Insectes Sociaux, Paris.
1978, Tome 25, n° 2, pp. 173-186.

CHANGES IN THE DISTRIBUTION OF THE NESTS OF *FORMICA RUFA* L. (HYMENOPTERA : FORMICIDAE) AT BLEAN WOODS NATIONAL NATURE RESERVE, KENT, DURING THE DECADE FOLLOWING COPPICING

By R. COLIN WELCH

Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, PE17 2LS, Cambs, England.

Reçu le 16 janvier 1977. Accepté le 30 avril 1977.

SUMMARY

The distribution of *Formica rufa* L. nests in 1.6 ha of neglected coppiced woodland in South-East England was mapped immediately after coppicing in 1965.

The fate of the original 29 nests was followed throughout the next 10 years. The stability of *F. rufa* nests in Britain is questioned.

The foundation of new daughter nests and the consequent development of polycaly is described and discussed.

The initial nest density was higher than that recorded from other localities. In the first two years after coppicing a rapid increase in the density of occupied nests was observed. This was followed by a steady decline until the density was 30 % lower than in 1965.

ZUSAMMENFASSUNG

Anderungen in der Verbreitung der Nester von *Formica rufa* L. (Hymenoptera : Formicidae) in Blean Woods National Nature Reserve, Kent, während des Jahrzehntes nach dem Abtrieb.

Die verbreitung der Nester von *Formica rufa* L. in einem 1,6 ha grossen vernachlässigten Niederwald So-Englands wurde unmittelbar nach dem Abtrieb im Jahre 1965 kartiert.

Während der nächsten 10 Jahre wurde das Schicksal der ursprünglich 29 Nester verfolgt. Die Beständigkeit von *F. rufa* — Nestern in Grossbritannien wird in Frage gestellt.

Die Gründung von neuen Tochterkolonien und die nachfolgende Entwicklung von Polykalie wird beschrieben ud diskutiert.

Die anfängliche Nesterdichte was höher als von anderen Lokalitäten angegeben. Während der ersten beiden Jahre nach dem Abtrieb wurde eine rasche Zunahme der Dichte der Nester beobachtet. Darauf folgte eien ständiger Rückgang, bis die Dichte 30 % niedriger lag als 1965.

INTRODUCTION

Although there is a wealth of literature on the species of wood ants comprising the *Formica rufa* group (COTTI, 1963) many aspects of their biology are still poorly known, in particular the method of nest formation and the prevalance of polygyny and polycaly in the various species. A population of *F. rufa* L. was studied in Blean Woods National Nature Reserve, Kent over a period of ten years with a view to gaining a better understanding of polycaly.

YARROW (1955), in discussing the distribution and biology of *F. rufa* comments, « The fascinating problem of colony founding in these ants is still very imperfectly understood and speculation based on very doubtful evidence has done little to assist ». « In what way and by what means new nests are begun, their number in any locality must be infinitesimal compared with the number of virgin females available as potential nest starters ». « The presence of large numbers of dealate females (100 or more is nothing unusual) together in isolated nests implies that some mated females must either return to the parent nest or never leave it, but it is very improbable that those which fly away ever find their way back ». He further adds « The peculiarly restricted distribution of nests in one small part of an apparently homogeneous area has brought forth the very plausible theory that some of these nests must be offshoots or branch nests of others and are populated by females and workers which have moved out from the parent nest, ... but that these branch nests arise in the way just described is not I think proven ».

However, ELTON (1932) had already witnessed the the splitting of a *F. rufa* nest into two subsidiary nests near Ringwood, Hants in April 1927. By September 1928 these had been abandoned in favour of the original nest site but in March 1929 the split was repeated and this time appeared permanent. This, and two other cases of nest splitting, was the direct result of some human interference, although JOSEPH (1958) describes two instances of a series of three small poorly formed nests adjacent to large established nests of *F. aquilonia* Yarrow in a birchwood in Strathspey, Inverness-shire. These, he concluded, had been formed by colonization from the larger nests. BÜTTNER (1971) observed the production of daughter nests in a colony of *F. polyctena* (Foerst.) in deciduous woodland in Germany and noted that this activity was greatly increased when the nest mounds were provided with a protective covering. HUGHES (1975) concluded that in North Wales *F. lugubris* Zett. was able to radiate into suitable habitats by budding, and had a capacity for quick and widespread colonization not shared by *F. rufa,* which appeared to be dependent on alate queens as a method of dispersion. KLIMETZEK (1970, 1972 and 1973), referring to five species of the *F. rufa* group in the south west Black Forest (of which *F. rufa* comprised between 48 % and 64 %) states that the location of nests was often changed by the abandonment of old nests and the construction of new ones. He observed

163 *F. rufa* nests in 1966, but within three years 119 nests had been abandoned and only 56 new nests formed to replace them, amounting to a 39 % decrease in total nest numbers.

The development of techniques for the introduction of wood ant colonies into forests, for the purpose of controlling defoliating insect pests, has resulted in increased interest in the *F. rufa* group in many European countries. Considerably more accurate field and experimental data are now available although much of it is concerned with *F. polyctena,* an undoubted polgynous polycalic species. In continental Europe *F. rufa* appears to have more varied habits. GÖSSWALD (1941) and ADLUNG (1966) distinguished between monocalic, monogynous nests and oligogynous colonies of up to 20 nests.

BETREM (1960) states that in England *F. rufa* is always polycalic, whereas in Germany it is mostly monocalic and only rarely oligocalic or polycalic. LANGE (1960) refers to monogynous colonies of *F. rufa* and OTTO (1968), in assessing the relative abundance of four species of the *F. rufa* group throughout the forests of West Germany, showed that the polygynous form of *F. rufa* was generally scarce. It only rarely attained 20 % of the total for all four species, and constituted less than 15 % of all *F. rufa.* Betrem *(loc. cit.)* quotes from other workers in Germany who have never found more than one queen in the monocalic colonies of *F. rufa.* ZAKHAROV (1974) has shown experimentally in Russia that when unequal development occurs within a single *F. rufa* nest the more powerful « colony » will form ancillary nests. Thus demonstrating the transition from an individual, monocalic form of nest existence to a polycalic or colonial form. Considerable confusion persists regarding monogyny and polygyny in *F. rufa* in Britain and the role of queens in the foundation of daughter nests. ZAKHAROV also refers to ancillary nests with no queen present as « forage buds » becoming « offshoots » when a queen is introduced.

F. rufa is widely distributed in England and Wales although it is mainly concentrated on well drained soils in southern England (BARRETT, 1968) and has often been known from a given locality for a considerable period. Of the localities recorded by NELMES (1938) a number have become extinct mainly as a result of urban development or clear felling and ploughing of woodland sites. Barrett has shown that, away from the areas of concentrated records, the incidence of extinction becomes significantly higher and he regards the chance of recolonization as remote. He further records a presumed extinction in 26 % of the 10 Km squares from which the species has been recorded. BARRETT does not discuss this beyond commenting that the disappearance of *F. rufa* from sites within the main areas « can usually be ascribed to increasing urban pressures », especially sites on London Clay, and he shows a 54 % extinction from all clay sites. In most cases where the wood persists, so does the *F. rufa* colony. This has been substantiated by BARRETT and FELTON (1965) in S. E. England and a survey which I carried out in East Anglia and the East Midlands during 1968. Although in both instances a number of new localities were found it is more likely that these had been previously overlooked or unrecorded than that

they represented a spread from known older sites. Indeed, thriving colonies now exist in some localities where *F. rufa* was recorded as extinct by Barrett. Clearly the species was either extremely localised and overlooked or, more likely, persisted at a very low density for a number of years.

Less cataclysmic changes may have resulted in the local extinction of *F. rufa*. SATCHELL and COLLINGWOOD (1955) suggest the decrease in the number of colonies near Windermere, in the Lake District, may be related to the invasion of disturbed woodland by *Pteridium aquilinum*, whilst BARRETT and FELTON record the sudden decline of a colony at Tubney Woods, Berkshire over a 7 year period correlated with the area becoming overgrown in places, although apparently suitable areas which remained were not colonised. *F. rufa* later became extinct at this site (BARRETT, *loc. cit.*). SATCHELL (1966) further postulates that where *F. rufa* is at the limit of its geographic range it is more susceptible to such pressures as increased habitat disturbance. Recently HUGHES *(loc. cit.)* has shown that over England and Wales there is a good quantitative and qualitative fit between the distribution of *F. rufa* and that of coppiced woodland. He adds that factors such as neglect of coppice and its conversion to plantation may also bring about a reduction in the range of *F. rufa*.

Some of the earliest records of *F. rufa* result from the quest by entomologists for myrmecophilous Coleoptera etc., and WALKER (1897) provides just such a record for Blean Woods, Kent. NELMES *(loc. cit.)* also records *F. rufa* as very numerous in Blean Woods between 1933 and 1938. Although it cannot be proven, there is strong circumstantial evidence for these records being from the same woodland block as that which now forms part of the Blean Woods National Nature Reserve.

SITE DESCRIPTION

Blean Woods National Nature Reserve lies to the west of Blean village three miles north-west of Canterbury in the parish of St. Cosmus and St. Damian in the Blean, East Kent. The work described below was done in an area referred to as Mincing Wood on the 1 : 25000 Ordnance Survey Sheet TR 16 (O.S./61 : 112609).

The experimental area occupies the western two thirds of Compartment 9. This consists of an area of 1.6 hectares bounded on the south by Middle Ride, in the west by the boundary fence of Grimshill Wood and along its northern margin by the line of the former Beech Ride. The eastern limit is a footpath running northwards from Middle Ride to meet Alder Ride in the north-east corner of the compartment.

The heavy London Clay forms a plateau which slopes gently to the north where the 76 metre contour runs parallel with, and just beyond, the compartment's northern boundary. WHEN SALE and ARCHIBALD (1960) laid out the Nature Conservancy's Working Plan for the reserve the area consisted of neglected mixed coppice, much of which was overgrown *Castanea sativa* coppice.

This, to a large extent, was almost certainly the result of earlier planting. The standard trees were mainly *Quercus petraea,* estimated to be about 25 years old and at a density of 100-125/ha.

In the winter of 1964/1965 the compartment was coppiced. All *Castanea* was cut and all other tree species left to provide future standards for the prescribed management to false high forest. In addition to the *Q. petraea* occasional *Fagus sylvatica, Sorbus torminalis, Betula pubescens, Ilex aquifolia* and *Malus sylvestris* were left. Many stools were left with several slender stems from which the best could be later singled. As a result the initial pole density was very high, being in excess of 300/ha. These poles were fairly evenly distributed but with a tendency to be less dense along the northern margin of the compartment. Most had weak crowns and cast little shadow. A number of large bushes of *Crataegus monogyna* and a few *Sarothamnus scoparius* were retained and clumps of *Ruscus aculeatus* persisted. The opening of what had been dense canopy woodland initiated a proliferation of herbaceous and shrubby species together with vigorous new growth the cut *Castanea* and *Corylus* stools. Seedlings and suckers of *S. torminalis* were also common throughout the area.

In the first years after coppicing a fairly dense mixed ground flora became established, of which the major constituents included *Anemone nemorosa, Hypericum pulchrum, Teucrium scorodonia, Asperula odorata, Euphorbia amygdaloides, Milium effusum, Luzula sylvatica* and *Holcus mollis. Lonicera periclymenum, Rubus* and *Rosa* spp. grew vigorously with the ensuing years so that by 1970 access to many parts of the compartment was very difficult. However, by 1973 the canopy formed by the regenerating coppice had closed sufficiently to begin to suppress the growth of bramble and briar.

METHODS

On 20 June 1965 J. C. FELTON visited Blean Woods and made a provisional map of the distribution of *Formica rufa* nests in and around the newly coppiced compartment 9. His initial map also included compartment 8 to the north (coppiced 1963-1964), compartment 5 to the east, and some marginal areas of compartment 10 in the south, both of which were well grown. FELTON selected the part of compartment 9 occupying the clay plateau and plotted the positions of 24 *F. rufa* nests. The two easternmost nests shown in figure 1 as nests 25 and 26 were noted by FELTON but were outside his selected area. It is considered probable that three other nests may have been present but were overlooked. Nest 35, close to the poorly defined margin with compartment 8, was first noticed on 27 April 1967 amid dense bramble, but was clearly not of recent origin. Similarly nest 42, first observed on the same date was already well established, as was nest 34 when first seen on 5 May 1966. On 8 May 1967 dozens of alate queens were seen on nest 42 providing further proof of its maturity. Thus it seems probable that 29 nests, whose distribution is shown by solid circles in figure 1, were occupied in 1965. During the next three years the site was visited regularly and although only two months are indicated on figures 2 and 3 these, and details on figure 1, are based on many more observations. Only one visit was made during each of the next three years, followed by three years of regular biannual spring and autumn visits.

In May 1966 FELTON revisited the area and marked occupied nests using wooden

stakes, 23 × 4 × 2.5 cm, with a red « Dymo » number tacked to each. The stakes were hammered into the ground, close to the western margin of each nest, so that approximately 7 cm stood proud of the soil surface. On this occasion only 17 nests were found but by early 1967 25 nests had been numbered in this manner. In 1966 a series of studies on the *F. rufa* at Blean Wood was started and during frequent visits I was able to observe the nests in compartment 9 in greater detail. In 1967, during a period of maximum activity in the colonization of new nest sites, it became obvious that a more precise method of mapping the nests was required. Subsequently during 1967 and early 1968 the whole experimental area was mapped on a 20 metre grid and all trees, nests, paths, ditches, etc. were accurately plotted and a base map produced (see fig. 1 and 4). This

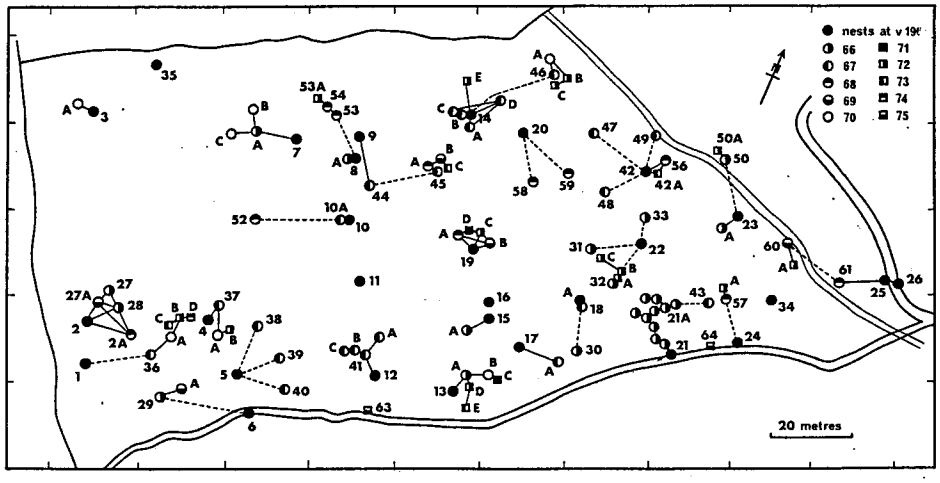

FIG. 1. — Distribution of *Formica rufa* L. nests in Compartment 9, Blean Woods National Nature Reserve, Kent, during the period 1965-1975.
Solid lines = migration observed.

ABB. 1. — Verbreitung der Nester von *Formica rufa* L. in Abteilung 9, Blean Woods National Nature Reserve, Kent, im Zeitraum 1965-1975.
Ausgezogene Linien : Nestwanderung beobachtet.
Gestrichelte Linien : Nestwanderung vermutet.

proved invaulable during the later part of the study when the vegetation was so dense that progress and orientation were difficult. This did not completely overcome the difficulty in finding new small nests but it did enable the known nests to be located and if a nest had died out the surrounding area could be searched more intensively for possible new nest sites. 'Figure 1 shows the spatial distribution of 121 sites occupied by *F. rufa* nests at some time during the period 1965-1975. The coding of half-shaded circles and squares indicates the year in which occupation of a site was first observed or estimated. Figure 2 gives an indication of the temporal distribution of these nests. It will be seen that some sites were occupied on more than one occasion. In both figures a continuous solid line is an indication of when movement between sites was observed. The broken lines mark the most probable source of origin for a newly occupied site. In figure 2 occupation of nest 5 will be seen to have ceased in the winter of 1966-1967, whilst in April 1967 three new nests, 38, 39 and 40, were observed for the first time, all 10-12 metres north and east of nest 5. Since it is more probable that nest 5 was abandoned, rather than the whole colony exterminated, the ants must

have migrated somewhere. At this same time nest 4 was observed migrating to nest site 37, nest 6 had already died out and nest 12 was colonizing site 41. Thus it is postulated that nests 38, 39 and 40 were formed by he splitting of nest 5. It was by this form of reasoning that the links between sites shown on figures 1 and 2 were established.

Initial plans to measure the size of each nest were not continued since GÖSSWALD and HORSTMANN (1966) had shown in *F. polyctena* that neither diameter nor height of the nest dome is a measure of the strength of the nest. The younger daughter colonies possess a relatively high dome whilst the older nests are worked more firmly into the ground.

NEST MIGRATION AND COLONIZATION OF NEW SITES

Although figure 2 shows nest 21 being replaced by a single nest 21 a between June 1965 and June 1966, reference to figure 1 indicates ten linked nest sites. On 29 June 1966 nest 21 was found to be dead and an arc of eight nest noda ran northwards into the open area of the compartment. These are considered to correspond with the « micromounds » described by ROSENGREN (1969) in *F. uralensis* Ruzsky. Three sites nearest the parent nest and another on a western branch of the main trail, had already been abandoned and were discernible only by a small accumulation of nest material. The terminal four noda all consisted of small concentrations of ants and building material. By 22 September 1966 a northern pair of small nest sites had been temporarily established but these and the two south west of nest 21 a contained very few ants. Nest 21 a had consolidated and all other sites were deserted. By 27 April 1967 only the one new nest (21 a) was occupied. Thus the re-establishment of a nest colony 12 metres from the parent nest had been observed although up to ten potential nest sites had been tried and an actual distance of 18 metres covered between the old and new nests. Similar behaviour has been observed by BÜTTNER *(loc. cit.)* in *F. polyctena* four new nest sites were occupied during one year up to 56 metres from the parent nest and the following year seven additional nests spread a further 20 metres.

ROSENGREN *(loc. cit.)* was of the opinion that in *F. uralensis* the abandoning of older mounds and the buildings of new ones by splitting was mainly the outcome of the ants' habit of overwintering regularly outside the mounds. The small temporary micromounds were often built on the overwintering chambers in the spring prior to the ants remigrating to the mother nest. However, there are many inter-specific behavioural differences between members of the *F. rufa* group including their method of overwintering. ROSENGREN found that in southern Finland one colony of *F. lugubris* completed a 48 meters seasonal migration between summer and winter nest sites, whilst no overwintering outside the main nest was observed in *F. polyctena.* In *F. rufa* the position is confused. EIDMANN (1943) states that overwintering outside mounds is not of general occurrence whilst KNEITZ (1964) describes the phenomenon as not uncommon. In a relatively stable polygynic population of two nests on a small islet in Finland, ROSENGREN found one overwintering site 12 metres from the parent nest and another, much larger one, only 3 metres distant. No evidence

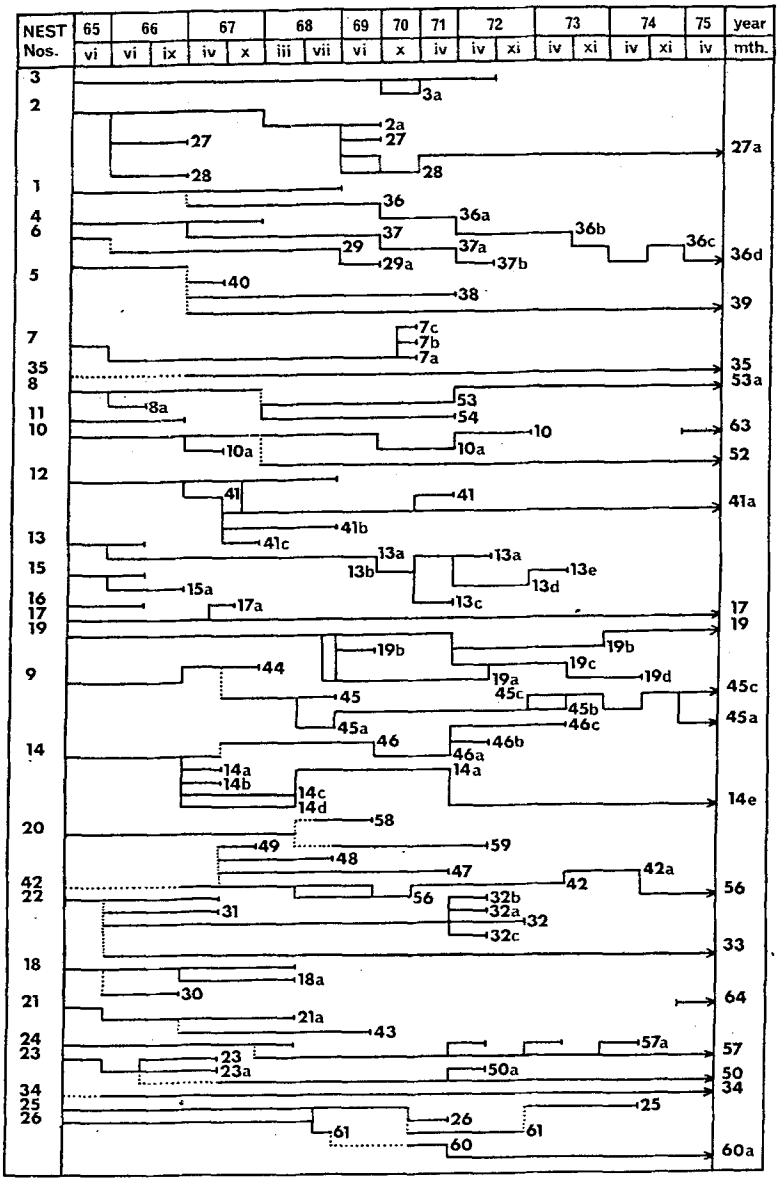

FIG. 2. — Dendrogram to show fate of 29 *Formica rufa* nests during the period 1965-1975.

Horizontal lines = continued occupation of nest site.
Vertical lines = migratory movement to new nest site.
Solid lines = occupation and migration observed.
Broken lines = occupation and migration postulated.

was found during the present study of overwintering away from the parent nest. However, on many occasions in early spring the emerging clusters of ants were seen to be a short distance from the main nest site. It was presumed that these ants had emerged from the parent nest but had moved to a more open situation where they could take full advantage of the limited solar radiation. Although it is just possible that some of these represented ants from separate overwintering sites close to the main nest, this is thought unlikely. Penetration of the heavy London Clay presents considerable difficulties for the ants unless access can be gained through the rotting root system of a dead tree. This is believed to be a major contributory factor in the failure of some new nests to survive their first winter, e.g. 27, 28, 44 and 15 a (fig. 2).

With the developing use of the *F. rufa* group as biological control agents against forest insect pests much information is available on the movement of artificially established nests. ADLUNG *(loc. cit)* states that the artificial establishment of *F. polyciena* is only successful in pine forests where sunlight is able to penetrate rather evenly to the forest floor, otherwise the ants move their nest to the forest margins. O'FLANAGAN (1967) describes how, seven weeks after its introduction into an Irish woodland, a *F. rufa* colony moved 73 metres and formed two small nests. After a further seven weeks the colony had moved a further 55 metres and was establishing a new nest at a site open to both east and south allowing the longest possible hours of sunshine. WELLENSTEIN (1968) working for 14 years on *F. polyctena* in pine forests along the Upper Rhine found that the ant colonies moved up to 100 metres in search of more favourable sites. During this period one third of all introduced nests observed by him either moved, subdivided, or both.

NEST DENSITY

At the time of coppicing, Compartment 9 at Blean Woods the 1.6 ha contained 29 occupied *F. rufa* nests, i.e. 18 per hectare. By early 1967, two years later, a maximum density of 26.9/ha was reached (see fig. 3). This dropped to a minimum of 10.6/ha in the autumn of 1974, with an average of 12.7/ha over the last three years of the study. This would appear to be a particularly high nest density. ELTON'S study area *(loc. cit.)* of 1.4 ha in the New Forest contained seven occupied nests, i.e. 5/ha. Bedford Purlieus, a mixed deciduous woodland of 208 ha, 5 km west of Peterborough, with a history of coppice

---

ABB. 2. — Schema der Entwicklung von 29 *Formica rufa* Nestern im Zeitraum 1965-1975.
Horizontale Linien : fortlaufende Besiedlung des Nestes.
Vertikale Linien : Abwanderung an einen neuen Nestsandort.
Ausgezogene Linien : Besiedlung und Abwanderung beobachtet.
Gestrichelte Linin : Besiedlung und Abwanderung vermutet.

management and some replanting with pine during the past 30 years, was found to have 155 *F. rufa* nests occupied in 1974 (PETERKEN and WELCH, 1975), i.e. an average density of 0.75/ha. However, the nests were present in compartments comprising less half the total area of the wood, at a density of 1.33/ha. The maximum density occurred in two adjacent compartments where 57 nests were present in 17.5 ha, i.e. 3.26/ha. BUETTNER *(loc. cit)* found a very similar range of densities for a natural population of *F. polyctena* in deciduous woodland in Germany. In an area of 10.5 ha the nest density varied over a five year period from 1.14 to 3.33/ha. In 135 000 ha of the Italian Alps PAVAN

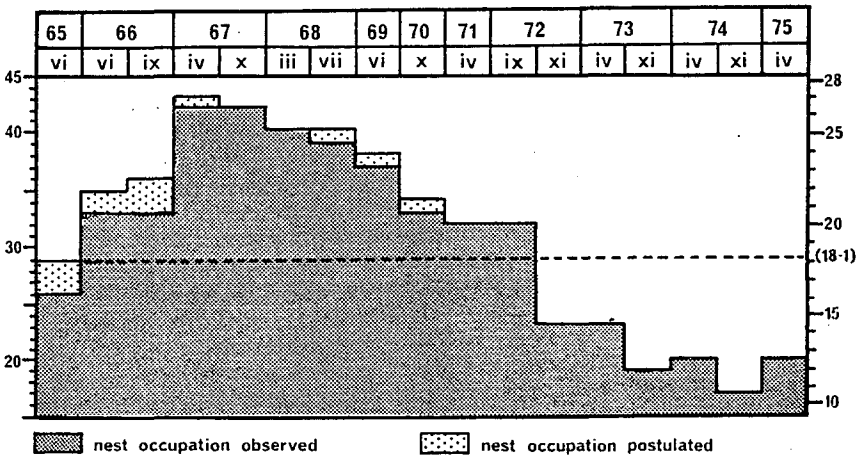

FIG. 3. — Numbers of occupied *Formica rufa* nests in 1.6 ha of coppiced woodland between 1965-1975.
Left-hand scale = nest numbers.
Right-hand scale = nest dentity/ha.

ABB. 3. — Zahl der bewohnten Nester von *Formica rufa* in 1, 6 ha Niederwald im Zeitraum 1965-1975.
Link Skala : Nestzahl.
Rechte Skala : Nestdichte/ha.

(1959) found four species of the *F. rufa* group with an average nest density of 1.85/ha.

Most other workers have recorded considerably lower nest densities. KLIMETZEK (1972) records a maximum of 15.9 nests/100 ha for five species of the *F. rufa* groupe in 1 640 ha of the Black Forest where *F. rufa* constituted up to 63 % of the species present. OTTO (1968) showed an average density of 2.5-5.8 nests/100 ha for six species of the *F. rufa* group in woods throughout West Germany, although *F. polyctena* and *F. rufa* comprised more than 90 % of all records. The maximum nest density he recorded for all species was 10.25/100 ha.

CONCLUSIONS

Of the 29 *F. rufa* nests present in compartment 9 in Blean Woods at the time of coppicing in 1965, only three (nests 17, 34 and 35, fig. 2 and 4) occupied the same sites throughout the succeeding ten years. Nest 17 produced one daughter nest some 10 metres to the east in early 1967, but this site was abandoned later the same year. Nest 19 was unusual in that the parent nest site was unoccupied for two years. During 1972 and 1973 up to three daughter nest sites were occupied but in spring 1974 one of these (19 d) died out and the other (19 b) was seen to recolonize the parent nest site where it remained until observations ceased the following year (fig. 2). Thus although it has been inferred that there is stability in the location of sites occupied by *F. rufa* colonies, in coppiced woodland, stability of individual nests is the exception rather than the rule. If HUGHES' (1975) correlations between the distribution of *F. rufa* and that of coppiced woodland hold true then such instability must be normal for this species in England and Wales. It should be borne in mind that the traditional methods of coppice management often resulted in the piecemeal cutting of small areas at different times of the year. This resulted in a mosaic of vegetation of varying ages. Today's mechanized coppicing takes place swiftly, over larger areas, and almost without exception, during the winter months. Ants emerging in the spring are thus faced with a « devastated » area which initially may not be able to support enough other invertebrates to provide them with prey.

Some indication of the changes among the invertebrates within the coppice cycle have already been obtained from studies at Monks Wood National Nature Reserve, Cambridgeshire (WELCH, 1969). It is in the second and third years after coppicing that the herbaceous flora is at its best and the various coppiced stools are producing vigorous new growth. Compared with the sparsely vegetated ground layer beneath the previous dark, dense canopy, young mixed coppice must provide greater numbers of both species and individuals as prey for *F. rufa*. It therefore came as no surprise to witness the increase in nest density during this period when the ants were able to exploit this more easily accessible food source. However, quite a large area to the west of the compartment remained uncolonized throughout the study period and no older abandoned nest sites could be identified in this region. A nest site possibly from an earlier period of active coppicing, was located close to the western boundary between nests 2 and 3.

It was expected that the density of *F. rufa* nests might eventually stabilize at a level similar to that which existed at the time of coppicing. In the winter of 1974/1975 compartment 10 was coppiced. It was expected that this opening up of the whole southern aspect of the study area could exert a considerable

influence upon the ants in the marginal strip in particular. Observations in other newly coppiced compartments in Blean Woods had shown that there was often a considerable re-colonization by *F. rufa* along the northern margin which acted as a sheltered sun trap. However, in these cases the ground sloped gently to the south, whereas in compartments 9 and 10 there is a gradual slope to the north. This may explain why this behaviour was not observed along the northern boundary of compartment 9 after coppicing.

In April 1975 two new nests (63 and 64) were already being established at the edge of the path between compartments 9 and 10. It is presumed that these owed their origins to nests within the latter compartment. With the threat of

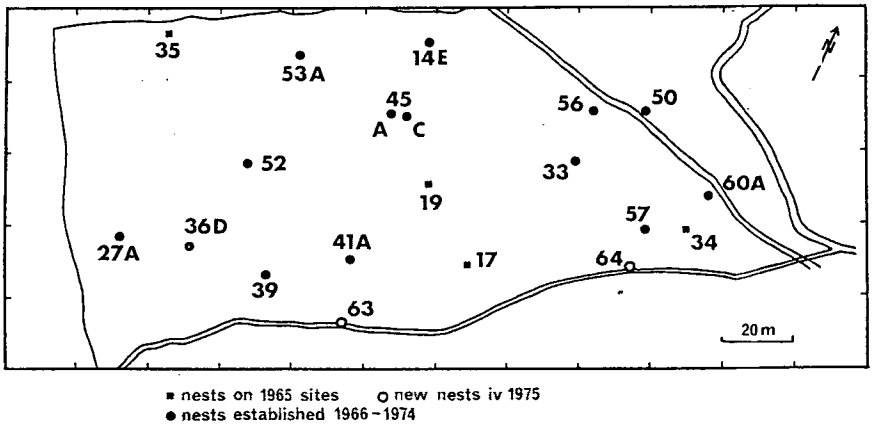

FIG. 4. — Positions of *Formica rufa* nests in April 1975, ten years after coppicing.

ABB. 4. — Verbreitung der Nester von *Formica rufa* im April 1975, zehn Jahre nach dem Abtrieb.

further immigration, and the end of the isolated nature of compartment 9, the decision was made to end this study after ten years. During that period the number of occupied *F. rufa* nests in the 1.6 ha study area had ultimately declined by about 30 %. It must remain conjecture whether the nest density in 1975 is the new stable density or whether it represents the trough prior to later stabilization at a higher level. Another visit to the area in a further five years may help answer this question.

ACKNOWLEDGEMENTS. — I am deeply indebted to J. C. FELTON, through whose initiative this study was started; for his continued help and encouragement and for reading the draft of this paper. I am also particularly grateful to G. J. MOLLER for help in producing the original base map and assistance in plotting the nest distribution.

APPENDIX

The numbers given to the majority of *Formica rufa* nests described in this study do not correspond with those used by FELTON. Since many of Felton's markers persist in compt. 9 at Blean Woods National Nature Reserve the following list will enable those nests to be identified.

Felton Marker Nos.	25	26	27	28	29	30	31	32	33	34	35	36	
Nos. in present study..	9	8	13A	18	22	17	35	40	39	38	36A	52	
Marker Nos.	37	38	39	40	41	42	43	44	45	46	47		
Present Nos.	41	21A	33	42	45	14A	14C	14D	46	47	48		
Marker Nos.	48	49	50	51	52	53	54	55	56	58	59	60	61
Present Nos.	31	32	30	49	50	23A	43	57	34	25	26	41A	41B
Marker Nos.	62	63	64	66	67								
Present Nos.	15A	2A	7A	29	36								

The following nest numbers are unchanged and are common to both systems : 1-7, 10-16, 19-21, 23 and 24.

REFERENCES

ADLUNG (K. G.), 1966. — A critical evaluation of the European research on use of Red Wood Ants (*Formica rufa* Group) for the protection of forests against harmful insects. *Z. ang. Ent.*, *57*, 167-189.

BARRETT (K. E. J.), 1968. — A survey of the distribution and present status of the Wood Ant, *Formica rufa* L. (Hym., Formicidae), in England and Wales. *Trans. Soc. Br. Ent.*, *17*, 217-233.

BARRETT (K. E. J.) and FELTON (J. C.), 1965. — The distribution of the World Ant, *Formica rufa Linnaeus* (Hymenoptera, Formicidae), in south-east England. *Entomologist*, *98*, 181-191.

BETREM (J. G.), 1960. — Ueber die Systematik der *Formica rufa*-Gruppe. *Tijdschr. v. Entom.*, *103*, 51-81.

BÜTTNER (K.), 1971. — Einfluss des Nestschutzes auf die naturliche Vermehrungsrate einer Waldamcisenkolonie (*Formica polyctena* Foerster) im Gemeindewald Schwarzenau. *Waldhygiene*, *9*, 118-123.

COTTI (G.), 1963. — Bibliographia ragionata 1930-1961 del gruppe *Formica rufa* in italiano, deutsch, english. *Min. Agr. For. Roma, Coll. Verde*, *8*, 413 p.

EIDMANN (H.), 1943. — Die Ueberwinterung der Ameisen. *Zeitsch. Morph. Oekol. d. Tiere*, *39*, 217-275.

ELTON (C.), 1932. — Territory among wood ants (*Formica rufa* L.) at Picket Hill. *J. Anim. Ecol.*, *1*, 69-76.

O'FLANAGAN (L. P.), 1967. — A note on *Formica rufa* (Wood Ant). *Irish Forestry*, *24*, 86-88.

GÖSSWALD (K.), 1941. — Rassenstudien an der Roten Waldameise *Formica rufa* L. auf systematischer, ökologischer, physiologischer und biologischer Grundlage. *Z. ang. Ent.*, *28*, 62-124.

GÖSSWALD (K.) and HORSTMANN (K.), 1966. — Untersuchungen über den Einfluss der Kleinen Roten Waldameise (*Formica polyctena Foerster*) auf den Massenwechsel des Grünen Eikenwicklers (*Tortrix viridana* L.). *Waldhygiene*, *6*, 230-255.

HUGHES (I. G.), 1975. — Changing altitude and habitat preferences of two species of wood - ant (*Formica rufa* and *F. lugubris*) in North Wales and Salop. *Trans. R. ent. Soc. Lond.*, *127*, 227-239.

JOSEPH (R. L.), 1958. — Aspects of the bionomics of *Formica aquilonia* Yarrow. *Entomologist*, *91*, 173-177.

KLIMETZEK (D.), 1970. — Zur Bedeutung des Kleinstandorts für die Verbreitung hügelbauender Waldameisen der *Formica rufa* - Gruppe (Hymenoptera, Formicidae). *Z. ang. Ent. 66*, 84-95.

KLIMETZEK (D.), 1972. — Veränderungen in einem natürlichen Vorkommen hügelbauender Waldameisen der *Formica rufa* - Gruppe (Hymenoptera, Formicidae) in Verlauf von drei Jahren. *Ins. Soc., 19,* 1-5.

KLIMETZEK (D.), 1973. — Die Variabilität der Standortansprüche hügelbauender Waldameisen der *Formica rufa* - Gruppe (Hymenoptera, Formicidae). *Mitt. bad. Landesver. Naturkunde u. Naturschutz.,* N.F. *11,* 9-25.

KNEITZ (G.), 1964. — Saisonales Trageverhalten bei *Formica polyctena* Foerst. (Formicidae, Gen. Formica), *Ins. Soc., 11,* 105-129.

LANGE (R.), 1960. — Modellversuche über den Nahrungsbedarf von Völkern der Kahlruckigen Waldameisen *Formica polyctena* Forst. *Z. ang. Ent., 46,* 200-208.

NELMES (E.), 1938. — A survey of the distribution of the wood ant *(Formica rufa)* in England, Wales and Scotland. *J. Anim. Ecol., 7,* 74-104.

OTTO (D.), 1968. — Zur Verbreitung der Arten der *Formica rufa* Linnaeus - Gruppe. *Beitr. Ent., 18,* 671-692.

PAVAN (M.), 1959. — Altivita italiana per la lotta biologica con Formiche del gruppo *Formica rufa* contro gli inselti dannosi alle foreste. *Publ. Min. Agr. For. Roma, Coll. Verde, 4,* 1-80.

PETERKEN (G. F.) & WELCH (R. C.), 1975. — Bedford Purlieus : its history, ecology and management. Monks Wood Symposium N°. 7, *Natural Environment Research Council,* 209 p.

ROSENGREN (R.), 1969. — Notes regarding the growth of polycalic nest system in *Formica uralensis* Ruzsky. *Noctulae Entomol., 49,* 211-230.

SALE (G. N.) & ARCHIBALD (J. F.), 1960. — Working Plan for Blean Woods Nature Reserve (N.N.R. 36). *The Nature Conservancy,* 76 p.

SATCHELL (J. E.), 1966. — Extinctions and Invasions — some case histories and conclusions, in The Conservation of Invertebrates ed. E. Duffey & M. G. Morris, Monks Wood Symposium N°. 1, *The Nature Conservancy,* 19-28.

SATCHELL (J. E.) & COLLINGWOOD (C. A.), 1955. — The Wood Ants of the English Lake District. *North-Western Nat., 3,* 23-29.

WALKER (J. J.), 1897. — *Microrrhagus pygmaeus* and other Coleoptera in the Blean Woods, Kent. *Entomologists' mon. Mag., 33,* 175-176.

WELCH (R. C.), 1969. — Coppicing and its effect on woodland invertebrates. *Jnl. Devon Trust Nat. Conserv., 22,* 969-973.

WELLENSTEIN (G.), 1968. — Weitere Ergebnisse über die Auswirkungen einer planmässigen Ausiedlung von Waldameisen und höhlenbrütenden Vögeln in Lehr — u. Versuchsrevier Schwetzingen. *Z. ang. Ornith., 3,* 40-53.

YARROW (I. H. H.), 1955. — The British Ants allied to *Formica rufa* L. (Hym., Formicidae). *Trans. Soc. Br. Ent., 12,* 1-48.

ZAKHAROV (A. A.), 1974. — Structure and formation of the colony in ants *Formica s. str.* (Hymenoptera, Formicidae). *Zool. Zh., 53,* 58-65 (in russian, British Library Translation Series RTS 10009).

Masson, éditeur, Paris. Dépôt légal : 1978. N° d'ordre : 5107. — 2e trimestre 1978.
Imprimé par Soulisse et Cassegrain, à Niort (France). D.L. n° 1603.
Printed in France. Commission paritaire : n° 27719.