A background study into the ecology of *Formica rufibarbis*

Insect conservation

The rate of species extinction has dramatically increased over the last century, so much so that it is hypothesised the world is in the midst of a sixth mass extinction (Thomas *et al* 2004). Local species extinction does not only affect the immediate species but can also cause a knock on effect throughout the ecosystem. There is abundant data supporting the decline and conservation of charismatic taxa such as birds and mammals but insect decline and conservation is often overlooked (Dunn 2005; Thomas 2005). Yet insects comprise 54% of the worlds described species compared with only 0.6% of birds (Thomas *et al* 2004). It is estimated that of every one million species 100,000 will be extinct by 2050 (Pimm & Raven 2000), and most of these extinctions are likely to be insects (Dunn 2005).

Butterfly and bumblebee decline has been recorded in the UK. Over 71% of butterfly species have declined over the last 25 years (Thomas *et al* 2004) and bumblebee populations have dramatically decreased during the last 60 years due to agricultural intensification and loss of habitat. This has resulted in three species becoming extinct, seven are of high conservation importance and over half are experiencing range contractions (Goulson *et al* 2004, 2008). If butterflies and bumblebees can be used as indicators for other insect groups, it could mean many of our insects are disappearing with no knowledge of their functional importance for wider communities. This could have strong implications for biodiversity and conservation.

The importance of hymenoptera (bees, wasps, sawflies and ants) is well documented due to their ecological dominance on the land (Wilson 1971). Social insects are functionally important at different trophic levels (Alonso 2000) and play critical ecological roles in; soil structure and turnover, nutrient recycling, plant protection

(Raine *et al* 2004) plant pollination and seed dispersal (Gammans *et al* 2005, 2006). However, social insects may be more susceptible to extinction (Chapman & Bourke 2001). Due to their sociality they may appear numerous than what they are, as a large majority of their workforce is non-reproductive. Dispersal is also often limited and this could lead to genetic inbreeding (Chapman & Bourke 2001).

Ants in particular comprise one of the most diverse, abundant and ecologically dominant animal groups in the world (Holldobler & Wilson 1990). They are among the leading predators of other insects and small invertebrates, and in many environments they are the principle herbivores and seed predators (Beattie & Hughes 2002). In the tropics they are the chief earth movers substituting earthworms (Wilson 1971). Some ant species are described as keystone species for their roles in seed dispersal or in general as ecosystem engineers (Bond & Slingsby 1984; Christian 2001; Gomez *et al* 2003). Ants are also regarded as indicator species, as changes in ant communities (after a disturbance) are indicative of other invertebrate groups (King et al 1998). Ants' impact on the terrestrial environment is great and they can provide useful information on an ecologically and numerically dominant group (Underwood & Fisher 2006).

Formica is a well studied genus of ants that exhibit an eclectic mix of social structures (e.g. polygyne and monogyne) both within and between populations of the same species (Deslippe & Savolainen 1995; Gyllenstrand et al 2002; Hannonen *et al* 2002; Hannonen & Sundstrom 2002). In the Holarctic temperate zone *Formica* is regarded as a keystone genus (Czechowski *et al* 2002). In the UK the *Formica* genus is of high conservation importance with seven of the eleven species having a Biodiversity Action Plan (BAP).

Formica rufibarbis

Formica rufibarbis is possibly the rarest animal resident in mainland Britain (Brian 1977; Pontin 2005) with only three colonies remaining at Chobham Common (NNR), Surrey. *F. rufibarbis* belongs to the class Insecta, order Hymenoptera, family Formicidae, genus *Formica*. *F. rufibarbis* is one of the most thermophilous species of the *Formica* genus (Pontin 1996) and it requires an open, dry and sun exposed habitat both for nesting and foraging (Czechowski *et al* 2002). Identification keys to the species are found in Bolton & Collingwood (1975), Skinner & Allan (1996) and Czechowski *et al* (2002).

Distribution

F. rufibarbis is quoted as a common species in many parts of Europe (up to Southern England) ranging across the Palearctic and is present in southern and central Europe as far north as 62 degrees latitude and spreads into Asia minor and Caucasus (Pontin 1996; Czechowski *et al* 2002; Czechowski & Radchenko 2006). However, their distribution across Europe may be great but no actual data exists on their abundance. It may be a misconception that this species is ‘common’ without having any quantitative information. The only other British location is the Isles of Scilly, where it predominantly remains on St. Martin’s Island where it was discovered in 1940 (Yarrow 1941; Pontin 2005; Beavis 2006). *F. rufibarbis* has a narrow distribution on the eastern end of St. Martin’s, Chapel Down (refer to Appendix 1 maps 1-3) where it is restricted from English Island point on the south to Burnt Hill on the north of the island (Beavis 2006). Beavis (2000) has also recorded *F. rufibarbis* on the small uninhabited islands of Great Ganilly and Nornour, part of the Eastern Isles, which are joined at low tide. Workers were recorded on a single occasion on the uninhabited island of Tean (Parslow 2007), but have not been seen since, suggesting temporary colonisation rather than permanent establishment (Beavis pers. Comm.).

All of the mainland British sites are (or were formerly) Surrey heaths (refer appendix 1 map 4). Donisthorpe (1927) lists records of *F. rufibarbis* nests around Weybridge, Reigate and Ripley pre- 1920 and there are also reports of one nest on Oxshott (1964) and at Chobham Common (1967) (Pontin 2005). More recently in 1992 a nest was found on Stickledown Range, Pirbright (Pontin 1996) which is now extinct due to a raid from the slave making ant *Formica sanguinea* in 2002 (Pontin 2002). Pre 2008 only one nest was thought to remain at Chobham Common, however two *F. rufibarbis* nests were located on a road side verge within 1m of each other in August 2008, suggesting a satellite/budding nest, which is a common mode of propagation in ants (Seppa *et al* 2008).

Habitat

Beavis (2006) gives an excellent detailed description of *F. rufibarbis* habitat on St. Martin's, Isles of Scilly:

'Chapel down consists of a flat windswept and particularly barren looking plateau, surrounded on all but its western boundary by steep rocky slopes and cliffs dropping down to the sea. The coastal fringe is interspersed with high exposed granite outcrops (carns) and sheltered hollows. The slopes are mostly occupied by heathland or a heather and grassland mosaic, but there are also areas of maritime grassland including thrift and birdsfoot trefoil, as well as patches of mixed bracken and bramble. The slopes are clearly more sheltered than the plateau, and the heather exhibits in a correspondingly less extreme fashion. On its western, inland, side Chapel Down grades into rough grassland and dense thickets of gorse and bramble, some of which are now beginning to be cleared. Historically the Down would have served as a 'common', outside the regular landscape but available for informal grazing by a hardy, and long extinct, insular breed of sheep'

The plateau is particularly unsuitable for colonisation as it is windswept and becomes waterlogged among the heather hollows (Beavis 2006). Therefore the nesting habitat of *F. rufibarbis* on St. Martin's can be described as a mosaic of sheltered maritime heathland and grassland with scattered granite outcrops. Nests are excavated in the ground or under rocks/stones (Czechowski *et al* 2002; Beavis 2006).

It is interesting to observe the apparent competitive displacement between *F. rufibarbis* and the closely related *Formica fusca*. The formers distribution is restricted to Chapel Down, where *F. fusca* is absent (Beavis 2006; Gammans & Robertson pers obser) and yet *F. fusca* is present on the rest of the island where *F. rufibarbis* is not present. The two species do not appear to overlap, however the reason for this is unknown (Beavis 2006). It should also be noted that the slave-maker ant, *Formica sanguinea*, to whom both species are host is not present in the Isles of Scilly.

It is therefore interesting why *F. rufibarbis* distribution is confined to the Isles of St. Martin's and absent from others such as Tresco, Bryher, St. Agnes and St. Mary's where the vegetation communities are similar. No other aculeate species distribution is restricted to Chapel Down or St. Martin's (Beavis 2006). *F. fusca* are present on Tresco, Bryher and St. Mary's so possibly *F. rufibarbis* is out competed, although *F. fusca* are not found on St. Agnes. Perhaps their microclimate is not suitable (Beavis 2006)? Or alternatively *F. rufibarbis* could have been artificially introduced by man to St. Martin's and has not been able to colonise these surrounding islands (Yarrow 1940).

On mainland Britain *F. rufibarbis* distribution is also restricted, with just three colonies remaining at Chobham Common (NNR), Surrey. It is possible this remaining population is a relic or alternatively it could again be an introduced species, which could explain why it is only found in land locked Surrey. Chobham Common consists of 517ha of lowland heath and is situated in the London Basin. Habitats include wet and dry heath, marsh grassland and bogs, interspersed with patches of woodland

(English Nature Research report, 2004). The soil has a high clay content which is generally thought to be unsuitable for this species (Pontin 2001). Prior to the discovery of two new nests (possibly one being a satellite) in 2008, only one colony remained on Chobham Common near Monument Car park in an area densely covered by bristle bent, *Agrostis curtisii,* and purple moor grass *Molinea caerulea*. The surrounding nest vegetation has been continually cut back by hand as it threatens to encroach. The two new nests were found on a grassy road side) verge (close to Monument car park) by Jonty Denton in August 2008 and subsequent visits have frequently seen workers foraging on the tarmac path. In 2009 an intensive survey is planned of Chobham Common for *F. rufibarbis* nests. As opposed to the Isles of Scilly, *F. sanguinea* is abundant on Chobham Common and poses a risk to *F. rufibarbis* reintroduction and colonisation.

Very little information exists on European nesting habitats of *F. rufibarbis*. Both Gomez *et al* (2003) and Suvak (2007) have reported *F. rufibarbis* as opportunists on grazed, cultivated and disturbed habitats in Girona (Spain) and Slovakia. *F. rufibarbis* has also been recorded as a secondary pollinator of the perennial herb *Scleranthus perennis* in dry, sandy disturbed environments in southern Sweden (Svensson 1985; 1986). Krunic *et al* (2005) also recorded *F. rufibarbis* foraging in orchards in Italy. This evidence strongly suggests that *F. rufibarbis's* European habitat is not just restricted to heathlands. The new road side verge nests at Chobham Common also support this view. Clearly more work is needed on *F. rufibarbis* habitat requirements.

Reproductive biology

Each nest may contain a colony of a few thousand workers along with one or more queens plus brood (Czechowski *et al* 2002). In mature and healthy colonies a new sexual generation containing gynes and/or males is usually produced each year, with mating flights most commonly occurring in late June early July (Czechowski *et al* 2002; Beavis 2006). Nests with a solarium or colonies nesting underneath pebbles/stones/tiles bring their brood up to the surface to ‘bask’ in temperatures of up to 35°C (Pontin 1998). In April eggs are laid with sexual larvae developing before worker. The majority of *F. rufibarbis* nests will produce either male or female sexuals however some nests were observed to contain both sexes on the Isles of Scilly (Gammans & Robertson unpublished data). Once developed, alates ‘wait’ within the nest until ideal weather conditions of clear, sunny warm days for the nuptial flight (Gammans & Dodd unpublished data). Mating takes place on a predominant stem near to the maternal nest, where the winged gyne ‘calls’ to males using a pheromone scent (Pontin 1996; 2005).

Two winged gynes were collected by Gammans & Dodd (unpublished data) on St. Martin’s in 2008. They were thought to be unmated as a virgin queen will immediately bite off her wings after copulation (Donisthorpe 1927). Two males were collected from two tiled *F. rufibarbis* nests in different locations and placed inside the universal tubes where the gynes were stored (one in each tube). No aggression was observed between the males and females. The males were removed either when the gynes wings were removed or on return to mainland UK. Both queens have since laid diploid worker larvae suggesting successful copulation occurred.

Prior to the two nests being discovered at Chobham Common, the original remaining *F. rufibarbis* nest produces only female alates. To date it is unknown whether the two new nests will produce male/female or both sex alates. If males are produced it will be possible to conduct further experiments into ‘test tube matings’.

Foraging behaviour

F. rufibarbis workers usually forage singly for invertebrate prey or carrion, such as moths, spiders, beetles, woodlice and other dead ant species from midden piles (Gammans & Dodd unpublished data), they will also take plant nectar and harvest aphid honey-dew were available (Pontin 1996). *F. rufibarbis* were observed nectaring hogweed, *Heracleum sphondylium*, on the Isles of Scilly (Gammans & Dodd pers obs). As this is not a heathland species it appears *F. rufibarbis* are opportunist foragers. Plant material is also collected such as thrift seeds (Beavis 2006). Workers have been observed collecting dead *Lasius flavus* workers from midden piles at the road side verge nests, Chobham Common and *Myrmica* alates from the Isles of Scilly (Gammans & Newell per obs; Beavis 2006).

Colony founding and genetics

Little is known of *F. rufibarbis* colony founding (Beavis 2006). To date the only study on *F. rufibarbis* genetic structure and population viability has been completed by Sumner *et al* (*in prep*) on the St. Martin's population. Nests of the latter were shown to have both polygynous and monogynous colonies, with average queen number being close to 2. Reproduction was found to be relatively equal between *F. rufibarbis* queens within the same nest but queens were unrelated. This may appear to be unusual as other studies on the *Formica* genus have found that equal queen reproduction is due to high relatedness. The higher the relatedness between queens the more genetically similar the workers, therefore they will show equal favour to queens. The less related the queens the greater the reproductive skew (Hannonen & Sundstrom 2003; Holzer *et al* 2008). Polygyny often arises through the secondly adoption of daughter queens which would result in higher relatedness (Holldobler & Wilson 1990; Sundstrom 1997). However *F. fusca* have been shown to adopt unrelated queens into a colony (Hannonen *et al* 2002; Hannonen & Sundstrom 2003).

Genetic analysis completed by Sumner *et al* (*in prep*) demonstrated that *F. rufibarbis* queens are facultatively multiply mated with males (polyandry). The males mated to the same queen are related (suggesting brothers) yet unrelated to the queen. In conclusion Sumner *et al* (*in prep*) suggests colonies are formed by co-founding (pleiometrosis) as opposed to colonies accepting queens or daughters through subsequent years, as the mates of different queens within the same nest were closely related. However if queens enter the nest in following years (secondary adoption) they may have mated with males from the same maternal nests- this is potentially possible due to the small population size on St. Martins (approximately 70 nests). A study by Deslippe & Savolainen (1995) showed *Formica podzolica* established 27% of their founding nests by pleiometrosis. Although as previously stated, polygyny commonly occurs in ant colonies by secondary adoption of daughters (Holldobler & Wilson 1990; Sundstrom 1997). Laboratory experiments were completed by Deslippe & Savolainen (1995) to investigate variation in queen number on larvae production and colony survival of *F. podzolica*. Artificial nests contained 1, 2-4 or greater than 8 queens. Results showed that small queen numbers (2-4) had the greatest colony egg production and survivorship as opposed to a single queen colony or greater than 8 queen density colony. Extrapolating this theory could have important implications for released *F. rufibarbis* colonies survival and production. Preliminary experiments should be completed to discover whether placing two queens together within a starting nest will increase larval production.

Sumner *et al (in prep)* suggests *F. rufibarbis* colonies are not polydomous (containing several nests per colony) on St. Martin's, which is claimed is normally attributed to limited dispersal. Sumner concludes *F. rufibarbis* has not saturated its environment and is freely able to disperse. However this would seem unlikely as *F. rufibarbis* distribution is restricted to Chapel Down on St. Martins with limited available habitat for colonisation (refer maps 1-3, Appendix 1). In addition the two new nests at the road side verge Chobham Common are within a close proximity to each other and initial observations suggest it could be a polydomous nest. Similar nesting structures were also observed in St. Martin's (Gammans unpub data). Further genetic studies are needed on the Chobham Common and St. Martin's populations to further examine this theory. Behavioural experiments should also be completed to examine whether the two Chobham Common (and St. Martin's nest) are still in social contact, as this implies a polydomous nest (Denis *et al* 2007; Seppa *et al* 2008).

Comparisons between workers from St. Martin's' (14 nests) and from Chobham Common colony (1 as thought at the time) were compared for similarity. Unfortunately sequence data yielded unclear results. Conversely preliminary analysis showed both populations to be distinct. More detailed genetic experiments are needed between the two UK populations; in addition Europe stock should be collected for comparison.

Additional genetic studies are needed for *F. rufibarbis* to gain a clear insight into their population structure, as results have been confusing. This information is vital for any project working with this species. Experiments should be combined with behavioural experiments where possible.

F. rufibarbis status

In Great Britain *F. rufibarbis* was listed as nationally rare in the originally Red Data Book for insects (Shirt 1987). It was upgraded to endangered by Faulks (1991) RD1 after providing more detailed accounts of aculeate decline. *F. rufibarbis* is a UK biodiversity action plan (UK BAP) priority species and has a Species Action Plan (SAP) that coordinates its conservation.

Causes of loss or decline of F. rufibarbis

Lowland heaths are priority habitats for invertebrates with many rare and characteristic species occurring (Habitat Action Plan Surrey 1999). Many invertebrates are dependant upon localized bare ground 'hot spots' providing a warm microclimate and shelter. Surrey heathlands are an important sanctuary for many of these rare invertebrate species including *F. rufibarbis* (Habitat Action Plan Surrey 1999). Reasons for *F. rufibarbis* loss or decline have been suggested by Pontin (1998);-

- Loss of suitable heathland habitat through urban or industrial development, agricultural improvement and afforestation.
- Loss of bare ground on heathlands for foraging and nesting
- Inappropriate heathland management.
- Excessive or untimely disturbance of nests through, for example, trampling, off-road vehicles, digging, and inappropriate mechanised scrub or heather clearance.
- Frequent, untimely or intensive heathland fires (although appropriate light burning may be beneficial).
- Growth of vegetation and shading out of nests (Chobham Common).
- Population size to small for genetic viability.

Lowland heathland is a priority for nature conservation because it is a rare and threatened habitat. During the last 50 years heathlands in the UK have decreased considerably (Chambers et al 1999). This is largely due to loss of traditional management practices, urbanisation and conversion to farmland (Bullock & Pakeman 1997; Sedlakova & Chytry 1999). The following points have been attributed to the loss of heathlands;-

- Lack of resources to fund land management (Habitat Action Plan Surrey 1999)
- Encroachment of trees and scrub (succession) (Natural England Research Reports 2004; Niemeyer *et al* 2007)
- Nutrient enrichment (Hardtle *et al* 2006; Niemeyer *et al* 2007)
- Fragmentation and disturbance from developments such as housing and road constructions (Habitat Action Plan Surrey 1999)
- Uncontrolled fires (Habitat Action Plan Surrey 1999)
- Agricultural improvement including reclamation and overgrazing (Habitat Action Plan Surrey 1999)
- Public opposition to management (Sedlakova & Chytry 1999)

- Loss of tradition management; grazing, controlled burning, cutting and removal of heather, turf stripping and periodic cultivation (Gimingham 1994)

It is generally thought that a return to traditional land management practises will provide and create mosaic heathlands which are suitable for a range of species including *F. rufibarbis*. However very little information is available to land managers to devise effective management plans, such as grazing management (Bullock & Pakeman 1997). For example the reintroduction of grazing can increase plant species richness, increase amount of bare ground, prevent shrub and tree invasion and control *Molinea Caerulea*. Yet difficulties arise in which animals and breeds to use, stocking rates, grazing season, proportion of land to be grazed and integration with other management techniques (such as burning, mowing, turf stripping) (Bullock & Pakeman 1997). Ants have shown different responses to grazing reintroduction and this will vary in different sites and with grazing intensity (Underwood & Fisher 2006). Pontin (1998) is concerned at the reintroduction of grazing where *F. rufibarbis* are present as they may be susceptible to trampling. A grazing trial with cattle at Chobham Common destroyed two *F. sanguinea* nests with very similar structures to *F. rufibarbis* nests. More research and case studies are needed on grazing management of heathlands and their effect on the invertebrate community. Grazing trials are needed on a variety of low land heaths with published results.

As previously stated, more information is needed on *F. rufibarbis* habitat requirements. European evidence suggests *F. rufibarbis* is capable of nesting in disturbed, grazed and cultivated land (Gomez *et al* 2003; Suvak 2007). More research is needed into the ‘ideal’ nesting and foraging habitats of *F. rufibarbis*.

The slavemaker Formica sanguinea

A potential threat to *F. rufibarbis* is the presence of the slavemaker ant *F. sanguinea*. Slavery (dulosis) is a form of social parasitism in which the slave making species exploits the labour of workers from a parasitized host colony to complete colony duties such as foraging, feeding and brood care (Holldobler & Wilson 1990; Mori *et al* 2001; Johnson *et al* 2002). The slave makers typically conduct raids on neighbouring host species killing and driving away the workers and stealing their brood. The pillaged brood eventually become workers which are fully incorporated into their parasitic colony even participating in future raids (Mori *et al* 2001).

F. sanguinea is a facultative slave maker (Mori et al 2001; Czechowski & Radchenki 2006), which, means the slavemaker's and hosts workers participate in all roles within a colony (D'ettorre et al 2002). An obligate slavemaker is dependant on host workers to perform specific tasks within a colony, such as food gathering, nest maintenance and care of the brood and queen (Visicchio *et al* 2000). Obligate slavemakers are dependent on host workers as part of their colony lifecycle.

The presence of *Formica sanguinea* is potentially a serious threat to its host *F. rufibarbis* (Mori *et al* 2001; Pontin 2002; Czechowski & Radchenko 2006). *F. sanguinea* forms a co-ordinated army to attack a *F. rufibarbis/fusca* or *cunicularia* nest to steal the brood (larvae and pupae), which is either reared or eaten and can result in the death of the slave provider nest (Pontin 2005). *F. sanguinea* raids generally take place after their nuptial flight and are thought to be a result of worker foraging continuation, expansion and predatory activity as opposed to specific raiding scouts (Wilson 1971; Mori *et al* 2001). Dealated (wings removed) queens have been observed participating in raiding swarms, digging at the entrance holes entering and not seen to remerge suggesting temporary parasitism (Mori *et al* 2001). Queens are also capable of independent colony formation or may return to their maternal nest.

Observed raiding swarms can be 10 to 12 m long and 30 to 50 cm wide consisting of hundreds of workers. Once the host colony is located, the entrance holes are cleared (many flights ensue) and eventually the nest is penetrated, hence the host workers burst scattering from the nest clutching brood. Raids can take several hours to complete. Raids are a common and frequent behaviour for *F. sanguinea* (Mori *et al* 2001) and can occur within a distance of 100m to a host nest (Wilson 1971).

Mori et al (2001) observes that workers of *F. rufibarbis* are fiercely aggressive to the slavemaker *P. rufescens*, workers are seen actively attacking scouts and successfully defending raids. D'Ettorre *et al* (2004) observed seasonal behaviour differences of *F. rufibarbis* workers to *P. rufescens* parasitized and un-parasitized areas. Workers from the latter were continuously aggressive all year round to *P. rufescens* scouts. Whereas in parasitized areas *F. rufibarbis* workers significantly increased their levels of aggression during the raiding and colony founding season.

Clearly *F. sanguinea* is a threat to *F. rufibarbis*. In Europe evidence suggests *F. rufibarbis* and *F. sanguinea* are able to share the same habitat and live side by side. However some points remain unclear. *F. sanguinea* is a facultative slavemaker and doesn't rely on slaves for colony functioning or founding (Wilson 1971). Whereas, the obligate slavemaker *P. rufescens* needs to parasitize a host nest and kill the queen for colony founding. Therefore is it in the interest of *F. sanguinea* to destroy its hosts nest and kill the queen- only if the intention is colony parasitism (which is usually temporary and rare) (Mori *et al* 2001). If *F. sanguinea* only steals the brood from its host it is not worth killing the queen/colony as they can return and take subsequent brood in future years and use it as a long-term resource. Evidence suggests host colonies regroup after an attack and persist as a colony (Wilson 1971; Mori *et al* 2001). In conclusion *F. sanguinea* is a threat to *F. rufibarbis* nests but this could be a temporary action. If an *F. sanguinea* raid does not kill the queen the colony can regroup and rebuild. More research is needed into the outcome of slave raids by *F. sanguinea*.

References

Agosti, D. Majer, J.D. Alonso, L.E. & Schultz, T.R (Editors) (2000) Ants: Standard Methods for Measuring and Monitoring Biodiversity (Biological Diversity Handbook). Smithsonian Books.

Beattie, A.J. & Hughes, L. (2002) Ant-plant interactions. In: Plant-animal interactions: and evolutionary approach (CM Herrera and O Pellmyr eds). pp 211-235. Blackwell Science, Oxford

Beavis, I.C. (2000) Aculate Hymenoptera on the Isles of Scilly. Entomologists Gazette **51**, 59-68

Beavis, I.C. (2006) Aculate Conservation Group Hymettus report 2006. English nature. Action for Biodiversity. Species recovery programme.

Beavis, I.C. (2007) *Formica rufibarbis* fabricius on the Isles of Scilly Report on studies in May 2006 and survey of earlier observations. Aculate Conservation Group Hymettus Ltd. Report for 2006. Midhurst, UK.

Bolton, B. & Collingwood, C.A. (1975) Handbooks for the Identification of British Insects: Hymenoptera: Formicidae. Royal Entomological Society.

Bond, W.J. & Slingsby, P. (1984) Collapse of an ant-plant mutualism: the Agentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology **65**, 1031-1037

Brian, M.V. (1977) Ants. New Naturalist series. Collins.

Bullock, J. & Pakeman, R. (1997) Grazing of lowland heath in England: Management methods and their effects on healthland vegetation. Biological Conservation **79** (1), 1-13

Chambers, F.M. Mauquoy, D. & Todd P.A. (2001) Recent rise to dominance of ***Molinia caerulea*** in environmentally sensitive areas: new perspectives from palaeoecological data. Journal of Applied Ecology **36** (5) 719 - 733

Chapman, R.E. & Bourke, A.F.G (2001) The influence of sociality on the conservation biology of social insects. Ecology Letters **4** (6), 650- 662

Christian, C.E. (2001) Consequences of a biological invasion reveals the importance of mutualism for plant communities. Nature **413**, 635-638

Czechowski, W. Radchenko, A. Czechowska, W. (2002) The Ants of Poland: (Hymenoptera, Formicidae). Museum & Institute of Zoology.

Czechowski, W. & Radchenko, A. (2006) *Formica lusatica* SEIFERT, 1997 (Hymenoptera: Formicidae), an ant species new to Finland, with notes on its biology and the description of males. Myrmecolische Nachrichten **8**, 257-262

Denis, D. Chameron, S. Costille, L. Pocheville, A. Châline, N. & Fresneau D. (2008) Workers agonistic interactions in queenright and queenless nests of a polydomous ant society. Animal Behaviour **75** (3), 791-800

Deslippe, R.J. & Savolainen, R. (1995) Colony foundation and polygyny in the ant *Formica podzolica.* Behavioral Ecology and Sociobiology **37** (1), 1-6

D'Ettorre, P. Mondy, N. Lenoir, L. Errard, C. (2002) Blending in with the crowd: social parasites integrate into their host colonies using a flexible chemical signature. Proceedings of the Royal Society Biological Series **269** (1503), 1911-1918

Donisthorpe, H. (1927) British Ants: their life- history and classification.

Dunn, R.R. (2005) Modern insect extinctions, the neglected majority. Conservation Biology **19**, 1030-1036

Elmes, G.W. (1989) The effect of multiple queens in small groups of *Myrmica rubra* L. Insectes Sociaux **5**, 137-144

Elmes, G. W & Wardlaw, J. C. (1983) A comparison of the effect of temperature on the development of large hibernated larvae of four species of *Myrmica* (Hym. Formicidae). Insectes Sociaux **30** (1) 106- 118

Elmes, G.W. Wardlaw, J.C. Schönrogge, K. Thomas, J.A. & Clarke, R.T. (2004) Food stress causes differential survival of socially parasitic caterpillars of *Maculinea rebeli* integrated in colonies of host and non-host *Myrmica* ant species. Entomologia Experimentalis et Applicata **110**, 53-63

Falk, S. (1991) A review of the scarce and threatened bees, wasps and ants of Great Britain. Peterborough: NCC.

Gammans, N., Bullock, J.M. & Schonrogge, K. (2005) Ant benefits in a seed dispersal mutualism. *Oecologia* **146**, 43- 49

Gammans, N. Bullock, J.M. Gibbons, H. & Schönrogge, K. Reaction of Mutualistic and Granivorous Ants to *Ulex* Elaiosome Chemicals. Journal of Chemical Ecology **32** (9), 1935 - 1947

Gimingham, C.H. (1994) Lowland heaths of west Europe: Management for conservation. Phytocoenologia **24**, 615-626

Gómez, C. Casellas, D. Oliveras, J & Bas, J.M (2003) Structure of ground-foraging ant assemblages in relation to land-use change in the northwestern Mediterranean region. Biodiversity and Conservation **12** (10), 2135- 2146

Goulson, D. Darvill, B. Ellis, J. Knight, M.E. & Hanley, M.E. (2004) Interspecific differences in response to novel landmarks in bumblebees. Apidologie **35**, 619-622

Goulson, D. Lye, G.C. Darvill, B. (2008) Decline and conservation of bumblebees. Annual Review of Entomology **53**, 191-208

Guerrieri, F.J & d'Ettorre, P. (2008) The mandible opening response: quantifying aggression elicited by chemical cues in ants. Journal of Experimental Biology **211**, 1109-1113

Gyllenstrand, N. Gertsch, P.J. & Pamilo, P. (2002) Polymorphic microsatellite DNA markers in the ant ***Formica exsecta***. Molecular Ecology Notes **2** (1) 67- 69

Hannonen, M. Sledge, M.F. Turillazzi, S. & Sundström, L. (2002) Queen reproduction, chemical signalling and worker behaviour in polygyne colonies of the ant *Formica fusca*. Animal Behaviour **64** (3), 477-485

Hannonen, M. & Sundström, L. (2002) Proximate Determinants of Reproductive Skew in Polygyne Colonies of the Ant *Formica fusca.* Ethology **108** (11), 961 – 973

Hannonen, M. & Sundström, L. (2003) Reproductive sharing among queens in the ant ***Formica fusca*.** Behavioral Ecology. **14** (6), 870-875

Hardtle, W. Niemeyer, M. Niemeyer, T. Assmann, T. & Fottner, S. (2006) Can management compensate for atmospheric nutrient deposition in heathland ecosystems? Journal of Applied Ecology **43** (4), 759 - 769

Hölldobler, B. & Wilson, E.O. (1990) The Ants. Belknap Harvard

Holzer, B. Chapuisat, M. & Keller, L. (2008) Foreign ant queens are accepted but produce fewer offspring. Oecologia. 157(4), 717-23

IUCN (1987) Position station on translocation of living organisms. http://iucn.org.themes/ssc/pubs/policy/transase.htm

IUCN/SSC (1995) Guidelines for reintroductions. http://www.iucn.org/themes/ssc/pubs/policy/reinte.htm

Johnson, C.A. Topoff, H. Vander Meer, R.K. & Lavine, B. (2002) Host queen killing by a slave-maker ant queen: when is a host queen worth attacking? Animal Behaviour **64** (5) 807-815

Kessock-Philip, R. Hurst, H. Rossington, S.R. & Holloway, G.J. (2004) Nesting ecology of *Formica cunicularia* (Report Number 612). English Nature.

King, J.R Andersen, A.N. & Cutter, A.D. (1998) Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. Biodiversity and Conservation **7** (12), 1627-1638

Kutter, H. & Stumper, R. (1969) Hermann Appel, ein leidgeadelter Entomologie (1892-1966). Proc. Sixth Congr. Int. Union Study Soc. Ins. (Bern), pp. 275-279.

Lake, S. Bullock, J.M. & Hartley, S. (2001) Impacts of livestock grazing on lowland heathland in the UK. English Nature Research Report no. 422. Peterborough.

McGibbon, R. (1999) Lowland Heathland (including Acid Grassland and Bog). A habitat action plan for Surrey.

Molenaar, F.M. (2007) Post-mortem examination protocol for ants. London, institute of Zoology.

Molenaar, F.M. & Sainsbury, A.W. (2007) The native insects quarantine unit: Set-up and quarantine protocol 2007. London, institute of Zoology.

Molenaar, F.M. & Sainsbury, A.W. (2008) Prevalence of microsporidia-like structures in free-living red barbed ants (*Formica rufibarbis*). London, Institute of Zoology.

Mori, A. Grasso, D.A.Visicchio, R. Le Moli, F. (2001) Comparison of reproductive strategies and raiding behaviour in facultative and obligatory slave-making ants: the case of *Formica sanguinea* and *Polyergus rufescens.* Insectes Sociaux **48** (4), 302-314

Niemeyer, M. Niemeyer, T. Fottner, S. Hardtle, W. & Mohamed, A. (2007) Impact of sod-cutting and choppering on nutrient budgets of dry heathlands. Biological Conservation **134** (3), 344-353

Parslow, R. (2007) The Isles of Scilly. Collins.

Pimm, S.L. (1991) The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities. University of Chicago Press

Pimm, S.L. & Raven, P. (2000) Biodiversity: Extinction by numbers. Nature **403**, 843-845

Pontin, J. (1996) Annual Report to English Nature on Formica rufibarbis. Surrey, UK.

Pontin, J. (1998) Annual Report to English Nature on Formica rufibarbis. Surrey, UK.

Pontin, J. (1999) Annual Report to English Nature on Formica rufibarbis. Surrey, UK.

Pontin, J. (2002) Annual Report to English Nature on Formica rufibarbis. Surrey, UK.

Pontin, J. (2005) Ants of Surrey. Surrey Wildlife Trust.

Raine, N.E. Gammans, N. Macfadyen, I.J. Scrivner, G.K. & Stone, G.N. (2004) Guards and thieves: antagonistic interactions between two ant species coexisting on the same ant-plant. Ecological Entomology **29** (3), 345 - 352

Sedláková, I. & Chytrý, M. (1999) Regeneration patterns in a Central European dry heathland: effects of burning, sod-cutting and cutting. Plant Ecology **143** (1), 77-87

Seppä, P. Fernández-Escudero, I. Gyllenstrand, N. & Pamilo, P. (2008) Colony fission affects kinship in a social insect. Behavioural Ecology and Sociobiology **62**, 589-597

Shirt, D.B (1987) British Red Data Books, NC Council, G Britain. Nature Conservancy Council

Skinner, G.J. & Allen, G.W. (1996) Ants. Richmond Publishing Company Ltd.

Sumner, S. Ciborowski, K. & Peniche, G. (*in prep*) Social and population genetic structure in the endangered red barbed ant Formica rufibarbis: implications for a reintroduction programme.

Sundstorm, L. (1997) Queen acceptance and nestmate recognition in monogyne and polygyne colonies of the ant ***Formica truncorum.*** Animal Behaviour **53** (3), 499-510

Suvák, M. (2007) The ants (HYMENOPTERA: FORMICIDAE) in the stubbles- fields of East Slovakia. Acta Zoologica Universitatis Comenianae **47** (1), 21–33

Svensson, L. (1985) An estimate of pollen carryover by ants in a natural population of *Scleranthus perennis* L. (*Caryophyllaceae*). Oecologia **66** (3); 373-377

Svensson, L. (1986) Secondary pollen carryover by ants in a natural population of *Scleranthus perennis L. (*Caryophyllaceae*).* Oecologia **70**, 631-632

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science **303**, 1879-1881

Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B-Biological Sciences **360**, 339-357

UK Species Action Plan for red-barbed ant
http://www.ukbap.org.uk/UKPlans.aspx?ID=312

Underwood, E.C. & Fisher, B.L (2006) The role of ants in conservation monitoring: If, when, and how. Biological Conservation **132** (2), 166-182

Visicchio, R. Sledge, M.F. Mori, A. Grasso, D.A. Moli, F. Le. Turillazzi, S. Moneti, G. Spencer, S. & Jones G.R. (2000) Dufour's gland contents of queens of the slave-making ant *Polyergus rufescens* and its host species *Formica cunicularia*. Ethology Ecology & Evolution **12**, 67-73

Yarrow, I.H.H. & Guichard, K.M. (1941) Some rare Hymenoptera Acualeata, with two species new to Britain. Entomologist’s Monthly Magazine **77**, 2-13

Wardlaw, J.C (1991) Techniques for rearing *Myrmica* ants (Hym.) and *Maculinea rebeli* Hir. Caterpillars (Lep., Lycaenidae). Entomologists Monthly Magazine **127**, 233-241

Wilson, E.O. (1971) Insect Societies. Harvard University Press.