Synthesis, Volume No. 13, Production Ecology of Ants and Termites, Ed. M V Brian).

Work at Furzebrook has two facets. One is a study of the species of ant that live in heathland; the distribution and density, the turnover and the factors which influence this. The

Plate 1. A more distant view of the mounds of Lasius flavus *in the same areas as Plate 10. Many pastures have substantial populations of this species yet show no mounds at all.*

Plate 2. Ant hills made by the yellow ant Lasius flavus *in old chalk pasture in Dorset where there is no ploughing or severe agricultural disturbance. These ant hills grow to considerable sizes (the one in the foreground is a metre at its base) and attain high densities. There is no doubt that these ants are important soil insects and have a considerable influence on the grassland that they inhabit, but a full study of this has never been made.*

other is the study of the social organisation of a relatively simple genus with species that range over many habitats. Combined, these two approaches cover a field that is ecological, sociological and physiological. In the account which follows, it has not been possible to describe the work in all its aspects and so three important parts have been selected for full treatment and the rest listed.

The Pattern of Species in Heathland

Two years after fire

A grid of sample sites was established on an 8 hectare area of heath in Hartland Moor NNR. The area chosen was suitably varied: wet bog with a dry knoll in the middle. The time chosen was also convenient, for the whole area had been burnt two years earlier and was showing signs of recovery (Plate 3). At each site, a number of measurements were made

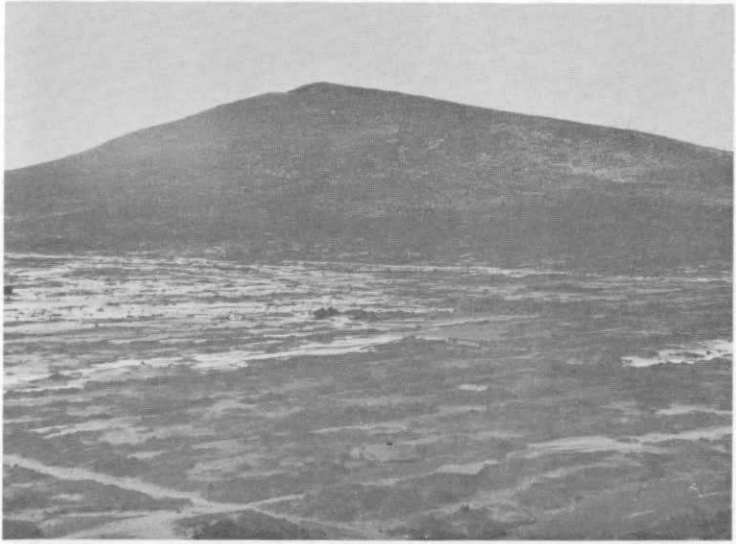

Plate 3. A photograph of the study area after the fire in September 1976. This photograph was taken in March. Notice the erosion caused by heavy rainwash, leading to the deposition of sand in the lower parts. In dry weather, both sand and ash blow from the exposed hillside into the lower, wetter regions. In the mid-line of the photograph, a series of tiles used, when the vegetation is lush and thick, to attract ants for nesting, can be seen beginning in the foreground and going up the hill into the distance.

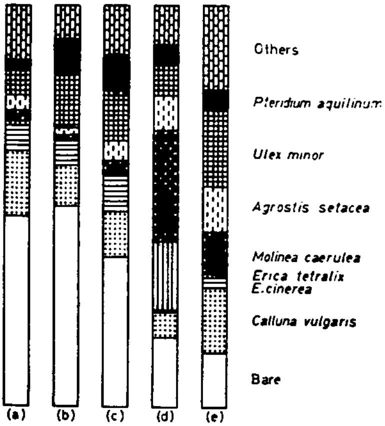

Figure 1. The proportions, bare and variously vegetated in the areas inhabited by ants and in those uninhabited. (a) No ants; (b) Lasius alienus; *(c)* Tetramorium caespitum; *(d)* Lasius niger; *(e)* Formica fusca.

with the aim of getting a description of the ant, plant (Figure 1) and soil variation. Ants were attracted to sugar lump baits in tins; plants were assessed in a metre diameter circle in terms of species and the area they covered; soil characteristics were measured as moisture, organic matter and integrated temperature of a month in June and July. The altitude of each sample point was also surveyed (Figure 2). As is usual in this sort of data, most of the variables turned out to be highly correlated, either positively or negatively, and, to simplify interpretation, three 'natural' groups were established using principle component analysis (Figure 3). The first of these groups (I) accounted for 73% of the variation in the data collected and was of supreme importance. It represented a combination of moderately high, dry, sandy warm soil, only half of which was vegetated. The plants in the main were *Erica cinerea* (bell heather) and *Ulex minor* (dwarf gorse). In short, this association is one that all naturalists recognise as 'warm dry heath' and is the sort of habitat which is known to attract ants in cool climates such as we experience in England. On this component or vector, starting at the warm dry end and going towards the cold wet end, the four ant species were strung out as follows:

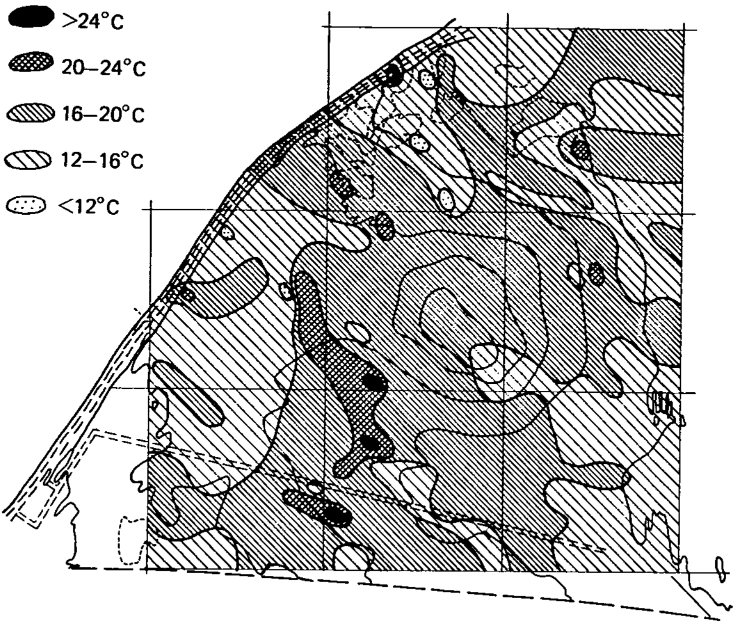

Figure 2 A map of the heathland area studied, with contours for height above sea level in metres; the July temperature distribution as obtained by integrating for the whole month just below the soil surface is also shown.

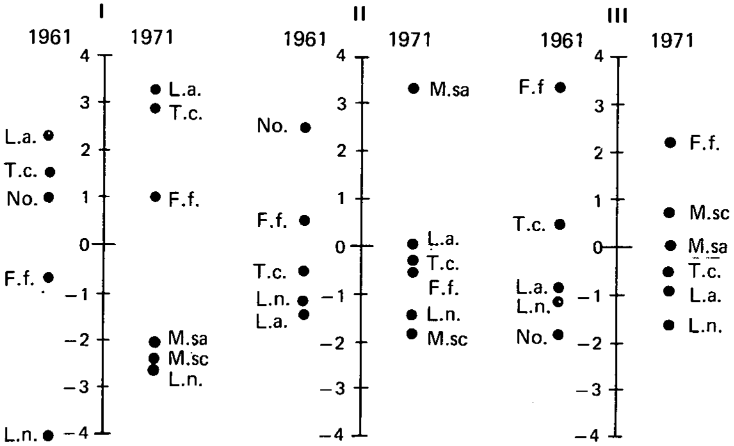

Figure 3. Species positions for the first three components (as deviations from the mean) of a principle component analysis of habitat factors for 1961 and 1971. L.a., Lasius alienus; *T.c.,* Tetramorium caespitum; *F.f.,* Formica fusca; *L.n.,* Lasius niger; *M.sa.,* Myrmica sabuleti; *M.sc.,* M. scabrinodis; *No, no ants.*

Lasius alienus (a continental formicine), *Tetramorium caespitum* (a continental myrmicine), 'no-ants', *Formica fusca* (an English formicine) and *Lasius niger* (a boreal formicine). Thus, there is an obvious relation between their position in the array which represents their sub-habitat on Hartland Moor and their geographical distribution. The other two groups (II and III) were less important and comprised only 13% and 12% of the variation respectively). The first of these represented a sub-habitat dominated by quite dense *Calluna vulgaris* (ling) in which 'no-ants' preponderated. The third represented a well vegetated, quite warm, grass/gorse sub-habitat, in which *Formica fusca*, a scrub climbing ant, stood out in contrast to the rest of the species.

Twelve years after fire

Ten years later the same points were resampled. The altitudes were exactly the same as before (fortunately!) but the degree of cover by plants was much greater everywhere and the proportion of ling in this vegetation had increased substantially. Every one of the baits attracted ants and there were more uncommon species such as *Tapinoma erraticum* from southern Europe. Nevertheless, the first group of variables still described the same type of habitat namely, warm dry heath, though this time it accounted for only 54% of the variability. The ant species again formed the same array in relation to the vector. Group II comprised 26% of the dispersion and represented a high level *Agrostis setacea/ Erica cinerea* community that had evidently established itself out of a zone undifferentiated in the earlier survey. It was outstanding for the high incidence of the ant *Myrmica sabuleti* a grassland species *par excellence*. The third component (with 13% of the variability) again represented scrub with *Ulex minor* and the ants were again in the same order in relation to it, headed by the scrub-foraging *Formica fusca*.

At the end of the 10-year period, only one species was actually less common than it had been before: *Lasius alienus*. This ant inhabits very open vegetation and cuts galleries below bare soil and it is not surprising that the growth of the heath plants has in general been so detrimental. It is obviously adapted to the early stages after a burn. Its place was taken by *Tetramorium caespitum*, an ant that also took over most of the 'no-ant' points of the earlier census and was clearly expanding its range as the plants regenerated. It can build nests of soil in vegetation and so reach the warmth of the sun and it depends on a seed-crop collected in autumn, stored over-winter and eaten in spring.

A closer examination of the points which changed species from *Lasius* to *Tetramorium* show that, in habitat characteristics, they were not different from those that *Lasius* retained. There is thus no evidence of habitat difference between these species, but it is clear that they are adapted to opposite ends of the sequence of post-fire habitat restoration.

In addition to these surveys, the general habits of the main species were studied in considerable detail. The most important characteristics are: the food they eat, where they forage for it (usually foraging is strikingly stratified); how they make their nest and whether they can adapt it to encroaching vegetation; how they defend their nest and their foraging area against other species of ant and other colonies of the same species; and, finally, how they reproduce, including the time of year at which they produce sexuals, and, especially, whether the young queens are able to select their habitat to any degree.

The coexistence of two species of Lasius

Only one example of the way species properties and behaviour influence distribution can be given. This concerns the pair of *Lasius* species: *L. alienus* and *L. niger*. Already it has been stated that the former has a more southerly geographical range than the latter. It is a species with small, brownish workers, that lack hairs rather than of large, black workers, that are covered with them; to the casual observer they appear to be livelier and more excitable. In the heath, *alienus* lives in warmer, drier, less vegetated, zones than *niger* which is found in cool wet dense vegetation; they are in fact at opposite ends of the first component. *Alienus* lives under the soil in an anastomosing set of galleries with shafts to the surface every few decimetres through which it throws its excavated soil and makes characteristic craters. *Niger* lives in grass tussocks and clumps of heath that protrude above the water table; its excavated soil is put in one heap into which it may later tunnel and so make a single mound nest. *Niger* also tries, with little success, to make covered foraging routes.

By living underground in bare areas, *alienus* can get the warmth it needs whilst avoiding the desiccation of dry wind and fierce sunlight (against which its pale brown pigment is useless). *Niger* by living above the surface and having a black hairy body can exploit the cool wet zones and resist such sunlight as filters through the vegetation cover; it can build up out of the water into the sunlight. Thus, the two are totally opposed in their adaptations: one is designed to live below and one above the soil surface. Food differences appear to be incidental for they both hunt for small prey. Whilst *alienus* catches centipedes and beetle larvae below ground, *niger* catches flies and bugs and spiders above. Both also culture aphids: *alienus* on shrubs of birch and dwarf gorse stems that it covers with soil, *niger* on the leaves and stems of various shrubs.

Studies of settling queens have shown that they too can detect these habitat differences, though what cues they use is a mystery. *Alienus* which flies in September and October may seek warm areas; *niger* which flies in July and August may seek moist areas. Yet we may be underestimating them; both may have more subtle ways of assessing a situation. The fact that the former flies late is probably an adaptation to southerly regions which often get rain in September after a hot dry summer. If the weather is bad in this country, the sexuals never leave the nest and are massacred.

In spite of the general difference in distribution, these two species do occasionally meet in heathland. *Niger* are then extremely hostile and collect round the exit holes of *alienus* galleries, attempting to grab any of their workers that come within range but not, it seems, venturing down the galleries too much. In this way, they stop *alienus* climbing bracken fronds to the extrafloral nectaries and going up birch shrubs to aphid clusters. They effectively hold them underground and accentuate the clear tendency to stratification. There is no doubt that these two *Lasius* species would meet more often were it not for the myrmicine ant *Tetramorium caespitum* which frequently inhabits a zone between them. At this moment, research is in progress into the extent to which these micro-distributions are in fact determined by competition.

The relation between two sub-families

One point of interest arose out of the survey. Each of the two major sub-families of ant (the Formicinae and the Myrmicinae) contributed one species to each of five reasonably distinct sub-habitats: dry heath, bog, grass heath, scrub and wood. The formicine species corresponding to these places were, in the same order: *Lasius alienus, L. niger, L. flavus, Formica fusca* and *F. rufa.* The myrmicines were: *Tetramorium caespitum, Myrmica scabrinodis, M. sabuleti, M. ruginodis,* and once more *M. ruginodis,* for the Myrmicinae do not have a Wood ant as distinct from a scrub ant. So, twice in the course of ant evolution, species have radiated into these sub-habitats. It is more difficult to see how two species co-exist in each sub-habitat, but it probably arises most often from a difference in colony size. Thus, all the *Myrmica* species have small colonies that range short distances for food, whereas both the *Lasius* and *Formica* species have large colonies with big feeding areas around each. This obviously does not explain the co-existence in dry heath of *Tetramorium caespitum* and *Lasius alienus* both of which have large highly organised colonies, but there are food differences (the former eats a lot of seeds) and differences in mound building capability which adapt them to different stages in post-fire regeneration. Differences in colony size and area foraged between species mean that some will fit into the 'coarsely-grained' parts of a habitat whilst others will fit into the more finely-grained areas. Even in predominantly coarse habitats, the larger colonies, because they are more highly organised will of necessity take up the major parts, whilst the smaller colonies occupy interstitial zones.

The Population Dynamics of *Tetramorium*

The territory system

Though this species is really at home on the continent, it is able to establish substantial colonies in warm areas near the southern coasts of England. In Dorset heathland, it inhabits places that are not too high to catch the wind and not too low to be waterlogged and where the vegtation is diverse and productive. It has well-marked feeding territories that are defended against other species and other colonies of the same species (Figure 4). This is achieved by building an underground network of permanent galleries with surface access shafts liberally distributed along them and by having an effective system of communication and mobilisation. Though only a small individual weighing less than 4 mg, it is able to defend areas of 44 m^2 (average) or 81 m^2 (maximum) (Plate 4). In these areas, on average, there are 11,000 workers, one queen and much brood (all sorts in summer, but only larvae in winter). There are thus 250 workers/m^2, with a rapid system of recruiting help if food or enemies are in the neighbourhood. Altogether a very effective presence!

The consumption of heather

To compare these ants with the heath vegetation that sustains them we have to think in terms of weight or energy-content. So, an average colony weighs 6.51 g and there are 1.5 kg/ha. A ten-year stand of heath vegetation (shoots only) can weigh 1×10^4 kg/ha (Chapman *et al* 1976). *Tetramorium* is thus 0.15 thousandths (0.15×10^{-3}) of the heather system by weight. The production of the two can also be compared. First that of the ant: it has to produce sufficient new ants each year to replace workers that die. Our best estimates are that this necessitates total replacement each year. Apart from the workers most colonies must produce sexuals to fill in any

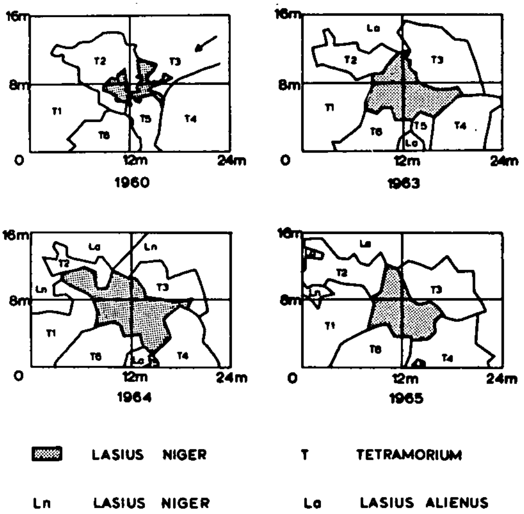

Figure 4. The territorial boundaries of a colony of Lasius niger *in four years (three of them successive). It has boundaries with several* Tetramorium *nests and a* Lasius alienus *area. T,* Tetramorium; *La,* Lasius alienus; *Ln,* L. niger. *Scale of distance in metres.*

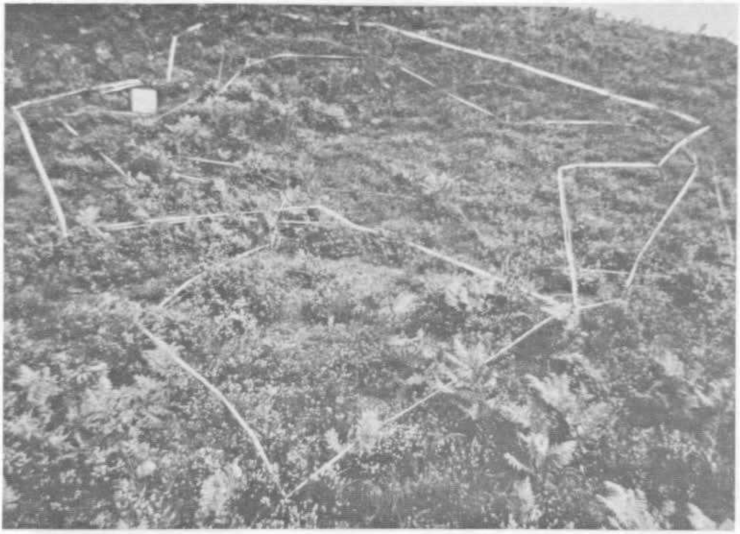

Plate 4. A territory of Tetramorium caespitum *outlined with tapes. The tile in the top left corner is 25 centimetres square and contains part of the brood system underneath it. This same colony was surveyed in several successive years, and the different tapes show that the territories change slightly from year to year, but not much.*

gaps due to the death of queens and to send out young queens in search of new terrain for colonisation. Data collected from fixed colonies over many years have provided the following estimate of production by *Tetramorium:* 0.26 g/m^2 or 2.6 kg/ha per annum. These are not big figures when compared with primary production by *Calluna* shoots: 250 g/m^2 in a 10-year post-fire heath (Chapman *et al* 1976). Though this is only one thousandth of primary production, it is about seven times the ratio ant/plant by weight: clearly *Tetramorium* is a relatively productive creature. Looked at in another way its ratio of production/colony-mass is 11.2/6.5 = 1.7, that is, each colony is capable of nearly doubling its own weight each year (this includes sexuals, almost all of which are emitted and dispersed).

There is one more point that can be made about production. The staple diet of this species is heath-plant seeds; both heathers and grasses are eaten (Plate 5), but the main seed-producer is ling (Plate 6). One year we calculated, from samples, that 241 g of seed (wet weight) was produced in the territory of an average colony. This is ample for conversion

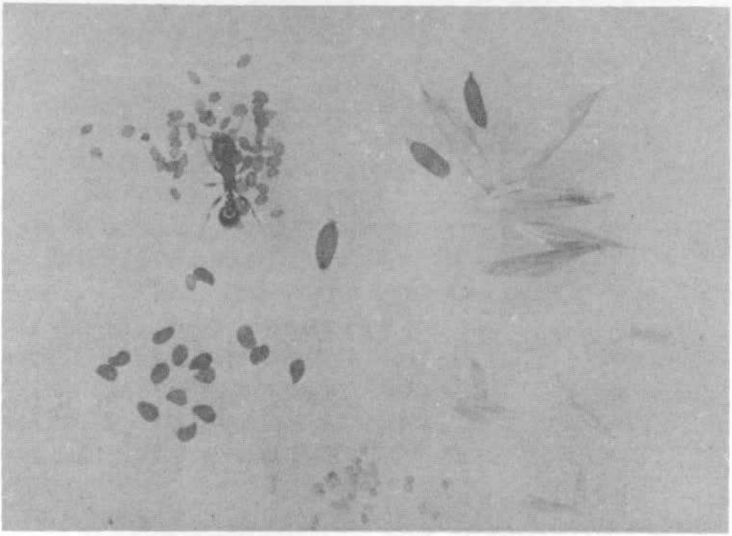

Plate 5. Some of the seeds that Tetramorium caespitum *eat, and a worker shown for comparison. The small seeds are those of ling, the larger ones those of bell heather* (Erica cinerea) *and the longer seeds* (*on the left*) *are those of a grass* (Agrostis setacea).

Plate 6. This photograph shows an excavation of a Tetramorium caespitum *nest in winter. Some of the galleries have been powdered with french chalk and show white against the dark soil. Others contain accumulations of pale brown seeds of ling. This is only the central part of one colony. The axe-handle is 30 cm long.*

into 11.2 g of new ant matter. The ratio of one to the other 11.2/241 or 4.6% is the food chain production efficiency.

Trends in production

To obtain all these data it was necessary to make a number of measurements on a set of about 30 colonies, lasting over a period of some eight years. Each year the number and weight of sexuals produced was estimated by collecting from wild nests in June as they ripen. The worker population of each colony was estimated by marking a sample with radio-active phosphorus and then doing a mark-recapture or Petersen index estimation. The territory area was obtained by dosing a colony with syrup containing radioactive phosphorus and then, a week or so later, finding by resampling how far it had spread (Plate 7). To get the size or mass of a colony, the weights and headwidths of a sample of workers were measured. It was then found that production was not steady: though it varied a good deal there was a trend of increase along with the regeneration of the biome after the fire. The

Plate 7. Using a Geiger-Muller probe to search for ants containing radioactive phosphorus and so obtain the area of dispersal or territory, of a colony of Tetramorium caespitum, *that had been fed this substance in a bait some days earlier.*

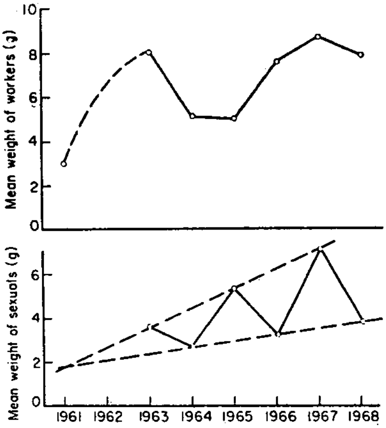

Figure 5. The mean weights of workers and sexuals from about 25 colonies of Tetramorium caespitum *L., for the period 1961–1968. It is suggested that sexual production has a 2-year periodicity; the dotted lines show the trends of increase for both high and low sexual production years.*

sexual component of production also showed a strong 2-year cycle, as though sexual-formation one year blocked sexual-formation the next (Figure 5). Apart from the upward trend in production, there were other interesting trends. The area foraged and defended, as well as its perimeter and the average size of workers, all increased. One can visualise the colonies of *Tetramorium* pushing out into the empty spaces left by the fire, as well as into areas inhabitated by *Lasius alienus* which they would destroy and eat. The resulting improvement in food supply would have enabled the formation of bigger workers that were better able to maintain these huge territories and, in turn, push them even further out from the base nest.

In accord with this initial expansion of colonies is the fact that, in the early post-fire years, territory and area had a profound effect on production: it clearly represented, at first, in the sparsely vegetated period of re-growth, the food supply of the colony. Later, its importance declined and the mass of workers in the colony replaced it as the vital factor governing production. This is easy to understand, for, as the heath shrubs grew and their seed production increased, food supply would be more than adequate and would include, of course, many insects that fed on the increasing amounts of plant

litter. The limiting factor to growth would then be the ability of a colony to gather food in and store it, hence the vital relevance of colony mass, for, the more and the bigger the workers, the more effective is the collecting power of a colony. In these circumstances, *Tetramorium* comes into line with a more primitive myrmicine species that does not defend external territories: *Myrmica sabuleti*. This lives in the grass heath sub-habitat, and studies over several years showed that its production was closely governed by the colony mass.
The biomass (colony mass/territory area) was calculated each year for each colony. The frequency distribution of the data was rather log-normal in form with a mode at 0.11–0.14 g/m^2 (Figure 6). Evidently there are a few colonies with a low biomass and a few with a very high one indeed, but most are below average (the mode less than the mean). Of great interest is the fact that the modal biomass was identical with the most productive biomass. It is difficult to see how much a regulation of density could arise other than by colonies expanding their territory only when they have the worker power to occupy it. If this hypothesis is accepted as plausible, it suggests that those with low biomass are young and those

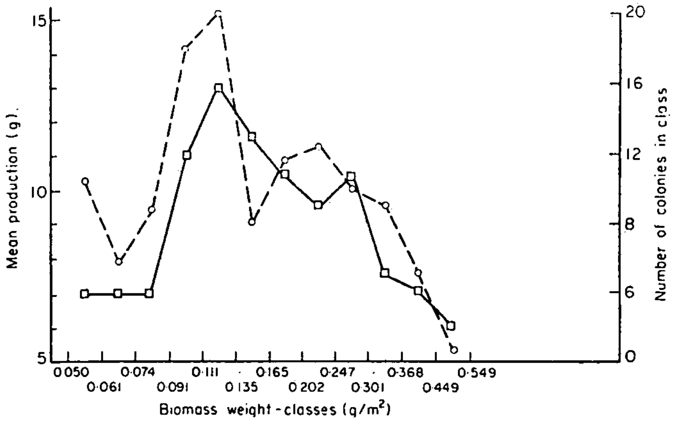

Figure 6. For equal log biomass classes ($\log_e g/m^2$) the number of colonies of Tetramorium caespitum *L.* (☐ *and continuous line) and the mean production of those colonies* (○ *and broken line) are plotted, using all the data for the years 1963–1967.*

with high biomass are older ones in the process of being compressed by competition with neighbouring colonies (or with other species).

The causes of mortality

A population study of a non-social insect would include a list showing the proportion of eggs that survive to each stage in the life history and the relative numbers eaten or otherwise destroyed by various predators and parasites. The number that die from accidents like wind, rain, trampling and so on would also be listed. The ant society exists to cushion these environmental hazards, and, in stable environments, not subject for example to erosion or to human interference, they are able to eliminate virtually all loss in the juvenile stages other than that caused by physiological defects e.g. lethal genes. In a lab study of the related species, *Myrmica rubra,* it was found that about 30% of eggs die from such causes. As the queen has to produce all the females and in some species the males as well (though, in many species, workers lay male-producing eggs), it is easy to calculate that the queen must lay about 16,000 eggs a year. These weigh about 800 mg and she weighs only 10 mg! Seventy per cent of these may form adults. All the males die the same summer; all the workers during the coming year; and any sexual females that do not manage to found a new colony or find a vacancy in an existing one will die during the winter. No quantitative analysis has been made of the incidence of mortality on workers after they have left the nest to forage. Risks from accidents and trampling and from predators such as spiders, beetles and birds are then quite high, though many birds and reptiles avoid eating ants. (This presumably is because they taste nasty and is the basis of much successful mimicry). In the end, if they avoid a violent death, they must senesce and die outside the nest, where they are soon scavenged or broken up by soil micro-organisms.

The sexuals are much the most vulnerable caste, especially during the nuptial flight. Most ants use a mass-exodus strategy for these flights. After leaving their pupal skin, the females, but not the males, build up their body reserves (Peakin 1972). Over wide areas, they then respond to a particular kind of weather and leave the nest at a particular time of day that varies from species to species and is quite characteristic. Synchrony of this sort attracts vast flocks of bird predators that normally feed in totally different places and ways. In spite of this, many ants escape destruction, and, after insemination, land to found a new colony or enter an old one. This survival depends on being able to find a refuge in the soil quickly; where conditions are bad, or where sites are already occupied by other ants, they must prolong their search, whilst all the time being in danger from many different types of ground predator. Other ants, with colonies already well established, are likely to encounter many of the survivors and destroy them. All these mortality factors are density-dependent. The species not only saturate the area of origin, but send an unknown number for emigration into new re-created ant habitats (such as freshly-felled woodland and new gardens). Even in fully occupied areas, old queens must be replaced every few years, but we have no figures for queen longevity in natural colonies. We are uncertain too whether they are replaced *in situ* by daughter queens or whether queens from other colonies are accepted, as for example in cases of complete queenlessness.

The Organisation of an Ant Society

A detailed examination of the organisation and growth of a colony under controlled laboratory conditions was designed to complement the field study just described (it also gave us work in winter). *Myrmica rubra,* a simple ant that hunts for prey in grassland, was chosen rather than the advanced *Tetramorium*. It is easily cultured indoors, its workers are large enough to manipulate, and its colonies are small and multi-queened, so that the viable ones can be collected without much difficulty.

The growth and development of a colony

Work has centred on the way colonies grow and develop, that is change in population composition. Eventually they reach a point where they begin to form sexuals, suitably called 'maturity'. In ants, the sex ratio is wholly under environmental and social control; it depends on whether an egg is fertilised by a sperm (giving a female) or not (giving a male). The release of sperm, which is stored for a whole life-time in a pouch near the exit of the queen's egg tube is responsive both to the season and to the state of the colony in many ants. In others, workers lay unfertilised male-producing eggs (they are never given sperm) and the queens lay fertilised female-producing ones. In such cases, the queens have control over whether and when, the workers do this (Plate 8). The queens also have a great influence on whether female larvae become workers or replacement queens. Hence, the analysis of development has involved an intensive study of the nature of the queen regulatory mechanism, as well as an examination of the susceptibility of the various life history stages (from egg to adult) to modification by social circumstances.

First, the development of a colony must be briefly described. A group of queens meet and excavate a cell in soil. They seal themselves in and lay eggs made from their fat body and their wing muscles. These eventually give young larvae which are fed on other eggs, and, in due course, mature into new workers. The first workers are always small, and, in this species, cause no hostility between queens (as they do in some species). They forage and the improved fresh food fosters growth and more broods of bigger workers. In this way,

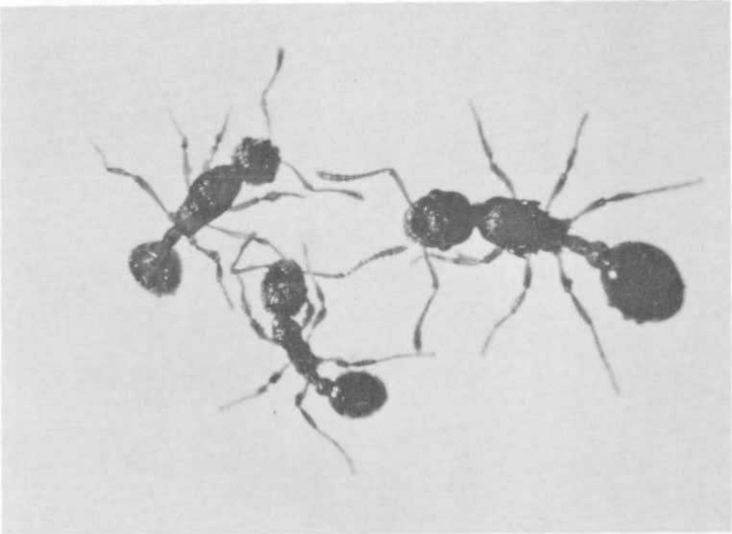

Plate 8. Three adult Myrmica rubra*; on right, a normal queen; on left, a microgyne; at lower centre, a worker.*

the young colony explores and exploits the food resources around it, going further and further afield as the workers get bigger and bigger. There is a limit to this as food gets costlier (in energy of transport) the further it has to be carried, for all food is taken into the central nucleus for processing. Moreover, redundant exploration must increase as forager density increases and return per worker inevitably diminishes.

Evidence collected by laboratory experiment suggests that, in fact, the colony ceases to grow and produce sexuals before this stage is reached. The cause of 'failure' is internal and to do with the capacities of the queens themselves: not only do they age, but, even at their best, their fecundity is limited. Fecundity, of course, improves with the size of worker force and hence of the food, but as few as 20 or at most 40 workers per queen can maximise her egg output, whereas, in natural colonies, the average member of workers per queen is, according to Elmes (1973), 75 (of course, fewer workers are needed under lab conditions where food is placed near the group). Thus, it is quite likely that, well before the collection of food resources becomes too costly; surplus worker power is diverted to the production of sexuals and thence, at least potentially, to colony division and dispersal. However, all our results point to the fact that queens exercise a strong, though not absolute, control over sexual production even when worker/larva and worker/queen ratios are high. They act as a valve that restrains sexual production and accumulates colony strength, rather than allowing it to dribble away; then it is released in a massive burst of sexual production. As already discussed, this is a good way of avoiding heavy aerial predation; but it is also beneficial to the species, in that it encourages exogamy and long range dispersal.

Control over the caste of females

Consider first the control over female development (Plate 9). Eggs are not all equal; those laid by young queens have a greater tendency, on reaching the last larval instar, to commence metamorphosis into workers. This seems without doubt to be a device for enabling young queens to obtain the assistance of workers with a minimum delay. Moreover, eggs laid about three weeks after the start of the season are also more likely to metamorphose. This has less obvious advantage,

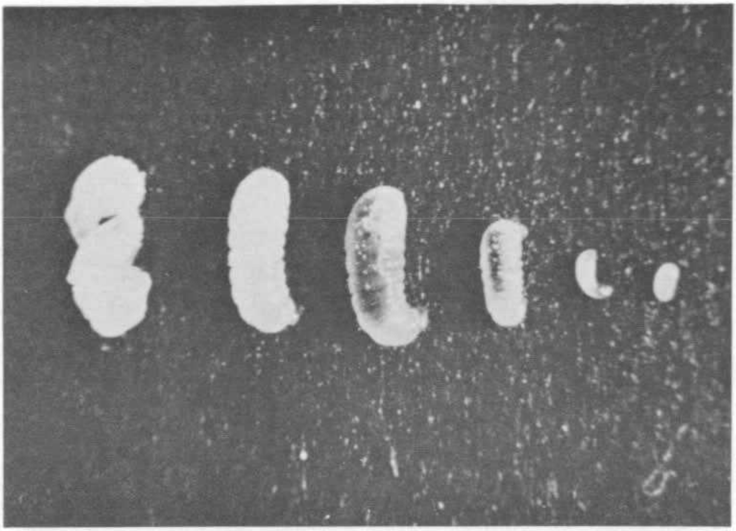

Plate 9. Stages in the life history of Myrmica. *Starting on the right hand side: egg, first-instar larva, two third-instar larvae, a pharate pupa and (left hand side) a pupa*

beyond helping all colonies to produce workers from eggs of the current season as well as from the hibernated larvae and so ensuring a quicker growth of the colony. In the last larval stage, there are also several crucial phases. The first one is when the larva is confronted with two alternative developmental paths: either to metamorphose into a worker or to grow slowly with very little development up to a limit when endocrine diapause overtakes it. Its tendency to metamorphose depends, as already stated, on its life as an egg in its mother queen, but also on how well it is fed as a larva; this in turn depends on whether it is brought up by spring workers or summer ones. The spring workers have just hibernated and they feed larvae energetically; moreover, they are extremely sensitive to queen stimulation and manage to cause more young larvae to metamophose if queens are present. Summer worker populations are composed largely of new workers that are disposed to feed themselves and build up their own stores as much as to feed larvae. They, in sharp contrast to spring workers, are quite insensitive to queen stimulation.

Larvae which hibernate below a certain size, namely the

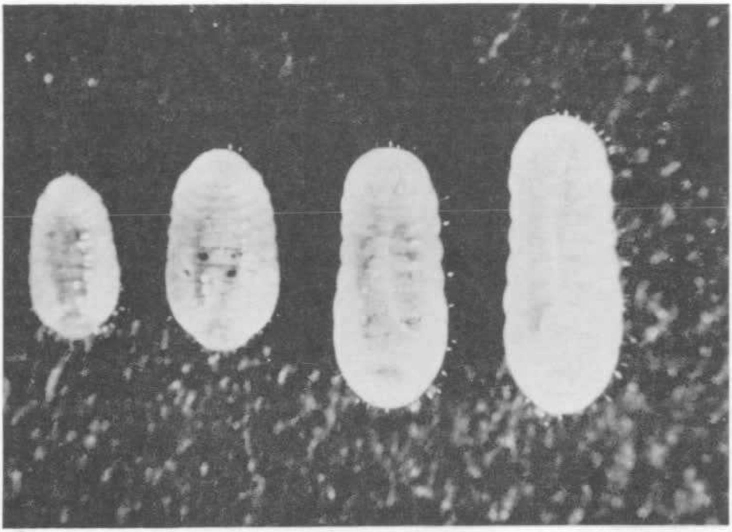

Plate 10. Two larvae on the left, cultured by workers with a queen; two larvae on the right cultured by workers without a queen. Notice the larger size of the latter and the absence of scars which workers inflict in the presence of a queen and which stimulate the metamorphosis of these larvae into workers.

threshold of metamorphosis into a worker, do not change during the cool winter, and, in spring, on encountering a revived and invigorated worker population, cross the threshold and grow into workers. Larvae that have passed the threshold before winter and that have reached diapause undergo a very important change during the cool weather. They acquire fresh growth potential and can be nourished by spring workers so that they grow to produce new large queens. This is however another point at which the influence of queens is brought to bear. Queens can reverse worker treatment so that, instead of giving the larvae priority over all others, they actually starve and attack them, feeding smaller larvae preferentially (Plate 10). Such 'slighting' prevents them becoming queens and they diverge hurriedly along a path ending in worker formation (Plate 11). Interestingly enough, the older queens that lay few worker-biased eggs are better at controlling worker brood rearing; they are not too old to suppress potential rivals very effectively. However, queens do vary in their ability to do this and there is plenty of evidence that, well before they die, their power attenuates and vanishes.

Control of male production

Now to consider male control. In *Myrmica*, workers produce the males, and queens have a very subtle way of blocking the

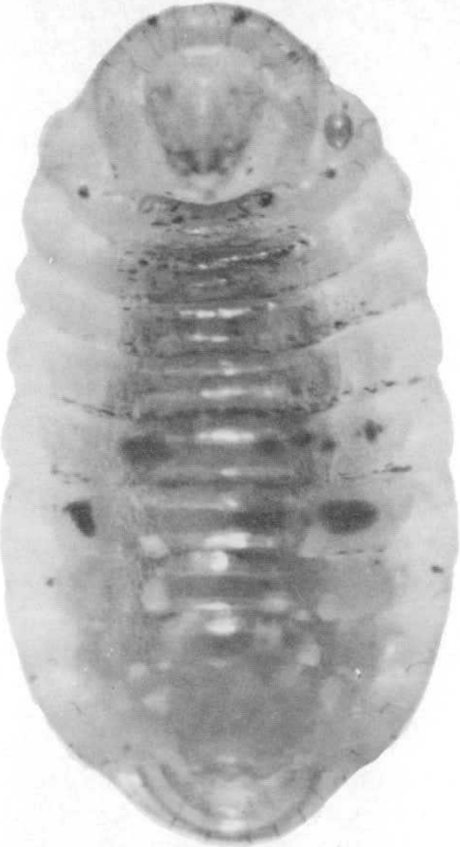

Plate 11. A larva of Myrmica rubra *which was capable of growing into a queen but has been cultured by workers with a queen of their own. As a result it has been both deprived of protein and attacked to such a degree that dark scars have formed on its surface. These two methods ensure that the larva grows very little and metamorphoses prematurely with the result that a worker instead of a queen is produced.*

formation of reproductive eggs by workers. Instead of inhibiting egg formation in the worker ovary, or of stopping oviposition so that the eggs are resorbed, queens do the exact opposite. They stimulate worker oviposition. The result is a premature or abortive egg which lacks a proper chorion and contains no germinal material. Such eggs are called 'trophic' as they make an invaluable encapsulated sterilised food store and contribute substantially to the diet of the queens and young larvae. In particular, the workers have the habit of adding these eggs to the eggs the queen lays so that a mixed cluster grows, composed of worker trophic and queen reproductive eggs. When the young female larvae hatch they are able, with very little movement, to discover a trophic egg, and to pierce and suck it. This gives them an excellent first meal and improves their chance of survival. As a result of this subtle intervention, the queen's progeny gain without she herself having to lay more eggs; her worker production is augmented whilst worker instigated male production is stopped.

The cessation of control

These controls over the growth of larvae of both sexes are used by the living inseminated queens during the growth of their colony. One may naturally now ask: 'How is this suppressive controlling effect switched off when the time becomes ripe for reproduction?' It could clearly arise as a result of dilution of the queen influence, but, to be quite sure, a short programme of research into how workers recognise their queens was initiated. It then transpired that the queen has no way of projecting her presence. Every worker must touch her periodically, for they cannot communicate information of this sort one to another. Such an arrangement might have been designed to ensure that a colony, as it grew and spread out into numerous chambers, diminished worker contact with the queens. An important point is that, even when, as is usually the case, there are several queens in the nest, they do not patrol and show themselves, but cluster tightly together near the egg mass. They thus occupy little more space than one queen alone. As control depends on mobility, it will be a function of worker density in the nest space; congestion has in fact been shown to reduce queen influence on metamorphosis.

Queens are effective in female control even if they are dead, as long as they are present in one piece with the head, thorax and abdomen correctly arranged. They must of course have been inseminated for virgin queens dead or alive have no control; copulation changes their behaviour and their scent. The effectiveness of queens can be destroyed by chemical extraction with lipid solvents, and it seems that the essential signal picked up by the workers is caused by a particular waxy material assisted by a specific body shape. For the inhibition of males, queens rely on a different and weaker signal. They must be laying eggs. In fact, the egg cluster that they produce by itself, effectively induces workers to lay trophic eggs. This may account for the fact that males are produced before queens in the growth of normal colonies; they appear soon after worker size has reached its maximum. Queens will stop laying before they die (so releasing male production) and die before they are ejected by the workers (so releasing queen production). More generally, their control over the nature of worker eggs is lighter than their control over the way workers nurse female larvae.

Other aspects of ant research

Facets of social insect research that have not been brought into this account for lack of space must simply be listed. They are:

(1) Worker activity measured by means of a specially designed electronic sensor.
(2) Digestive enzymes in workers and larvae of various species related to their food.
(3) The genetics of populations of *Myrmica* and the study of a polymorphism that is closely linked genetically with microgyne frequency.
(4) The recognition of larvae (both worker-forming and sexual-forming) by workers.
(6) The linkage of colony cycles with seasonal cycles.
(7) Male production and colony maturation in a *Myrmica* colony.
(8) The basis of colony discrimination in species of *Myrmica.*
(9) The function of juvenile hormone in caste determination.

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After Fire

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