Conservation Biology of *Cryptocephalus* species and Other Threatened UK Beetles

by

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

Abstract

The conservation biology of species within the genus *Cryptocephalus* (Chrysomelidae) and the weevil *Cathormiocerus britannicus* was the focus for this PhD. Four main questions were addressed in the research: a) did the BAP process select the *Cryptocephalus* beetles of genuinely high conservation concern? b) what are the ecological requirements of the adults and larvae? c) what is the vagility of the adults and how genetically differentiated are disjunct remaining populations and how does the population genetic structure affect re-introductions? and d) what is the species status of the putative endemic, *C. britannicus*.-

The conservation prioritisation process may have overlooked some *Cryptocephalus* species that are of genuine conservation concern and it is suggested in future that species are selected objectively based on as much data as possible.

Targeted autecological work showed that the *Cryptocphalus* adults are acutely thermophilic. The integrity of a population seems to be dependant on the presence of trees in a dynamic scrub habitat that offer a juxtaposition of conditions that are suitable for both adults and larvae. Dispersal and molecular studies showed that the rare species have very limited powers of dispersal resulting in a complex population genetic structure. A fact that should be considered when re-introductions are planned. This research also highlights the use of captive rearing and experimental releases as a means of gathering ecological data on rare insect species.

The species status of *Cathormiocerus britannicus* was found to be questionable, highlighting the need for a much more efficient use of the resources that are available for insect conservation.

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I dedicate this PhD to my loved ones: Mum, Dad, Andy, Tim and Melanie. Their support was essential.

List of Abbreviations, Acronyms and Symbols

AMOVA	analysis of molecular variance
ANOVA	analysis of variance
BAP	Biodiversity Action Plan
bp	base pair
COI	cytochrome oxidase I
COII	cytochrome oxidase II
CTAB	hexadecyltrimethylammoniumbromide
DFA	discriminant function analysis
dNTP's	deoxynucleotide triphosphates
ESU	evolutionary significant unit
HAP	Habitat Action Plan
ITS2	internal transcribed spacer 2
IUCN	International Union for the Conservation of Nature
mtDNA	mitochondrial deoxyribose nucleic acid
NNR	National Nature Reserve
PCA	principal component analysis
PCR	polymerase chain reaction
RDB	Red Data Book
rDNA	ribosomal deoxyribose nucleic acid
Taq	*Thermophilus aquaticus*

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PLATES

Chapter 1. General introduction

Invertebrates comprise the greatest component of animal diversity on the planet. Of these the insects have been said to comprise more than 50% of all known species (Groombridge, 1992). The insects are fundamental components in all terrestrial and freshwater ecosystems except those of the Polar regions (Brown, 1991; Morris *et al.,* 1991). However, the conservation of this large and very important group has until recently been largely ignored. Only during the last quarter of a century the discipline of insect conservation has developed (Pyle *et al.*, 1981; Samways, 1984) and until recently nearly all insect conservation efforts have been focused on butterflies (New *et al.*, 1995). Measures that may be successful in conserving vertebrates or plants do not guarantee the maintenance of insect populations. The very characteristics that make many invertebrates so vulnerable, such as their small size and restricted distributions may also facilitate their protection (IUCN, 1986). The propagation of insect conservation as a science has allowed the evolution of conservation management for insects. This process was slow as it was only gradually appreciated that; (a) species in decline are often dependent on artificial or greatly modified habitats, and (b) animal and plant communities are often dynamic in nature (Morris, 1987). Particularly important was the realisation that habitat diversity is related to successional stages that have been maintained over millennia in the UK by traditional agricultural and silvicultural techniques (Duffey & Watt, 1971). Numerous species of conservation concern in the UK depend on early-successional and open anthropogenic habitats (Hambler & Speight, 1996).

The beetles (Coleoptera) are the most species rich order within the insecta. Unlike the Lepidoptera, for example, which are unrepresentative of many lifestyles and habitat types, the beetles are ubiquitous and exhibit many different lifestyles. The diversity of the Coleoptera enables their conservation to illuminate many of the problems and solutions that may be encountered in the conservation of other insects. Following the 1992 International Convention on Biodiversity (the Rio 'Earth Summit') the British government published its response, 'Biodiversity: The UK Action Plan' (UK Steering Group, 1995). This listed 467 invertebrate species of conservation concern in the UK. Individual or group action plans and 'priority' or 'species' statements have been proposed for 237 of these species in subsequent reports (UK Biodiversity Group, 1999a; b). Criteria formulated by the BURD group (UK Database for Ranking Biodiversity) were used for the selection of these species for inclusion in the Biodiversity Action Plans. The list comprised many beetle species, of which there are approximately 4100 species in the UK (Hyman and Parsons, 1992). Of these, approximately 950 (23.2%) species are deemed to be of conservation concern (Hyman and Parsons, 1992). To enable the conservation of rare taxa it is of paramount importance to be able to identify the factors that have contributed to their decline. Habitat loss, as a result of agricultural activity, urbanisation or inappropriate habitat management, has long been cited as the cause of the precipitous decline of some species (Hambler & Speight, 1995; Rackham, 1995). Specific anthropogenic habitat threats are documented in the BAP for over half the presumed extinct insect species in the UK (Shirt, 1987; UKBG, 1999). For example, less than 10% of heathland cover in Europe remains, due to the manifold effects of afforestation, agricultural and industrial activity and urbanisation (Rose *et al.*, 2000). Britain, in the last 2000 years has lost approximately 80% of its wetlands (Merritt, 1994; Rackham, 1995) and in the last 5000 years roughly 90% of its forests (Department of the Environment, 1994; Rackham, 1994).

Conservationists of insects are faced with many problems, of which being able to identify a certain species and taxonomic units within is of utmost importance. Specific knowledge of the autecology of the species is also required. Successful conservation depends on an understanding of a species' biology and life history. Elucidating the micro-habitat preferences, feeding preferences and dispersal ability and other features of a rare species is therefore an integral part of any insect conservation programme, once the animals in question can be identified. For very rare or inconspicuous species information of this nature is still so scarce that it is almost impossible to make statements about the requirements of a particular species. Human intervention in the form of habitat management can even lead to extirpation if the ecological requirements of the species are not understood (Ehrlich & Ehrlich, 1981).

Conservation resources need to be concentrated on those species, which have genuinely declined and whose taxonomic status is assured. An often-asked question is how should conservation be prioritised. Should the species be considered as the unit of conservation or does each sub-population or population merit individual conservation efforts? A population unit that is ecologically or genetically distinct from other populations typically merits separate management and a high priority for conservation (Ryder 1986). Recognition of these distinct populations enables conservation efforts to be concentrated on any groups of individuals that may be in need of special protection. Tailored management strategies can be formulated for these populations or groups of populations (Soltis and Gitzendammer 1999; Johnson & Jordan, 2000). This subject also has important implications for re-introductions, as efforts must be made to conserve genetic diversity that may have developed or been retained between disjunct populations of particular species.

This thesis approaches the subject of insect conservation from a number of angles with several species within the genus *Cryptocephalus* (Coleoptera: Chrysomelidae) and another beetle within the genus *Cathormiocerus* (Coleoptera: Curculionidae) as study species. Field studies to elucidate the habitat preferences of three *Cryptocephalus* species were an integral part of this research. Consultant entomologists were employed during the field seasons to survey sites for the *Cryptocephalus* species and to collect specimens for molecular studies.

Chapter 2

This chapter examines prioritisation in insect conservation using the genus *Cryptocephalus* as a model. The objectives were to investigate the extent to which the beetles in question have declined together with an examination of the robustness of selection of a certain species onto the Biodiversity Action Plan. European data on the species were also collated to assess the rarity of the *Cryptocephalus* species on the continent.

Chapter 3

Three *Cryptocephalus* species were studied in depth in this thesis. There are several other species where no reliable population is known. The objective of this chapter was to collate all the known information on all of these species including the ones where reliable populations were identified. This information includes data from various surveys undertaken by consultant entomologists that were employed over the three years. Information from literature searches, personal communications and anecdotal sources were collated to provide a synthesis of information on each species. Miscellaneous data for *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* that were not appropriate for other chapters was included in this chapter.

Chapter 4

Certain life stages of some insects exhibit varying levels of crypsis or can only be found in very small numbers. Gathering information on the biology of a species with low abundance or cryptic stadia can be very difficult. Larvae are generally difficult to locate, therefore, understanding the requirements of this life stage can be a very frustrating process. This chapter details the use of a novel technique that was developed in the first year of research to recover released *Cryptocephalus* larvae so that ecological information could be gained.

Chapter 5

The habitats of larval and adult *Cryptocephalus* beetles are very different and at each site for *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* exist a very small number of trees where there is a juxta-position of suitable larval and adult habitat. The '*mother knows best*' hypothesis was a central theme of this chapter as these species provide an interesting system in which to study the relationship between female oviposition preference and offspring performance. Defining the characteristics of these suitable trees together with feeding preference studies of captive adults and larvae were the main objectives of this chapter.

Chapter 6

The objectives of this chapter were to examine the over-wintering survival of released *Cryptocephalus coryli*, *C. decemmaculatus* and *C. nitidulus* larvae recovered using the technique described in Chapter 4. A link between ground cover characteristics and predation would also be sought. The research was carried out in the context of the '*mother knows best*' hypothesis to examine the link between female oviposition preferences and larval survival. The results from this chapter would be used to provide guidelines on how the chances of success of larval releases could be improved for the purposes of re-introduction programmes that are described in the Species Action Plans.

Chapter 7

Mark release recapture experiments were undertaken on populations of *Cryptocephalus decemmaculatus* and *C. nitidulus*. The objectives of this chapter were to estimate population sizes, understand the mechanisms by which the adults move through their habitat and estimating the flight period and life expectancy of the beetles.

Chapter 8

The rare *Cryptocephalus* species exist in disjunct populations. The genetic differentiation within and between these populations was compared to other *Cryptocephalus* species with more contiguous distributions. The main objective was to gain an insight into the distinctiveness of each sub-population or population so that habitat management and re-introductions could be carried out in a way to preserve genetic diversity. The findings of this chapter were discussed with reference to the findings of Chapter 7.

Chapter 9

The techniques that were used to investigate the genetic differentiation between *Cryptocephalus* populations were also used to investigate differentiation at the species level. The putative endemic, *Cathormiocerus britannicus* (RDB1) was compared genetically and morphometrically to *C. myrmecophilus* in order to examine if the RDB 1 species with a biodiversity action plan deserves its species status and therefore, its high conservation status.

Chapter 10

There are many rare UK insect species where no reliable populations are known. This chapter discusses the use of moderately sized releases as a tool for learning ecological information about these rare species. The genus *Cryptocephalus* is used as a model as a great deal of information has been obtained from releases and captive rearing.

Chapter 11

The gathering of detailed information on the autecology of selected species is very important in the formulation of management proposals for sites where *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* are presently found. Habitat preference data from Chapter 5 is used to make recommendations for the sympathetic management of these sites. Other objectives of this chapter were to collate information on management (beneficial or detrimental) that has already taken place. Suggestions are also given for the ways in which current sites could be managed to produce a matrix of areas that possess suitable habitat.

Chapter 2. Which *Cryptocephalus* beetles most deserve conservation priority?

2.1. Introduction

Prioritisation of resources for the conservation of species combines subjective and objective components. Larger species, especially vertebrates, have a higher public profile than smaller species, but also often require large-scale efforts if they are to be conserved. This is reflected in the relatively generous funding that is provided for the conservation of mammals, birds and other vertebrates (R. Key, pers. comm.). In contrast, the funding available for insect conservation is small (R. Key, pers. comm.). Furthermore, much of this funding is targeted towards species in high profile insect groups: butterflies and dragonflies. The relatively small levels of resources available for the other insects make it particularly important that priority should be given to those species for which there is most cause for concern (and for those species where practical considerations mean that results are likely to be achieved). This depends on accurate information on their conservation status.

Prioritisation of UK insects of conservation concern is largely in accordance with international guidelines (together with domestic modifications) established by the IUCN. The IUCN criteria aim to categorise the extent of threat posed to species, rather than their degree of rarity (Shirt, 1987). In descending order of threat the IUCN categories are Red Data Book (RDB) 1 (Endangered), RDB2 (Vulnerable), RDB3 (Rare), RDB EX (extinct). They are supplemented by the ‘domestic’ category of Nationally Scarce (usually subdivided into Notable A and Notable B).

The criteria for a species to be classed as Endangered in the UK can be summarised as a) occurrence in vulnerable habitats, b) rapid decline; c) presently extant in five or fewer 10 km squares and e) possibly extinct (not recorded within 100 years). Species classed as Vulnerable have exhibited a decline throughout their range and/or depend on vulnerable habitats. Classification of a species as Rare depends on their populations being recorded from 15 or fewer 10 km squares, or if their populations exist in more than 15 10 km squares, then they are dependent on very small areas of vulnerable habitat. The Notable categories are defined on the number of grid squares that a species is found in. The Species of Conservation Concern list (SoCC) was formerly known as the UK Database for Ranking Biodiversity (BURD). Maintained by JNCC, it provides an assessment of the extent of conservation concern for plants and animals in this country, sumarising data covering global threat, international importance, national threat, decline and distribution within the UK. Species included on the list satisfy one or more of the following criteria: they are a threatened endemic or globally threatened, have more than 25% of the world population in the UK, have numbers or range that have declined by more than 25% in 5 years, occupy less than 15 ten kilometre squares, or are listed under international legislation

Following the 1992 International Convention on Biodiversity (the Rio 'Earth Summit') the British government published its response, 'Biodiversity: The UK Action Plan' (UK Steering Group, 1995). This listed 467 invertebrate species of conservation concern in the UK. Individual or group action plans and 'priority' or 'species' statements have been prepared for 237 of these species (UK Biodiversity Group, 1999a, b, 2000). Although based on the BURD list, criteria such as population or range decline and international threat could only rarely be applied to many of the invertebrate species due to the deficiencies in the available data (Key, *et al.,* 2000).

BAP priority species were nominally selected according to criteria set out in the 1995 Steering Group report (UK Biodiversity Steering Group, 1995*).* These aim to identify those species that are most at risk in the UK, while also taking into account the species' broader distributions and vulnerability. A list of Species of Conservation Concern that summarises current conservation status is maintained by JNCC (SoCC, formerly the UK Database for ranking Biodiversity (BURD). The criteria for inclusion can be summarised (DETR, 2001) as:

1. Numbers or range have declined substantially in the last 25 years;
2. Endemic to the UK or with more than a quarter of the world population here;
3. Under a high degree of threat internationally, and
4. Covered by relevant conventions, directives and legislation.
5. In "some instances" a distribution of fewer than 15 ten km squares also merits inclusion.

Clearly many of these criteria are dynamic, with values that change over time due to more data becoming available and real changes in the distribution and abundance of species (Key *et al*., 2000). Invertebrates, and particularly insects, contribute far more BAP species than do vertebrates or higher plants. Compared to continental Europe and most other areas, Britain has a relatively depauperate invertebrate fauna, but one which has been intensively recorded (Bratton, 1991; Collins and Thomas, 1991). Determination of those insects and other invertebrates that are of conservation concern should therefore be easier in Britain than in less well-recorded parts of Europe and elsewhere. However, with the exception of butterflies, some moths, dragonflies and water beetles (Heath *et al.,* 1984; Moore, 1976; Foster, 1991) insufficient data meant that two of the four criteria listed above could rarely be included with confidence during BAP prioritisation (Key *et al.,* 2000). The requirement for a '50% decline in range or numbers within the last 25 years' could rarely be met because estimates of UK population size are available for very few insect species, while few recent distribution records, compared with records that may have been accumulated over a century or more, may merely reflect changes in collection effort, rather than a true decline, especially if it is an inconspicuous species. 'International Threat' was also a difficult criterion to apply, because of a lack of recording data and of co-ordination across Europe. As a result, the broader conservation status of most UK insects is uncertain.

Here I provide estimates of the European status and rate of decline in the UK of *Cryptocephalus* beetles (Chrysomelidae). As with the majority of insect species, these criteria were not available when their current BAP priorities were assigned. A revised estimate of the beetles' relative conservation status is then presented, and compared with their current BAP prioritisation. The acquisition of similar data for other insects should be considered ahead of revisions of their conservation status.

2.1.1. Cryptocephalus 'pot beetles'

Beetles of the cosmopolitan genus *Cryptocephalus* are known as 'pot beetles', a name which relates to the characteristic biology of the larvae. *Cryptocephalus* adults feed on leaves and petals and are generally oligophagous, though a few species have more restricted host ranges (Erber, 1988). Larvae are found in leaf litter and eat mainly dried and decaying leaves (Lesage, 1985), although fresh plant material may also be required before pupation (Masutti, 1960). Adults are generally thermophilic, capable of flight and can often be found sitting in exposed positions on the leaves of trees and shrubs. Females oviposit from such perches, covering each egg in faeces to form an egg case that is dropped onto the ground below. Once hatched, the larvae progressively enlarge the case with their own droppings, forming the larval "pot", which they carry around with them (Erber, 1988). Over-wintering in northern latitudes takes place in the larval stage, with pupation and adult emergence taking place in the spring (Steinhausen, 1994). Most UK species are thought to be univoltine, but some appear to require more than one year to complete their development.

The genus *Cryptocephalus* is represented in Europe by 84 species, of which 19 occur in Britain (Kloet and Hincks, 1964) while a 20th, *C. violaceus*, is now extinct (Table 2.1). The UK *Cryptocephalus* species have broad ranges, often extended throughout the Palaearctic (Table 2.1). The genus has a high proportion of species recognised as being of conservation concern. Seven species were listed in the Red Data Book of insects (Shirt 1987) and six (32 % of the UK species) have a Species Action Plan or Priority Statement (UK Biodiversity Steering Group, 1999). Some of the species have only very small population sizes in the UK. No more than ten *C. primarius* individuals have been found in the last decade (see Chapter 3) and the last known

English population of *C. decemmaculatus* is no larger than 600 individuals (see Chapter 7). The proportion of *Cryptocephalus* species that are of conservation concern (Endangered, Vulnerable, Rare, and Notable A & B) is unusually high (Table 2.2). It has a higher proportion of such species than comparable genera within the Chrysomelidae, other chrysomelids in total and the remainder of the UK Coleoptera as a whole (as listed in Kloet & Hincks, 1964). The University of Leeds and Suffolk Wildlife Trust are Lead Partners for these species and they are the subject of active ecological research programmes funded by English Nature.

Table 2.1. The BAP and RDB status of British *Cryptocephalus* beetles. RDB status is from Shirt (1987), repeated in Hyman and Parsons (1994), BAP status is from UKBG (2000).

Species	RDB Status	BAP Status	Habitat	Global Range
C. aureolus	Notable B	No status	calcareous slopes	Palaearctic
C. biguttatus	Vulnerable	No status	wetland	W. Palaearctic
C. bilineatus	Notable B	No status	unimproved grassland	Palaearctic
C. bipunctatus	Notable B	No status	scrub transition / calcareous slopes	W. Palaearctic
C. coryli	Endangered	Action Plan	scrub transition	Palaearctic
C. decemmaculatus	Vulnerable	Priority Statement	scrub transition on wetland	W. Palaearctic
C. exiguus	Endangered	Action Plan	wetland	W. Palaearctic
C. frontalis	Notable A	No status	scrub transition	W. Palaearctic
C. fulvus	No status	No status	unimproved grassland	Palaearctic
C. hypochaeridis	No status	No status	calcareous slopes	Palaearctic
C. labiatus	No status	No status	mature / ancient trees	W. Palaearctic
C. moraei	No status	No status	unimproved grassland	W. Palaearctic
C. nitidulus	Endangered	Action Plan	scrub transition	Palaearctic
C. parvulus	Notable B	No status	scrub transition	Palaearctic
C. primarius	Endangered	Action Plan	calcareous slopes	S.W. Palaearctic
C. punctiger	Notable A	No status	scrub transition	W. Palaearctic
C. pusillus	No status	No status	mature / ancient oaks	W. Palaearctic
C. querceti	Vulnerable	No status	mature / ancient trees	W. Palaearctic
C. sexpunctatus	Vulnerable	Action Plan	scrub transition	W. Palaearctic
C. violaceus	Extinct	Extinct	calcareous slopes	W. Palaearctic

Table 2.2. The status of UK Cryptocephalus species compared with other genera of chrysomelid beetles and with beetles in general.

		Endangered, Vulnerable, Rare, Notable A and B		Indeterminate / insufficiently known		No status	
	Total	**n**	**%**	**n**	**%**	**n**	**%**
Cryptocephalus	19	14	73.7	0	0.0	4	21.1
Donacia	15	9	60.0	0	0.0	6	40.0
Chrysolina	16	8	50.0	0	0.0	8	50.0
Longitarsus	41	21	51.2	2	4.9	18	43.9
Psylliodes	14	5	35.7	1	7.1	8	57.1
Cassida	12	5	41.7	0	0.0	7	58.3
Other chrysomelids	236	107	45.3	6	2.5	21	8.9
Coleoptera	4100	1030	25.1	372	9.1	2550	62.2

2.2. Prioritisation of Cryptocephalus species: are the BAP priority species the most threatened?

2.2.1. Criteria for the current BAP listing

No UK *Cryptocephalus* species are endemic, or listed on international protocols. In the absence of data relative to any criteria other than distribution, the current BAP list is, not surprisingly, linked strongly with the numbers of recent distribution records (Figure 2.1).

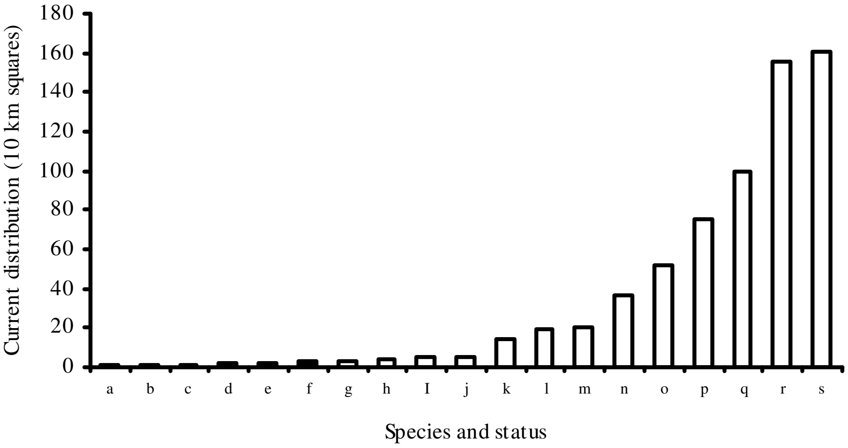

Figure 2.1. The abundance of British *Cryptocephalus* species, based on the number of ten kilometre squares they occupy. ***a = C. exiguus (E), b = C. nitidulus (E), c = C. primarius (E), d = C. decemmaculatus (V), e = C. sexpunctatus (V), f = C. coryli (E), g = C. querceti (V), h = C. punctiger (nA), I = C. biguttatus (V), j = C. frontalis (nA), k = C. bilineatus (nB), l = C. hypochaeridis, m = C. bipunctatus (nB), n = C. parvulus (nB), o = C. moraei, p = C. aureolus (nB), q = C. fulvus, r = C. pusillus, s = C. labiatus.*** **E = endangered, V = vulnerable, nA = nationally scarce A, nB = nationally scarceB.**

2.2.2. Additional criteria 1: Decline within the UK

The historical and present-day distributions of *Cryptocephalus* species in the UK were plotted at the scale of Watsonian vice-counties, based mainly on data acquired from the National Recorder for Chrysomelidae (Dr Mike Cox, pers. comm.). Literature searches and field surveys yielded further information. Rates of decline for each species were summarised as an extinction ratio (the number of sites lost / the number of sites historically occupied).

Since British records began many *Cryptocephalus* species have experienced a decline in distribution and one species, *C. violaceus* was last recorded in 1864 (Table 2.3).

Table 2.3. The decline of the British *Cryptocephalus* species, ranked according to their extinction ratios.

Species	Present RDB Status	No. of sites apparently lost	Present sites	Extinction ratio (proportion of sites lost)	Number of VC's Where ever recorded	Average No. of sites lost per occupied VC
C. violaceus	Extinct	1	0	1.00	1	1.00
C. sexpunctatus	Vulnerable	25	2	0.93	16	1.56
C. frontalis	Notable A	28	3	0.90	17	1.64
C. exiguus	Endangered	5	1	0.83	5	1.00
C. biguttatus	Vulnerable	14	3	0.82	9	1.56
C. coryli	Endangered	17	4	0.81	11	1.56
C. nitidulus	Endangered	12	3	0.80	8	1.55
C. decemmaculatus	Vulnerable	5	2	0.71	6	0.83
C. primarius	Endangered	5	2	0.71	5	0.80
C. bilineatus	Notable B	18	14	0.56	11	1.64
C. punctiger	Notable A	7	6	0.54	7	1.00
C. bipunctatus	Notable B	30	26	0.54	29	1.03
C. aureolus	Notable B	63	72	0.47	44	1.43
C. moraei	No status	36	53	0.40	32	1.13
C. hypochaeridis	No status	17	26	0.40	14	1.21
C. parvulus	Notable B	17	33	0.34	23	0.74
C. labiatus	No status	75	157	0.32	69	1.09
C. fulvus	No status	45	111	0.29	44	1.02
C. querceti	Vulnerable	1	3	0.25	5	0.20
C. pusillus	No status	44	167	0.21	59	0.75

Some species of conservation concern, have, historically, only ever been recorded from a small number of sites (e.g. *C. exiguus, C. querceti,* and *C. primarius*). Conversely, other species such as *C. sexpunctatus,* which were once regarded as being locally common, are now extremely rare. Other species that were once relatively widely distributed have also shown marked declines, and are clearly likely to be at particular risk. In particular, the extinction ratio of *C. frontalis* (0.90) is much higher than those of *C. coryli* (0.81), *C. exiguus* (0.83) and *C. decemmaculatus* (0.71), yet it is not a BAP priority species (UK Biodiversity Steering Group, 1999). The proportion of sites that have been lost appears to be related to the number of sites where they have been recorded, with most of the species that have never been recorded from less than about 40 sites suffering losses in excess of 50%, while all the more widespread species have lost a smaller proportion of sites (Table 2.3, Figure 2.2).

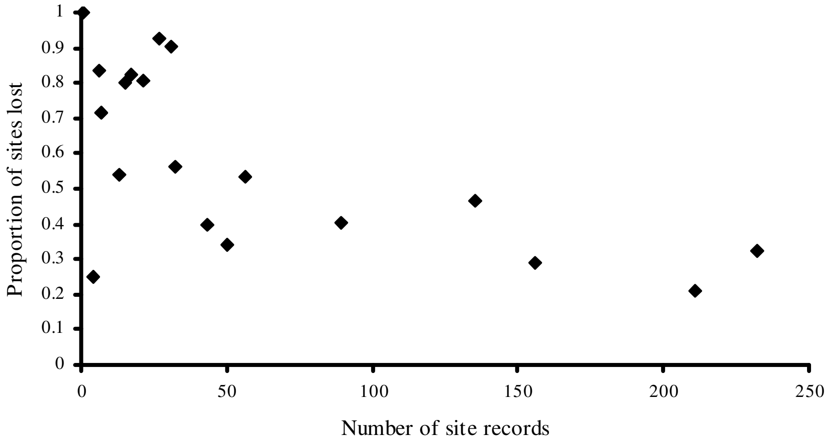

Figure 2.2. The relationship between the number of sites recorded for British *Cryptocephalus* species and the proportion of sites where the beetles have been lost.

Some caution is needed however, as this pattern might be generated by the more common species only being recorded systematically in recent years, as they were of little interest to amateur collectors. When records at the level of vice-county are compared, a different pattern emerges. The number of sites lost is independent of the number of vice counties where the beetles had been recorded (Table 2.3, Figure 2.3). This confirms the impression that the genus as a whole has been in decline, not just those species that are BAP listed, but the rarer species were starting from a lower baseline of abundance.

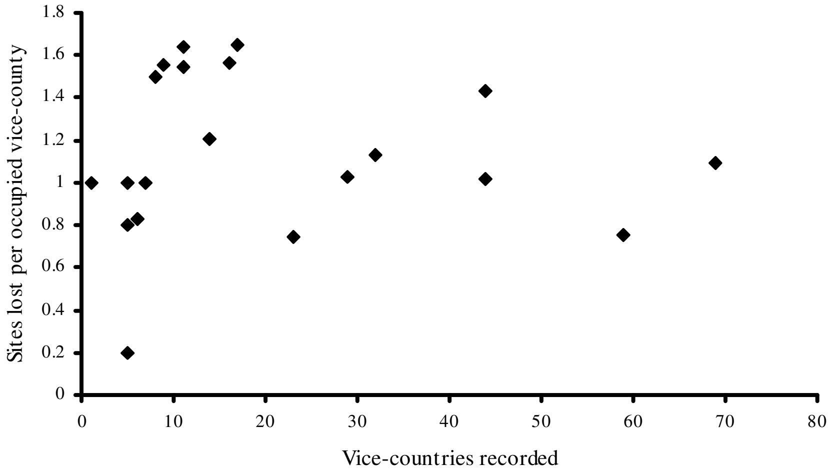

Figure 2.3. The relationship between the number of vice-counties where British *Cryptocephalus* species have been recorded and the mean number of sites per occupied vice-county that have been lost.

A lack of recent records may be a genuine indication of decline, or may be a consequence of sites not being re-surveyed. Peter Hodge, an authority on UK Coleoptera, kindly provided the data for Appendix 1, based on his personal knowledge of sites and collecting visits that have taken place over many years. The collections were not systematic, but do provide a means of assessing the frequency of re-discovery of *Cryptocephalus* from sites where they have been recorded, and the proportion of the sites that now appear totally unsuitable for the species (Table 2.4). Most of the known sites for the rarer *Cryptocephalus* species are included within the 199 site re-surveys (some based on multiple visits), 30.1% of which succeeded in finding the beetles. Only very intense surveying can confirm the absence of a species, so this does not necessarily indicate a very high rate of species loss from the sites. Nonetheless, of the 137 sites with habitat data where a species was not re-recorded, 36.5% are now considered by Mr Hodge to be no longer suitable for the species.

Table 2.4. Decline in *Cryptocephalus* species, as measured by the success of re-surveys. At sites where the beetles were not re-discovered, an indication is provided of whether or not the habitat has been greatly changed and is highly unlikely to still be suitable (habitat information was not available for some sites). Based on data provided by Peter Hodge.

Species	**Re-survey results**		**Habitat at sites where not re-recorded**	
	Present	Absent	Suitable	Unsuitable
C. aureolus	8	5	3	2
C. biguttatus	1	15	10	5
C. bilineatus	4	1	12	0
C. bipunctatus	1	14	14	0
C. coryli	4	18	8	10
C. decemmaculatus	2	3	0	3
C. exiguus	1	4	3	1
C. frontalis	2	3	3	0
C. fulvus	6	8	8	0
C. hypochaeridis	2	8	8	0
C. labiatus	6	1	1	0
C. moraei	3	5	5	0
C. nitidulus	3	12	2	10
C. parvulus	2	9	6	3
C. primarius	2	5	3	2
C. punctiger	3	5	4	1
C. pusillus	6	4	4	0
C. querceti	2	4	2	1 (1?)
C. sexpunctatus	2	15	2	12 (1?)

Re-survey failure rates varied between about 20 and 90% between the species, but were not linked to their present-day abundance, probably because many factors can influence the likelihood of survey success (Figure 2.4). The highest failure rates at previous sites were with the very rare *C. sexpunctatus*, and the more widespread *C. biguttatus* and *C. bipunctatus.* Neither of the latter species are BAP listed, but this result suggests they may need closer attention than is apparent from considering their current distribution alone (Figure 2.1). The decline in *C. bipunctatus* does not seem to be related to gross habitat change whereas for *C. sexpunctatus* and possibly *C. biguttatus* this is likely to have been an important contributor to their decline. Habitat loss does appear to have been more significant among the rarer *Cryptocephalus* species as a group, compared with the more widespread species (Figure 2.5).

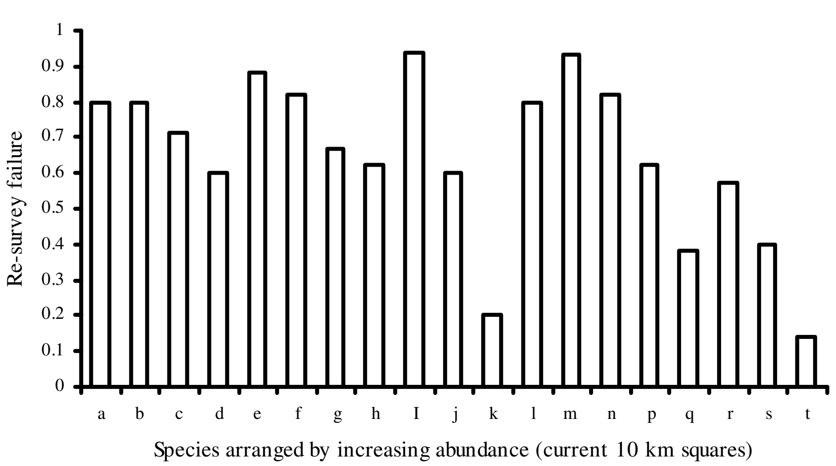

Figure 2.4. Rates of failure to re-confirm the presence *Cryptocephalus* species during survey visits by P. Hodge. See Figure 2.1 rubric for definition of letters on x axis.

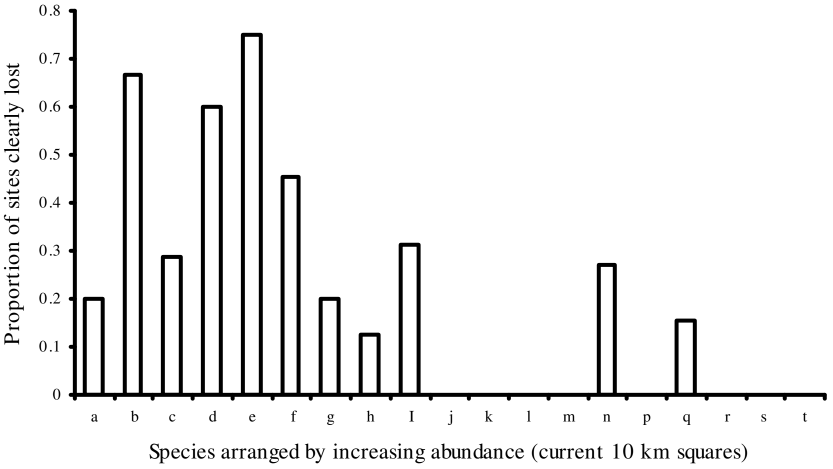

Figure 2.5. Sites re-surveyed for *Cryptocephalus* by P. Hodge where the habitat is clearly no longer suitable. See Figure 2.1 rubric for definition of letters on x axis.

2.2.3. Additional criteria 2: Status in mainland Europe

European distribution records were assembled and compared with the abundance of the beetles in the UK (Table 2.5, Figure 2.6). It is clear that the species with very limited distributions within the UK range from having relatively limited European distributions (*C. nitidulus* and particularly *C. primarius*), through to species that are relatively ubiquitous (*C. coryli, C. sexpunctatus*). Among the British species, *C. primarius* appears to be the only "south-western" species, with no northern and eastern continental records.

Table 2.5. The European distributions of the British *Cryptocephalus* species. A = absent; P = present.

Species	**Denmark**	**Norway**	**Sweden**	**France**	**Belgium**	**Nether.**	**Luxem.**	**Germany**	**Spain**	**Italy**	**Austria**	**Switz.**	**Poland**	**Cz/Slv**	**Latvia**	**Romania**	**Bulgaria**
C. aureolus	P	P	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. biguttatus	P	P	P	P	P	P	P	P	A	P	P	P	P	P	P	P	P
C. bilineatus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. bipunctatus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. coryli	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. decemmaculatus	P	P	P	P	P	P	P	P	A	A	P	P	P	P	P	P	P
C. exiguus	A	P	P	P	P	P	P	P	A	A	P	A	P	P	P	P	P
C. frontalis	A	P	P	P	P	P	P	P	A	A	P	A	P	P	P	P	P
C. fulvus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. hypochaeridis	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. labiatus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. moraei	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. nitidulus	A	P	P	P	A	A	A	P	A	A	P	P	P	P	P	P	P
C. parvulus	P	P	P	P	P	P	P	P	A	A	P	A	P	P	P	P	P
C. primarius	A	A	A	P	A	A	P	P	P	A	A	P	A	A	A	A	A
C. punctiger	P	P	P	P	P	P	P	P	A	A	P	A	P	P	P	P	P
C. pusillus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
C. querceti	P	P	P	P	A	A	A	P	A	A	P	A	P	P	P	P	P
C. sexpunctatus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P

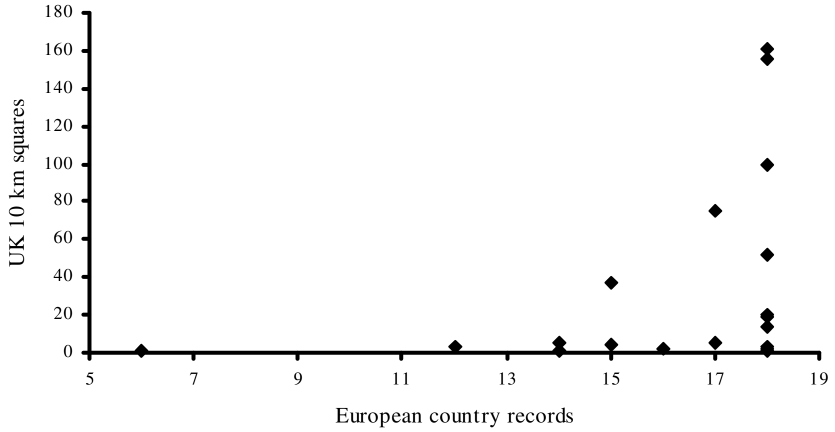

Figure 2.6. The relationship between the abundance of *Cryptocephalus* species in Britain and the number of European countries where they have been recorded.

Personal communications from recognised chrysomelid specialists (see acknowledgements), combined with information from Red Data Books (or analogues) (Ehnstrom, *et al.*, 1993: Geiser, 1998) made possible a comparison of the conservation status of *Cryptocephalus* species in Britain with that in some other European countries (Germany, France, Spain, Norway and Sweden). Abundance ratings were allocated as follows: 0 (Extinct), 1 (Endangered), 2 (Vulnerable), 3 (Rare), 4 (equivalent to Notable A or B) and 5 (Common). A mean rarity rating for each species across these countries was then calculated.

It appears that certain British species (e.g. *C. nitidulus, C. coryli*) are rare throughout much of their European range (Figure 2.7). Conversely, *C. violaceus*, which is extinct in Britain, can be locally common in other parts of its range and *C. decemmaculatus* (which is restricted to one English site and one Scottish site) is considered to be more common on the continent. Taking the genus as a whole, there was a weak, but significant positive correlation between the rarity of the species in Britain and their rarity in the continental European countries ($\nu = 19$, Pearson's Product Moment Coefficient $r = 0.5$, $P < 0.05$), confirming that species less common in the UK also tend to be less common in continental Europe. None of the common British species appeared to be rare on the continent.

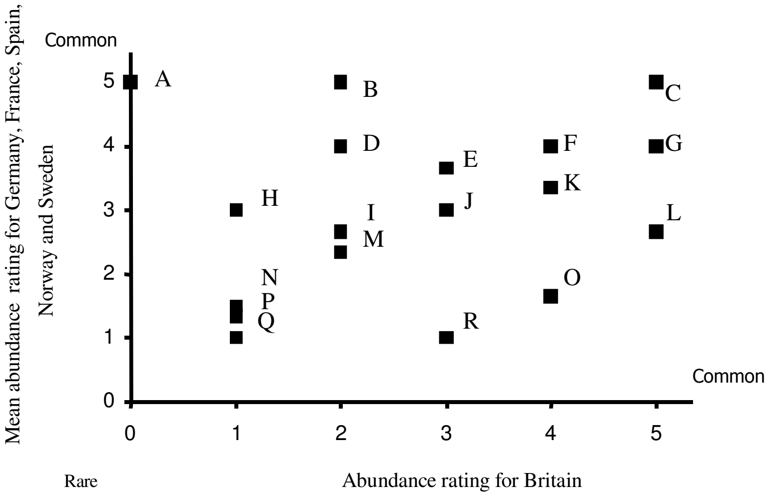

Figure 2.7. The rarity of British *Cryptocephalus* beetles in relation to their status on the continent. (A = *Cryptocephalus violaceus*, B = *C. decemmaculatus*, C = *C. fulvus*, D = *C. querceti*, E = *C. aureolus*, F = *C. parvulus*, G = *C. hypochaeridis*, *C. labiatus* and *C. moraei*, H = *C. exiguus*, I = *C. bigutattus*, J = *C. frontalis*, K = *C. bipunctatus*, L = *C. pusillus*, M = *C. sexpunctatus*, N = *C. primarius*, O = *C. bilineatus*, P = *C. nitidulus*, Q = *C. coryli*, R = *C. punctiger*).

2.3. Discussion

Resources available for the conservation of vulnerable invertebrate species are, at best, scant and those that are available need to be applied with as much objectivity as possible. Subjective decisions concerning which species merit high conservation priority can only result in, at times, misguided selection and the selection of taxa for high conservation priority therefore needs to be based on as much data as possible.

Most species-based conservation efforts in the UK are currently being channelled towards Biodiversity Action Plan (BAP) priority species, while habitat management is being directed via parallel Habitat Action Plans. Determination of which species among the 100,000 or so to be found in the UK (Hawksworth, 2001) should be included on BAP lists is therefore central to current conservation efforts. Little funding is available for those species that fail to meet the criteria for inclusion on BAP lists and currently only 10% of BAP resources can be allocated towards non-BAP species, consolidating the need for accuracy and objectivity in the prioritisation of conservation.

Many of the criteria used to identify species for the BAP are difficult to apply and some have inherent limitations. The UK has very few endemic species and only a tiny minority of (usually large or conspicuous) insects are covered by conventions and legislation. This has meant that selection of insect species for BAP prioritisation has necessarily depended mainly on assessments of their known ranges, supplemented by *ad hoc* knowledge of individual species.

The distribution and abundance of insects can change very rapidly and prioritisation of species should ideally be as dynamic as the populations of those insects that need to be conserved. In practice, however, because of these problems, the BAP prioritisation of insects for conservation has in the main been based on accumulated distribution records, which equate more with rarity than with risk.

Cryptocephalus merits its high conservation prioritisation relative to other genera of beetles in Britain. It has one of the highest frequencies of RDB beetles despite containing, mainly large, non-cryptic species that are unlikely to be under reported in comparison with other beetles. Within the genus, current BAP prioritisation accurately reflects the present day abundance of the species, though four non-BAP taxa (*C. querceti, C. punctiger, C. biguttatus and C. frontalis*) are currently known from very few sites. Rate of decline (as measured by extinction ratio) has been high among all the BAP-listed species, but has also been as high in *C. frontalis*, and *C. biguttatus*. Decline, as measured by re-survey failures, was not closely related to current abundance, but pointed to *C. biguttatus* (and *C. bipunctatus*) having unexpectedly high rates of loss. Amongst the non-BAP species, *C. biguttatus* also has the highest proportion of sites that have suffered gross habitat changes.

European status was not explicitly taken into account when determining which species would require species action plans, but the status of *Cryptocephalus* in Britain is largely reflected in continental Europe as well. *C. coryli, C. nitidulus, C. primarius* are not only very rare in Britain, but also very rarely seen in Europe. Although the range of some of these species is extensive (*C. coryli* and *C. nitidulus* reach Korea and Japan, respectively; Takizawa, 1975; Warchalowski, 1991), they are seldom, or never, found in abundance (Warchalowski, 1991; B Enstrogm, pers. comm.). In contrast, *C. primarius* has only a relatively small distribution in Europe, and where it does occur it is of very high conservation concern, which emphases the importance of this species which is also extremely rare in the UK. Among the non-BAP species *C. biguttatus, C. bilineatus*, *C. frontalis* and *C. pusillus* appear to be of more conservation concern at the whole European level than in the UK alone although all four of these species are in some way more cryptic than *C. coryli, C. nitidulus* or *C. primarius*. The demise of the Essex emerald moth is a prime example of why continental information should be gathered on rare British insects. This moth became in extinct in the UK and it was believed that re-introductions could be carried out using continental specimens (P. Waring, pers. comm.). Unfortunately, after a great deal of continental survey work it was conceded that the Essex Emerald had become globally extinct (P. Waring, pers. comm.).

It has been argued that thermophilic species, such as *Cryptocephalus* beetles, that depend on ephemeral, mid successional habitats have never been naturally common in Britain but that anthropogenic disturbance has permitted northerly range extensions (Thomas and Morris, 1994). Although this may be true for some insect species of conservation concern in Britain it is evident that *Cryptocephalus* beetles rare in Britain are also often rare in continental Europe. This is in contrast to other rare British insects that can be widespread and common on the continent (Thomas and Morris, 1994).

In conclusion, the current BAP-priority species clearly deserve this designation, but the additional data provided here suggests that there are additional species, in particular *C. biguttatus and C. frontalis* that also probably merit inclusion. Among the BAP-listed species, the rarity of *C. primarius* overseas perhaps appropriately makes it the species that should be of primary conservation concern in the UK.

Chapter 3. The rare species of UK Cryptocephalus: the current state of knowledge and a possible way forward.

3.1. Introduction

Detailed ecological studies of an insect species are dependent upon the reliability and availability of that species in sufficient numbers for observations to be made. Many Biodiversity Action Plan (BAP) listed insects have seen little progress in terms of implementation of their action plans because they are simply too rare for worthwhile studies to be carried out. The conservation biology of *C. coryli*, *C. decemmaculatus* and *C. nitidulus* detailed in this chapter and Chapter 5 reflect this limitation, in that these were the species where reliable populations were discovered. This contrasts with the information gathered here from text sources and site visits on those species in the genus that are of conservation concern but could not be found reliably: *C. primarius* and *C. exiguus* (both RDB1); *C. sexpunctatus, C. biguttatus* and *C. querceti* (all RDB2) and *C. frontalis* (Notable A).

3.1.1. Materials and Methods

Searching through British and European texts produced the majority of the data in this overview. Information on historic distributions was collated mainly from the *Entomologist's Monthly Magazine* and *The Entomologist's Record and Journal of Variation*. Other records of these species were obtained from the national Chrysomelidae recorder (M. Cox. Pers. comm.). Field surveys of sites for *Cryptocephalus primarius*, *C. querceti* and *C. sexpunctatus* entailed searches for adults using beating trays, sweep nets and simple visual searching. Where gaps in our knowledge of current distributions were identified, consultant entomologists were employed (with funding from English Nature) to survey sites for *C. exiguus*, *C. primarius, C. querceti* and *C. sexpunctatus*. Searches for larvae were also conducted. Here, the ground beneath adult host vegetation was examined carefully and in some cases ground material was collected and taken back to the laboratory where it was sieved.

3.2. Cryptocephalus coryli (Linnaeus 1758)

3.2.1. Description

Cryptocephalus coryli is a one of the largest *Cryptocephalus* beetles in the UK. Females can reach 8 mm in length (Plate 1) whereas males can reach 6 mm (Plate 2). Clear sexual dimorphism is apparent as females have an all red pronotum. The pronotum in males is all black. Females are also bulkier than males with relatively shorter prothoracic limbs and antennae. Like other *Cryptocephalus* beetles, the females have an obvious depression in the middle of the pygidium that is used to rest the egg in during the formation of the egg case. Larvae are whitish with a dark brown sclerotised head capsule and prothorax (Plate 3). The body inside the larval case is held in a 'C' shape. As with all *Cryptocephalus* larvae, *C. coryli* larvae have well developed legs. The egg case of this species (Plate 1) is relatively smooth and elliptical.

3.2.2. Distribution

3.2.2.1. UK distribution trends

Table 3.1 and Figure 3.1 shows the past and present distribution of *Cryptocephalus coryli* in the UK. Old records suggest that this species had a widely scattered distribution throughout Eastern England with a very disjunct location in Scotland (Fowler, 1890; Fowler & Donisthorpe, 1913; Harwood, 1947; Shirt, 1987; Hyman & Parsons, 1992). Only single specimens have ever been found at many of the localities listed in Table 3.1 and it has always been considered to be rare (Fowler, 1890). Specimens have been recorded from scrub invading heathland, calcareous grassland and woodland rides. Headley Warren (Surrey), where specimens have frequently been reported, has long been known among coleopterists wanting specimens of *C. coryli*. Sherwood Forest (Notts.) was another site once regarded as 'good' for *C. coryli* as well as other species (Kidson-Taylor, 1909). Up to 13 specimens were taken during each visit to this locality by J. Kidson-Taylor and his associates (Kidson-Taylor, 1904, 1906 and 1909), where *C. coryli* was beaten or picked from young birches and oaks during June. Unfortunately, due to the vague records left by collectors in the early 1900's, the precise location of the area within Sherwood Forest where *C. coryli* was recorded is unknown. In 1991 specimens were first recorded from North Unhill Bank in Oxfordshire, and their presence was confirmed in 1998. Populations are also currently found at Headley Warren, Kirkby Moor and Box Hill. Historically, relatively large populations have been found at Box Hill and Headley Warren, but recently the largest populations of *C. coryli* have been found at Kirkby Moor and Headley Warren.

Table 3.1. Records of *Cryptocephalus coryli*. Recent records in bold.

Site	Grid Ref.	Year of Record	Source
Blean Woods Complex (E. Kent)	TR16	1967	M. Cox , pers. comm., 1999.
Cobham Park (W. Kent)	TQ6868	1942	M. Cox , pers. comm., 1999.
Cobham Woods (W. Kent)	TQ6968	1932	M. Cox , pers. comm., 1999.
Darenth Wood (W. Kent)	TQ5873	1910	Maidstone Local Record Centre.
Westerham (W. Kent)	TQ4454	Unknown	Shirt, 1987.
Box Hill (Surrey)	**TQ1852**	**1908-1999**	**Shirt, 1987, G. Collins pers. comm., 2000,.**
Dorking (Surrey)	TQ1649	1986	M. Cox , pers. comm., 1999.
Headley Warren (Surrey)	**TQ188539**	**1914-2000**	**G. Collins, , pers. comm; 1999. Pers. obs., 2000.**
Mickleham (Surrey)	TQ1753	1923	Hyman and Parsons, 1992.
North Unhill Bank (Berks.)	**SU561833**	**1991**	**Hodge and Williams, 1997. M. Harvey, pers. comm.**
Stockgrove (Beds.)	SP9129	Unknown	Shirt, 1987.
Bedford Purlieus (N.hants.)	TL042995	1935-1970	M. Cox, pers. comm., 1999.
Cannock Chase (Staffs.)	SK0017	1910	M. Cox, pers. comm., 1999.
Kirkby Moor (N Lincs.)	**TF225625**	**1987-2001**	**M. Cox, pers. comm., 1999. Pers. obs., 1999, 2000. A. Binding, pers. comm., 2001**
Linwood Warren (N Lincs.)	TF132875	1955	M. Cox, pers. comm., 1999.
Middle Rasen (N Lincs.)	TF1091	1965	H. Henson, pers. comm., 1999.
North Wood (N Lincs.)	TF130870	1946	M. Cox, pers. comm., 1999.
Langford Moor (Notts.)	SK8555	1899	M. Cox, pers. comm., 1999.
Sherwood Forest (Notts.)	SK66	1908	Kidson-Taylor, 1904.
Witchampton (Dorset)	ST9806	1939	M. Cox, pers. comm., 1999.
Kincraig (Invernesshire)	NH64	1946	Harwood, 1947.

3.2.2.2 European distribution

The continental distribution of this species comprises a large part of the Palaearctic and it can be found from the UK to Korea (Warchalowski, 1991). On the continent it occurs only rarely and locally (Warchalowski, 1991), apparently displaying a distribution, pattern of abundance and habitat preference similar to that in the UK (D. Telnov, pers. comm.).

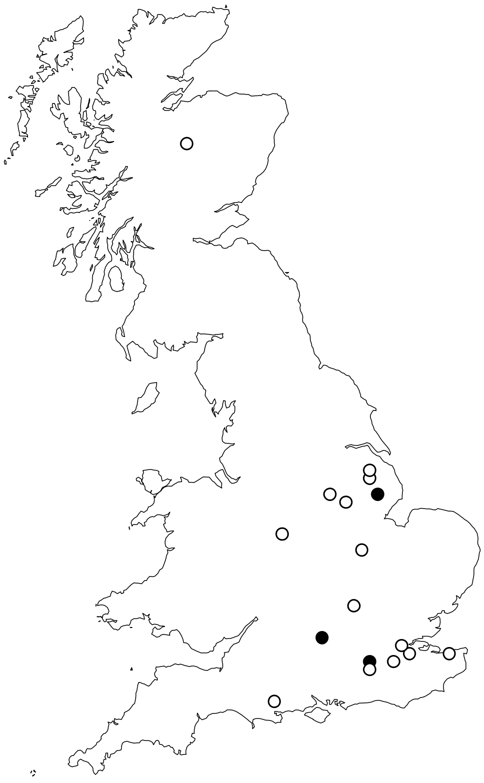

Figure 3.1. Past and present distribution of *Cryptocephalus coryli* [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.2.3. Surveys

3.2.3.1. Materials and Methods

Table 3.2 shows the 36 sites that were surveyed for *Cryptocephalus coryli* as part of this study in 1998, 1999 and 2000. The sites were either where the beetle had historically been recorded (*n* = 4) (Table 3.1) or areas that appeared to be suitable for the beetle. The methods employed for the surveys were visual searching of foliage, beating using a 1m^2 beating tray or, in areas of very young, scrubby growth, sweep netting. Tall trees were sampled with a beating tray and 2 m long beating stick. Surveys were carried out in May and June, corresponding to the adult flight period. Previous records indicated that this species had been found on *Betula pendula, Corylus avellana, Craetagus monogyna, Populus tremula* and *Quercus robur.* All of these species were searched for *C. coryli* if they were present.

Table 3.2. Sites surveyed for *Cryptocephalus coryli* during 1998, 1999 and 2000.

Site	Grid Ref	Surveyers	Comments
Kirkby Moor Nature Reserve (Lincs)	TF2163	A. Binding, all years R. Piper, 1999 and 2000.	*C. coryli* recorded in good numbers in 1997, 1998, 1999 and 2000.
Moor Farm Nature Reserve (Lincs)	TF2263	A. Binding, all years R. Piper, 2000.	No *C. coryli* found during 1998, 1999 and 2000 surveys.
Linwood Warren (Lincs)	TF1387	A. Binding, 1998.	No *C. coryli* found during 1998 survey
Middle Rasen Plantation (Lincs)	TF1091	A. Binding, 1998.	One male *C. coryli* found in 1965. No *C. coryli* found during 1998 survey.
Usselby Plantation (Lincs)	TF1092	A. Binding, 1998.	No *C. coryli* found during 1998 survey.
Clumber Park (Notts)	SK6275	A. Binding, 1998.	No *C. coryli* found during 1998 survey.
Ostlers Plantation (Lincs)	TF2162	R. Piper, 1999.	One female *C. coryli* found during 1999 survey.
North Unhill Bank (Oxon)	SU5683	P. Hodge, 1991. M. Harvey, 1998.	*C. coryli* recorded in 1991. One male found in 1998.
Colley Hill (Surrey)	TQ2452 and TQ2451	G. Collins, 1998.	No *C. coryli* found during 1998 survey.
Headley Warren (Surrey)	TQ188539	G. Collins, 1996. P. Hodge, other years.	*C. coryli* recorded from early 1900's. Found in good numbers in 1996, 1997, 1998, 1999, and 2000.
Headley Heath (Surrey)	TQ1953	G. Collins, 1998.	No *C. coryli* found during 1998 survey.
White Hill (Surrey)	TQ186539	G. Collins, 1998.	One female *C. coryli* found during 1998 survey.
Bow Hill (Surrey)	TQ1752	G. Collins, 1998.	No *C. coryli* found during 1998 survey.
Ranmore Common (Surrey)	TQ1349	G. Collins, 1998.	No *C. coryli* found during 1998 survey.
Albury Downs (Surrey)	TQ39492	G. Collins, 1999.	No *C. coryli* found during 1999 survey.
Clandon Downs (Surrey)	TQ050492	G. Collins, 1999.	No *C. coryli* found during 1999 survey.
Blatchford Downs (Surrey)	TQ102487	G. Collins, 1999.	No *C. coryli* found during 1999 survey.
White Downs (Surrey)	TQ109487, TQ110487 TQ122492, TQ125495, and TQ127495	G. Collins, 1999. R. Piper, 1999, 2000.	No *C. coryli* found during 1999 and 2000 surveys.
Westcott Downs (Surrey)	TQ 134500	G. Collins, 1999.	No *C. coryli* found during 1999 survey.
Juniper Bottom, Box Hill (Surrey)	TQ179527	G. Collins, 1999.	No *C. coryli* found during 1999 survey.
Liquor Box, Box Hill (Surrey)	TQ179519	G. Collins, 1999.	One female *C. coryli* found during 1999 survey.
Brockham Warren (Surrey)	TQ200513	G. Collins, 1999.	No *C. coryli* found during 1999 survey.
Horsell Common (Surrey)	TQ012608	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Chipstead Bottom (Surrey)	TQ267572	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Juniper Hill (Surrey)	TQ237520	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Buckland Hills (Surrey)	TQ233523	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Wingate Hill, Surrey	TQ263523	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Juniper Hill (Surrey)	TQ237520	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Dawcombe (Surrey)	TQ218526	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
South Hawke (Surrey)	TQ372538 and TQ377542	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Beech Plantation (Surrey)	TQ386543	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Quarry Hangars (Surrey)	TQ320536	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Hawk's Hill (Surrey)	TQ161552	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Sheepleas (Surrey)	TQ088521	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Addington Hills (Surrey)	TQ354644	G. Collins, 2000.	No *C. coryli* found during 2000 survey.
Kincraig area, Invernesshire	NN378453 and NN389564	J. Webb and R. Piper, 2000.	No *C. coryli* found during 2000 survey.

3.2.3.2. Results

Of the potential sites for this species only Ostlers Plantation yielded one female *Cryptocephalus coryli*, in 1999. It is doubtful if this discovery represents a hitherto unknown, self-sustaining population, as the area is close enough (300 m) to a Kirkby Moor sub-population to simply represent a displaced beetle. No *C. coryli* were found at any of the other potential sites. Of the historic locations surveyed during 1999 the Liquor Box section of Box Hill (Collins, 1999) yielded an adult female. This site was previously thought to have lost its *C. coryli* population and was the only historic location that yielded a *C. coryli* specimen in any of the surveys over the three years, despite an absence of recent past, positive records there. Intensive surveys of Sherwood Forest and Cannock Chase may still yield *C. coryli* populations in future surveys. These two large areas still possess extensive areas of habitat that superficially appear to be suitable for this species, not all of which could be surveyed adequately.

3.2.4. Life cycle

Adult *Cryptocephalus coryli* beetles are usually found in May and June, although there are records from July and August. Larvae of this species have been found beneath the adult host-plants where they feed on leaf litter. Some of the captive bred larvae of this species have been shown to take longer than one year to complete their development, an observation that was supported by the discovery of active, immature larvae in June.

3.2.5. Searches for wild larvae

Studies of the larvae of *Cryptocephalus coryli* have centred on feeding preferences in captivity (Owen, 1999). However, nothing is known of the ecology of wild larvae. The methods detailed in Chapter 4 were used to elucidate some aspects of larval ecology. Before this technique was employed searches were made for wild larvae beneath trees where adults had been seen ovipositing. Only very few larvae or their cases were found. All of these were found at Kirkby Moor in June 2000. Six larval cases were found in all. Two of these contained living larvae that were not mature enough to pupate, two other cases were both broken. The last two cases were fully grown, intact and buried, aperture end down, one in friable soil and one in moss. The adult from the first case had already emerged by cutting the distinctive cap from the posterior end of the case. The second of these intact cases was intact and contained a dead adult male *C. coryli*, found inside the case apparently facing the wrong direction for emergence. The discovery of active non-mature larvae in June indicates that it may take some larvae two years to reach maturity as they will not have had time to mature that year.

3.2.6. Captive rearing

3.2.6.1. Materials and methods

Larvae were maintained in captivity using the protocols described in Chapter 5. In order to initiate diapause larvae were placed in successively cooler incubators during November and December of 2000 (20, 13, 8 and 5 °C; four days in each of the first three incubators). The larvae were maintained at 5 °C for the winter. Food was added to the containers intermittently over this period as even at 5 °C some feeding continued. Successively warmer incubators were then used to bring the larvae out of diapause and into pupation.

3.2.6.2. Results

Approximately eight captive bred *Cryptocephalus coryli* females laid a total of 1449 eggs during the summer of 2000. Of the total number of eggs laid 909 (62.7%) hatched. A further 345 (23.8%) of the larvae died during their 1st instar. The majority of the larvae were subsequently used in the experimental releases that are detailed in Chapter 6. Eighty seven of the eggs that were laid did not possess a case. Of these only six hatched but these larvae managed to survive until, at least their 1st instar. These larvae were then lost; either they were cannibalised by their con-specifics or they may have constructed themselves a case during their 2nd instar.

3.2.6. Habitat requirements

The detailed habitat preferences of this species are described in Chapter 5.

3.2.7. Reasons for decline

Cryptocephalus coryli was once a relatively widespread species in the UK, although historical records and extant populations suggest that this species was never abundant. Populations of *C. coryli* have been recorded on scrub in heathland and calcareous grassland. Adults recorded from conifer plantation rides probably represent populations forced into this type of habitat when heathland and calcareous grassland areas were planted with conifers. The decline of this species has been linked to the decline of coppicing (Warren and Key, 1989), but this question shall be fully addressed in Chapter 5.

3.3. Cryptocephalus decemmaculatus (Linnaeus 1758)

3.3.1. Description

Female *Cryptocephalus decemmaculatus* beetles can reach 4 mm in length (Plate 4) whereas males can reach 3 mm (Plate 5). The species is characterised by having five black spots on each elytron with a distinctive yellow mark on the pronotum (Plate 4 and Plate 5). The markings are very variable and at least ten varieties are known within the world range (Burlini, 1955; Warchalowski, 1991). The variety *C. decemmaculatus var. bothnicus* is a melanic form that is known from the UK. Clear sexual dimorphism is non-apparent, although females are bulkier than males, with relatively shorter prothoracic limbs and antennae. The larvae are brownish-white with a black sclerotised head capsule and prothorax (Plate 6). The body inside the larval case is held in a 'C' shape. As with all *Cryptocephalus* larvae *C. decemmaculatus* larvae have well developed legs.

3.3.2. Distribution

3.3.2.1. UK distribution trends

Figure 3.2 shows the past and present distribution of *Cryptocephalus decemmaculatus* in the UK. Only eight disjunct sites (Table 3.3) and one unconfirmed site are known, with a small cluster in the northwest of England (Stott 1929; Allen, 1960d; Allen, 1970a; Shirt, 1987; Hyman and Parsons, 1992). Only two sites currently support this species. All of the records have been from bog or wet heath sites. Three of the site records are based on single specimens and *C. decemmaculatus* has always been considered to be rare (Stott, 1929; Allen, 1970a). Prior to 1981 the only known UK sites for this species were Chartley Moss in Staffordshire where it had been known since 1879 (Stott, 1929), Burnt Woods in Staffordshire, a single record from Abbots Wood in East Sussex (Allen, 1970a), Camghouran in Perthshire (Stott, 1929) and a single specimen from Braemar in Aberdeenshire (Allen, 1960d). In 1981 a very good population of this species was found at Wybunbury Moss in Cheshire while specimens were discovered at Chat Moss (Lancs) and the Muir of Dinnet (Aberdeenshire) in 1986.

Table 3.3. Records of *Cryptocephalus decemmaculatus*. Figures in parentheses after year of record indicates number of specimens captured. Recent records in bold.

Site	Grid Ref.	Year	Reference
Chartley Moss (Staffs.)	SK0028	1876-1979 (many)	Stott, 1929. M. Waterhouse, pers. comm., 1999.
Wybunbury Moss (Cheshire)	**SJ695503**	**1981-2001 (many)**	**M. Cox, pers. comm., 1999. Pers. obs., 1999, 2000 & 2001.**
Camghouran (Perthshire)	**NN595563**	**1864-2000 (many)**	**Stott, 1929; P. Hodge, pers. comm., 1993, pers. obs. 2000.**
Abbots Wood (E. Sussex)	TQ5607	Unknown (1)	Allen, 1970a.
Chat Moss (Lancs.)	SJ7096	1983 (?)	M. Cox, pers. comm., 1999.
Braemar area (S. Aberdeenshire)	NO1491	1959 (1)	Allen, 1960d.
Muir of Dinnet (S. Aberdeenshire)	NO4399	1986 (1)	M. Cox, pers. comm., 1999.
Burnt Woods (Staffs.)	SJ7434	1870 (many)	Stott, 1929.

3.3.2.2. European distribution

On the continent this species has been recorded from the Western Palaearctic region, with the eastern limit to its range in western Siberia (Warchalowski, 1991). Captures of this species on the continent are relatively rare and usually of only a few specimens (Warchalowski, 1991).

Figure 3.2. Past and present distribution of *Cryptocephalus decemmaculatus*. [White symbols = extant populations (positive surveys within last five years); Black symbols = putative extinct populations).

3.3.3. Surveys

3.3.3.1. Materials and Methods

Table 3.4 shows the sites that were surveyed for *Cryptocephalus decemmaculatus* in 1999 and 2000. The sites that were examined were areas where the beetle had historically been recorded or areas that appeared to be suitable for the beetle. The methods employed for the surveys were visual searching of foliage, foliage beating using a $1m^2$ beating tray and sweep netting on areas of dwarf, scrubby growth. Records indicate that this species has been found on small *Salix* sp. and small *Betula pubescens* trees.

Table 3.4. Sites surveyed for *Cryptocephalus decemmaculatus* during 1999 and 2000.

Site	Grid Ref	Surveyors	Comments
Chartley Moss, Stafffordshire	SK0228	J. Webb, 1999 and 2000	Recorded from this site from 1870's to 1979. None found during 1999 and 2000 surveys.
Fenns and Whixhall Moss, Shropshire	SJ4835	J. Webb and Ross Piper, 1999	No *C. decemmaculatus* records. None found during 1999 survey. *C. parvulus*, and *C. labiatus* recorded.
Wybunbury Moss, Cheshire	SJ6950	R. Piper 1999-2001; J. Webb, 1999	*C. decemmaculatus* recorded since 1981. Large numbers found in 1990, 1991, 1999, 2000 and 2001. *C. parvulus*, *C. labiatus* and *C. pusillus* recorded during 1999 and 2000 surveys.
Camghouran, Perthshire	NN5455	R. Piper and J. Webb, 2000	*C. decemmaculatus* recorded since 1860's. Found in small numbers in 1993. Larvae found in 2000 survey.

3.3.3.2. Survey results

The historic location of Chartley Moss, where many specimens were collected up to 1979, yielded no *Cryptocephalus decemmaculatus* in 1999 or 2000 (Webb, 1999; J. Webb, pers. comm.). Similarly, no *C. decemmaculatus* were found during the survey of the very extensive Fenns and Whixhall Moss (1999). A single unconfirmed record exists for this site although no specimen is available and the record was by a non-specialist in a pitfall trap (Clayson, 1994). It is possible that more intensive surveys of these two sites will enable the presence of *C. decemmaculatus* to be confirmed. Wybunbury Moss and Camghouran both currently support this species, but the potentially suitable area for the species at Camghouran is approximately 60 m^2. Two other sites in Scotland where this species was recorded were not surveyed because precise locality data are not available. Both of these records were based on single specimens, which is also the case for the record from East Sussex (Abbot's Wood). *C. decemmaculatus* was found to be abundant at Wybunbury Moss during the 1999, 2000 and 2001 surveys. Adults could be found in most areas on the inner portion of the Moss that had south facing aspects. Three main sub-populations existed which are listed as A, B and C in (see Plate 25). Area D also appeared to be suitable but did not yield any beetles in 1999 and 2000.

3.3.4. Life cycle

Adults of this species are usually found in May and June, although singletons can be found at the end of August. Observations of wild larvae show that the immature stages of this species can be found beneath the adult host plants feeding on leaf litter. Captive larvae have been shown to take longer than one year to complete their development, and a long development time is also indicated by the presence of active, immature larvae at Wybunbury at the beginning of spring.

3.3.5. Searches for wild larvae

Searches beneath *Salix cinerea* bushes at Wybunbury Moss in the summer of 2000 using a beating tray to sort through moss and litter debris yielded seven *Cryptocephalus decemmaculatus* cases. All of these cases were fully grown and had been broken into. Due to the damage on the cases it was difficult to tell if adults had eclosed. During a visit to the site in June 2001 a single live larvae (3-4 mm long) was found clinging to a *S. cinerea* leaf 1.3 m above the ground. Characteristic larval feeding damage was present on the leaf. During the summer of 2000 the site for this species in Rannoch was visited and a search for larvae was made. Sorting through litter yielded six larvae. None of these larvae were fully grown and all but one was alive. The living larvae were small (≤ 3 mm).

3.3.6. Adult mortality

Dead beetles were found by visual searching of host plants and the ground. Spiders' webs were scrutinised in particular. Mortality of adults was apparently low. The only observed cause of mortality was capture in the webs of *Enoplognatha ovata* (Araneae: Theridiidae). The spiders were observed feeding on the adults, which were trapped in the webs. Eighteen adults were observed in webs. Twelve (66.12%) of these were male. One adult male was also observed being eaten by a crab spider of the genus *Xysticus* (Araneae: Thomisidae). The very low mortality observed in the adults is probably as a result of the black and yellow warning colouration . Many chrysomelids have been shown to produce chemical deterrents (Pasteels et al, 1984). Of these many feed on *Salix* species (Tahvanainen *et al*, 1985).

3.3.7. Captive rearing

Around nine wild caught *Cryptocephalus decemmaculatus* females laid a total of 1271 eggs during the summer of 2000. Of the total number of eggs laid 748 (58.9%) hatched. A further 283 (22.3%) of the larvae died during their first instar. The majority (300) of the remaining larvae were used in the experimental releases detailed in Chapter 6. 145 larvae remained in captivity and 23 (1.8 %) of these died before reaching maturity. A further 30 larvae (1.6%) reached maturity but did not pupate after diapause and carried on feeding.

Adults were reared in the containers shown in Chapter 5 (Figure 5.15). Adults that were reared in captivity were individually marked when they hatched from their larval cases. Pupating larvae were monitored every day so that eclosed adults could be located and placed in cages (Figure 5.15). Marking involved the use of a modified mechanical pencil that was to act as a borer. This device was used to bore out round labels (0.9 mm dia.). Printed on these labels was a code composed of a letter and a number enabling 260 permutations. The labels were backed with double sided tape and once bored out from the sheet the label could be stuck to the mid-portion of the left elytron by depressing the lead in the mechanical pencil. Once marked the sex of the adult and the date hatched was recorded. The cages with the adults were monitored daily and dead individuals were removed. The code on the label was read with the use of a hand lens (Specwell, Japan). The date the individual died was then recorded. Adults with deformities were also recorded. When hatching appeared to have finished, the remaining cases were opened with a scalpel and the reason for the non-emergence of the adult was recorded.

Of a total of 145 *Cryptocephalus decemmaculatus* larvae originating from wild Wybunbury Moss females 78 adults hatched (53.8%), thirty (20.7%) continued to feed. 66.6% of the adults that hatched were male. Fourteen (9.7%) of the adults that pupated failed to hatch and 41.7% of these were deformed. Most of these deformed adults were male (85.7%). The only deformity observed was manifested in a twisting of one of the elytrons. Of the unhatched adults only 2 were female and one of these was deformed. 2.6% of the adults that hatched exhibited the same deformity that was seen in the unhatched adults and also displayed a paralysis of the metathoracic limbs and wings. In captivity the mean longevity for females was mean = 27 ± S.D. 3.9 days and mean = 18 ± 3.6 days for males. There was a significant difference in the median longevity of males and females [males (n = 40), 18 ± 4 days, median = 18 days; females (n = 18), 27 ± 4 days, median = 27 days; Mann-Whitney Z = -5.183, P = <0.001].

The adults hatched during a period of two weeks with most of the hatching being synchronised 3-8 days into the emergence of the imagos. Similar synchrony was observed in the *Cryptocephalus decemmaculatus* population at Wybunbury Moss where for a week in late May or early June large numbers of *C. decemmaculatus* adults could be seen on a very small number of *Salix cinerea* trees.

Cryptocephalus decemmaculatus was the only species in this study reared successfully in captivity during 2000-2001. The life span of the adult beetles is relatively long for a chrysomelid. Adults of other species within the same sub-family as the *Cryptocephalus* beetles have been shown to survive for approximately 30 days (Lesage and Steifel, 1996). Captive rearing of the beetles showed that adult males out-number females by two to one, although this may be an artefact of captive rearing. Males are also less long lived than females. Male *C. decemmaculatus* adults are smaller than females, thus, are less 'expensive' to produce, but only if male and female eggs are different sizes (Charnov, 1982). Females are also responsible for the time consuming act of oviposition, which, in these beetles is compounded by further time constraints imposed by encasing each egg in faeces. Covering a single egg in faeces can take as long as 20 mins (Tilden, 1949; Pers. obs.). Monitoring the observed deformity in captive bred adults over successive captive generations will enable a more thorough understanding of the possible deleterious effect of captivity on a population originating from a small number of individuals.

Almost all the captive adults that hatched did so within the space of two weeks indicating that there is a strong synchronisation of adult emergence. This strategy ensures that each beetle's chances of finding a mate are increased. A strategy that entailed adults emerging over a longer period of time would decrease the chance of finding a mate. The strategy employed by *Cryptocephalus decemmaculatus* and probably *C. coryli* and *C. nitidulus* makes populations very vulnerable to the effects of inclement weather during the adult period. Should poor weather prevail for a large part of the early summer adults would find it very difficult to move freely around on their host-plants, feed, fly or mate such is their extreme dependence on warm conditions

The adult female captive *Cryptocephalus* beetles in this study laid ≈200 eggs each. Other beetles in the same sub-family have been shown to lay 800 eggs (Lesage & Steifel, 1996). The percentage of eggs that failed to hatch was remarkably high. Further studies are required to elucidate if these eggs are unfertilised. A large proportion of these unhatched eggs were not covered with faeces. This dichotomy may be due to the ovipositing female detecting the fertility state of each egg or a lack of roughage. Every egg is manipulated in the hind tarsi for a considerable amount of time before the encasing process and it may be possible that the female detects a difference between fertilised and non-fertilised eggs. The exact nature of the difference, if there is one, remains to be seen, although it may be that embryogenesis has commenced in the fertilised eggs whilst they are still in the oviduct. These eggs may be slightly larger and heavier than non-fertilised eggs. Further investigation of this observation may prove to be very rewarding.

3.3.8. Adult translocations

Five female and five male *Cryptocephalus decemmaculatus* were translocated from area A to area D (Plate 25) during the summer June of 1999. Area D is separated from the open part of the bog by a large expanse of mature woodland and this species had never been found there. Scrub clearance was carried out in area D during the winter of 1998/1999 in an attempt to make this area suitable for *C. decemmaculatus.*

Area D was not surveyed in 2000 due to flooding but in 2001 three adult *Cryptocephalus decemmaculatus* females were found in this area, complete surveying of the area was difficult due to the very wet conditions there. These adults are likely to represent the descendents of the ten adults released in 1999.

Evidence from the experimental translocation of adult *Cryptocephalus decemmaculatus* at Wybunbury Moss suggests that it may be relatively simple to introduce this species to sites that are suitable for adults and larvae. If the adults beetles found in area D during 2001 represent the descendents of the adults released in 1999 then a founder population of ten adults may be sufficient to propagate a self sustaining population. In nature a founder population of a relatively sedentary species such as a *Cryptocephalus* beetle may be very small. A self-sustaining population of the butterfly *Proclossiana eunomia* was initiated from four individuals (Neve *et al*., 1996). It is plausible that a single gravid female chancing upon an area of suitable habitat can propagate a self-sustaining population. This prompts the question, however, that if this is the case then why are these beetle so rare? Events of a gravid female beetle moving or being moved (by strong winds) from their natal sites may be commonplace, but the chances of her landing in an area that offers optimal conditions for larval development and adult activity are very small indeed. More investigation is needed here to further examine if a self-sustaining population of these rare *Cryptocephalus* beetles can develop from a very small founder population.

3.3.9. Habitat requirements

The habitat requirements of this species are described in Chapter 5.

3.3.10. Reasons for decline

The decline of *Cryptocephalus decemmaculatus* has not been marked compared to some of the other *Cryptocephalus* species. Very few sites have ever existed for this species and in some areas it can be abundant. Extensive surveys of mid and northeast Scotland may relocate this species at sites where populations were identified relatively recently. In a broad sense the threats that are posed to this species are scrub removal, scrub maturation and habitat drainage. By itself, drainage may not be a threat, but it is likely that drier conditions prevailing over a site may result in greater scrub growth and eventual maturation. The threats to this species are discussed in greater detail in Chapter 5.

3.4. *Cryptocephalus nitidulus* (Fabricus 1787)

3.4.1. Description

Cryptocephalus nitidulus is a medium sized *Cryptocephalus* beetle. Females can reach 5 mm in length (Plate 7) whereas males can reach 4 mm (Plate 8). Teneral adults have a blue metallic sheen that becomes green in mature adults. The legs are yellow-brown. Clear sexual dimorphism is not apparent, although females are bulkier than the males with relatively shorter prothoracic limbs and antennae. The separate faecal plates that form the egg case of this species are raised and obvious (Plate 9).

3.4.2. Distribution

3.4.2.1. UK distribution trends

Figure 3.3 shows the past and present distribution of *Cryptocephalus nitidulus* in the UK. Historically 15 sites (Table 3.5) are known for this species (Fowler, 1890; Holland, 1903; Champion, 1908; Fowler & Donisthorpe, 1913; Atty, 1983; Shirt, 1988; Halstead, 1988; Drane, 1990) with a cluster in the southeast of England. The most northerly known site was Sherwood Forest (Nottinghamshire), but no discrete location of capture is known for the specimens from this site as is also the case for a number of the other sites. Currently only three sites are known, all of which support strong populations of this species. Specimens have been recorded from scrub invading heathland, calcareous grassland and woodland rides.

Table 3.5. Records of *Cryptocephalus nitidulus*. Recent records in bold.

Site	Grid Ref.	Year	Source
Ashdown Forest (Kent)	TQ4529	1916	M. Cox, pers. comm., 1999.
Nr. Bournemouth (Dorset)	SZ09	Unknown	Shirt, 1987.
The New Forest (S. Hants)	SU30	Unknown	Shirt, 1987.
Cobham Woods (W. Kent)	TQ6968	Unknown	Maidstone Local Records Centre.
Darenth Wood (W. Kent)	TQ5873	Unknown	Maidstone Local Records Centre.
Box Hill (Surrey)	**TQ1852**	**1900-present**	**Shirt, 1987. I. Menzies, pers. comm., 2001.**
Coulsdon, (Surrey)	TQ3058	1919	Hyman and Parsons, 1992.
White Downs (Surrey)	**TQ1249**	**1986-present**	**P. Hodge, pers. comm., 1999. Pers. obs., 1999, 2000.**
Headley Warren (Surrey)	**TQ188539**	**1905-present**	**P. Hodge, pers. comm., 1999. Pers. obs., 1999, 2000.**
Mickleham, Surrey (Surrey)	TQ1753	1897-1927	M. Cox, pers. comm., 1999.
Wychwood Forest (Oxon)	SP3315	1905-1955	Hyman and Parsons, 1992.
Colesbourne (E. Gloucs)	SP01	1922-1946	M. Cox, pers. comm., 1999; I. Menzies, pers. comm., 1999.
Chobham (Surrey)	SU9761	1908	Champion, 1908.
Gulf Scrubs, Colesbourne (E. Gloucs)	SP0214	1945	I. Menzies, pers. comm., 1999.
Sherwood Forest (Notts)	SK66	Unknown	Shirt, 1987.

3.4.2.2. European distribution

Cryptocephalus nitidulus has been recorded throughout the Palaearctic (Warchalowski, 1991) as far east as Japan (Takizawa, 1971). Relict populations can be found in the Pyrenees and Catalonia (Warchalowski, 1991). In Scandinavia it is a relatively widespread species particularly in Sweden (B. Engstrom, pers. comm.) where it can be found along woodland rides. Most continental records describe this species as being caught rarely, usually as single specimens (Warchalowski, 1991).

Figure 3.3. Past and present distribution of *Cryptocephalus nitidulus*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.4.3. Surveys

3.4.3.1. Materials and Methods

Table 3.6 shows the sites that were surveyed for *Cryptocephalus nitidulus* in 1999 and 2000. The sites that were examined were areas that appeared to be suitable for the beetle together with one site that once supported the species. The methods employed for the surveys were visual searching of foliage and foliage beating using a 1m^2 beating tray. Tall trees were sampled with a beating tray and a 2 m long beating stick. On areas of very young, scrubby growth a sweep net was employed. Records indicate that this species has been found on *Betula pendula, Corylus avellana, Craetagus monogyna* and *Populus tremula.* All of these species were searched for *C. coryli.*

Table 3.6. Sites surveyed for *Cryptocephalus nitidulus* during 1999 and 2000.

Site	Grid Ref.	Surveyors	Comments
Albury Downs (Surrey)	TQ39492	G. Collins, 1999.	No *C. nitidulus* found during 1999 survey.
Clandon Downs (Surrey)	TQ050492	G. Collins, 1999.	No *C. nitidulus* found during 1999 survey.
Blatchford Downs (Surrey)	TQ102487	G. Collins, 1999.	No *C. nitidulus* found during 1999 survey.
White Downs, West of Effingham road (Surrey)	TQ109487,	G. Collins and R. Piper, 1999 and 2000.	Many *C. nitidulus* found during 1999 and 2000 surveys.
White Downs, West of Pickett's Hole (Surrey)	TQ110487	G. Collins and R. Piper, 1999 and 2000.	Many *C. nitidulus* found during 1999 and 2000 surveys.
White Downs, East of Pickett's Hole (Surrey)	TQ122492,	G. Collins and R. Piper, 1999 and 2000.	Many *C. nitidulus* found during 1999 and 2000 surveys.
East White Downs (Surrey)	TQ125495,	G. Collins and R. Piper, 1999 and 2000.	Several *C. nitidulus* found during 1999 and 2000 surveys.
Westcott Downs (Surrey)	TQ 134500	G. Collins, 1999.	No *C. nitidulus* found during 1999 survey.
Juniper Bottom, Box Hill (Surrey)	TQ179527	G. Collins, 1999; I. Menzies, 2000.	No *C. nitidulus* found during 1999 survey. Several found during 2000 survey.
Liquor Box, Box Hill (Surrey)	TQ179519	G. Collins, 1999.	No *C. nitidulus* found during 1999 survey.
Brockham Warren (Surrey)	TQ200513	G. Collins, 1999 and 2000.	No *C. nitidulus* found during 1999 and 2000 survey.
Headley Warren (Surrey)	TQ1854 and TQ1953	G. Collins and R. Piper, 1999 and 2000.	Many *C. nitidulus* found during 1999 and 2000 surveys.
Colley Hill (Surrey)	TQ243522	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Horsell Common (Surrey)	TQ012608	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Chipstead Bottom (Surrey)	TQ267572	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Juniper Hill (Surrey)	TQ237520	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Buckland Hills (Surrey)	TQ233523	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Wingate Hill (Surrey)	TQ263523	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Juniper Hill (Surrey)	TQ237520	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Dawcombe (Surrey)	TQ218526	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
South Hawke (Surrey)	TQ372538 and TQ377542	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Beech Plantation (Surrey)	TQ386543	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Quarry Hangars (Surrey)	TQ320536	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Hawk's Hill (Surrey)	TQ161552	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Sheepleas (Surrey)	TQ088521	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Addington Hills (Surrey)	TQ354644	G. Collins, 2000.	No *C. nitidulus* found during 2000 survey.
Colesbourne (E. Gloucs.)	SP01	I. Menzies, 2000.	No *C. nitidulus* found during 2000 survey.

3.4.3.2. Survey results

Of the above surveys in 2000 *Cryptocephalus nitidulus* was re-discovered at Boxhill. The above sites were surveyed due to their similarity to sites that currently support *C. nitidulus*. It was difficult to survey many of the sites that once supported *C. nitidulus* as the old records often give no discrete locations. The survey of the Colesbourne site in Gloucestershire that once supported this species did not yield any specimens, possibly due to the site becoming heavily overgrown. Wychwood Forest also once supported a strong population of *C. nitidulus,* but it was decided not to re-survey this area as this has always been a well surveyed site and the last *C. nitidulus* specimens were caught here in the 1950's. It is hoped that with further investigation discrete areas within Sherwood Forest where *C. nitidulus* was recorded will be identified, enabling surveys to be conducted.

3.4.4. Life cycle

Adults of *Cryptocephalus nitidulus* can be found from early May and into July. Larvae of this species have been found to feed on leaf litter beneath the adult host plants. Active, immature larvae have been found in June in the wild suggesting that at least some of the larvae may take more than one year to complete their development. This observation is also supported by the slow development of larvae bred in captivity.

3.4.5. Searches for wild larvae

The only site that yielded wild larvae during June of 2000 was a small section of the White Downs where there was a very high proportion of bare ground. Seven larvae were found in total and half of these were represented by broken cases. Of the other three larvae one was very small (≈ 2 mm) and still active. The remaining two larvae were fully grown and the case aperture was sealed. These cases were opened in the laboratory and were found to contain the pupal cocoon and pupae of a hymneopteran parasite. These parasites were identified as the wingless ichneumons of the genus *Gelis* (Plate 10). *Gelis* sp. have been described parasitising other Chrysomelidae larvae (Dysart *et al.* 1973; Momoi, 1973; Cox, 1994) but never *Cryptocephalus* species. The *Cryptocephalus* larvae within these cases had been almost entirely consumed leaving just the sclerotised head capsule and pro-thorax. Parasitism must take place when the *Cryptocephalus* larvae are mature otherwise the larval case would not be large enough to accommodate the relatively large mature larva and pupa of the *Gelis* parasite. This would entail that the female parasite must be active in the winter and into the very early spring to be able to parastise larvae of the correct size before they seal their case. Active female *Gelis* ichneumons were found at the site during December of 1999. No intact, fully-grown, non-parasitised larvae were found during the searches suggesting that these larvae may be burrowing into the soil, although, the soil at the site is not particularly friable. Another possibility is that the larvae pupate in the many soil fissures. Searching these was very difficult without destructive sampling. Another possibility is that the larvae are associated with the lichen on host-trees as is mentioned in some of the older literature (Donisthorpe, 1938). The trunks of *Betula pendula* host trees were examined but no larvae were found.

3.4.6. Captive rearing

Four wild caught *Cryptocephalus nitidulus* females laid 535 eggs during the summer of 2000. 322 (60.2%) of these eggs hatched. A further 161 (30.1%) of the larvae died during their first instar. The majority of these reared larvae were used in the experimental releases detailed in chapter seven. Of the 126 larvae that remained 88% reached maturity. Only 5.5% of these larvae pupated. The remaining larvae continued feeding. Only egg and 1st instar mortalities (Figure 5.35) could be assessed in the larvae.

Cryptocephalus nitidulus larvae reached maturity (n = 126) when reared in captivity, however only four adults hatched (1 female and 3 males). A further two adults failed to hatch but upon examination the reason for the death of these adults within their cases was not apparent. Many of the larvae that were reared had already passed through one diapause and these larvae had carried on feeding into their third year. The adults that did hatch lived for 22 days (female) and mean = 20 days ± S.D. 1 day (males).

3.4.7.Habitat requirements

The detailed habitat requirements of this species can be seen in Chapter 5.

3.4.8. Reasons for decline

Cryptocephalus nitidulus could once be found relatively widely and abundantly, however, today its range is much contracted, although in suitable areas it can still be found in relatively large numbers. Over-collecting may have accelerated the extinction of certain populations of this beetle. Wychwood Forest was visited by generations of entomologists who came to collect the many rarities, including *C. nitidulus*. Another chrysomelid species (*Gynandrophtalama affinis*) was another rarity from this site and it too was heavily collected, which may have helped drive the population to extinction. Broadly, *C. nitidulus* has similar habitat requirements to *C. coryli*. The threats that are posed to this species are more fully discussed in Chapter 5.

3.5. Cryptocephlaus primarius (Harold 1872)

3.5.1. Description

Adults of *Cryptocephalus primarius* are slightly smaller than *C. coryli.* On each elytron of this species there are typically five small black spots (Plate 11), although the patterning can vary greatly, especially in continental populations. Both male and female adults have a black pronotum. The legs of *C. primarius* are uniformly black. Females are bulkier than males with relatively shorter prothoracic limbs and antennae. The separate faecal plates that form the egg case of this species are raised and obvious (Plate 12).

3.5.2.Distribution

3.5.2.1.UK distribution trends

Figure 3.4 shows the known past and present distributions of this species in the UK. As elsewhere, the species is regarded as present if it has been captured in the last five years. Table 3.7 lists the records that have been collated on the captures of this species. Most specimens have been recorded from the south (Powers, 1859; Richards, 1927; Hobby, 1955; C. Wiltshire, pers. comm.) with two disjunct specimens recorded from Scotland (Skidmore, 1966). In the last decade this species has only been recorded in very small numbers from two locations on the Cotswolds.

Table 3.7. Records of *Cryptocephalus primarius*. Figures in parentheses after year of record indicates number of specimens captured.

Site	Grid Ref.	Year	Sources
Cholsey Downs (Berks.)	SU5886	1927(1); 1955(5)	Richards, 1927; Hobby, 1955.
Gog Magog Hills (Cambs.)	TL4953	1859 (1); 1938 (1)	Powers, 1859. Hobby, 1955.
Colesbourne (E. Gloucs.)	SP01	1942 (1); 1944 (1)	M. Cox , pers. comm., 1999. I Menzies, pers. comm., 1999.
Breakheart Hill (W. Gloucs.)	**ST7596**	**1991 (5)**	**C. Wiltshire, pers. comm., 1999.**
Rodborough Common (W. Gloucs.)	SO8503	1890 – 1985 (several)	M. Cox , pers. comm., 1999. I. Menzies, pers. comm., 1999.
Stinchcombe Hill (W. Gloucs.)	**ST7498**	**1990 (3); 1999 (1); 2000 (1)**	**C. Wiltshire, pers. comm., 1999.** **P. Hodge, pers. comm. 2000.**
Nr Loch Rannoch (Perthshire)	NN3352	Unknown (2)	Skidmore, 1966.

Figure 3.4. Past and present distribution of *Cryptocephalus primarius*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.5.2.2. European distribution

On the continent this species has a South-Western distribution with records for the Iberian peninsula and south-mid France. (Warchalowski, 1991). No records exist for anywhere further east than Eastern France (Warchalowski, 1991). European authors state that it is caught very rarely and usually as single specimens (Burlini, 1955; Warchalowski, 1991).

3.5.3. Life cycle

As with other species of this genus, adults are found in the late spring and early summer. All of the captures of *Cryptocephalus primarius* have been made in May and June. It is speculated that the larvae of this species feed on litter beneath the unconfirmed host-plants, although no wild larvae have ever been found. In common with some other *Cryptocephalus* species it is probable that the larvae of this species can take two years to reach maturity (Owen, 1996).

3.5.4. Habitat requirements

Because of the paucity of specimens (the available records suggest that perhaps less than 50 individuals have ever been captured in the UK) the ecology of this species is very poorly known. All of the known specimens have been swept or found via visual searching on south facing areas of calcareous grassland. Four days of searching during the summers of 1999 and 2000 at Breakheart Hill and Stinchcombe Hill sites did not yield any *C. primarius* (Pers. obs), although single females were found in 1999 and 2000 at these sites(C. Wiltshire pers. comm.; P. Hodge, pers. comm.). Specimens captured via sweeping suggest that adults will utilise the upper portions of its putative host-plant, however, both of the recently caught specimens were found at the base of *Helianthemum nummularium* plants. It is not clear whether this location of capture represents the habitat of the adults or is simply a result of the beetles dropping from the flowers of the host-plant due to the reflex of thanatosis (Jolivet, 1952). *H. nummularium* appears to be the preferred adult food plant of this species in captivity when given a choice between this species, *Corylus avellana*, *Salix* sp. and *Quercus* sp. (C. Wiltshire, pers. comm.). *C. primarius* is nonetheless often found in association with *Salix* spp*, Corylus avellana* and *Quercus* sp. on the continent (Warchalowski, 1991)

3.5.5. Reasons for decline

The historical data indicates that very few UK sites have ever been known for this species and when present it has never been abundant. The decline of this species has therefore not been as marked as in some others of the genus. The largest numbers of individuals appear to have been recorded from Rodborough Common in the 1940's (I. Menzies. pers. comm.), although no records have been found to define just how many were caught here. It is unlikely that more than 50 specimens of this beetle have ever been found in Britain and almost 70 years elapsed between the first and second records for this species (Powers, 1859; Richards, 1927). The European distribution of *C. primarius* and its occurrence in habitats with very warm micro-climates lends weight to the theory of a species on the northern edge of its range.

Due to the lack of basic biological information on this species, formulating recommendations for habitat management is very difficult. Field observations have linked it to a relatively short sward and an abundance of *H. chamaecistus* on sheltered, south facing slopes. These observations would therefore imply that the maintenance of sheltered, but relatively scrubless south facing calcareous slopes is important. Grazing management with sheep (or preferably rabbits as the effect of trampling by larger grazers could be an important consideration in terms of larval survivorship) is likely to be essential. The last specimen caught at Rodborough Common was in 1985. The sward at the site appears to be taller than 50 years ago (I. Menzies, pers. comm.) and this may be one reason why this locality appears to be no longer favourable for *C. primarius*. Gathering information on the basic ecological requirements of this species via research is crucial if populations are to be managed and enhanced.

Of the sites that currently support this species Stinchcombe Hill is owned by a board of trustees who keep the site free from invading scrub. A local farmer who grazes cattle on the site owns Breakheart Hill, where there is no conservation-orientated management. Clearly there is a need to encourage careful agricultural practices at this site

3.6. *Cryptocephalus exiguus* (Schneider 1792)

3.6.1. Description

Cryptocephalus exiguus is the smallest British *Cryptocephalus* beetle with adults ranging from 2 to 2.8 mm in length. *C. ex*iguus is completely black with a matt pronotum due to fine longitudinal lines. Superficially, it is very similar to *C. labiatus*.. The legs of this species are slightly yellowish. As with all the *Cryptocephalus* species males have relatively longer antennae than females.

3.6.2. Distribution

3.6.2.1. UK distribution trends

The known past and present distribution of this species in the UK is shown in Figure 3.5. Table 3.8 lists the records that have been collated on the captures of this species. Very few sites for this species, past or present, are known. The majority of records for this species are from the east of England (Rye, 1871; Bedwell, 1899; Thornley, 1899; Morley, 1899; Rye, 1864; Mendel, 1987; Mendel, 1998), with a disjunct record represented by specimens from Somerset (Mendel, 1998). The only recent records for this species are from Pashford Poors Fen in West Suffolk (Mendel and Collier, 1997; Mendel, 1998).

Table 3.8. Records of *Cryptocephalus exiguus*. Figures in parentheses after year of record indicates number of specimens captured. Recent records in bold.

Site	Grid Ref.	Year	Sources
Oulton Broad (E. Suffolk	TM5092	1898 (1)	Bedwell, 1899.
Barton Mills (W. Suffolk)	TL7274	1899 (2)	Morley, 1899.
Pashford Poors Fen (W. Suffolk)	**TL7383**	**1980 (1); 1986 (1); 1997 (2); 2000 (1)**	**Mendel, 1987.**
Bure Marshes (E. Norfolk)	TG3316	1870 (?)	Edwards, 1893.
Freshney Bog (N. Lincs)	TA2308	1898-1954 (many)	Thornley, 1899.
Nr Weston S.M. (Somerset)	ST36	1860 (5)	Crotch, 1863 in Mendel 1998.
Wroxham (E. Norfolk)	TG 3016	1906 (1)	Mendel, 1998.

Figure 3.5. Past and present distribution of *Cryptocephalus exiguus*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.6.2.2. European distribution

This species is found throughout the Western Palaearctic, where it can be caught in moist meadows and at their edges (Warchalowski, 1991). The northerly and southerly limits to its European range are in Finland and the Alps respectively and it is found eastwards into Siberia (Warchalowski, 1991).

3.6.3. Life cycle

All the confirmed capture dates of *Cryptocephalus exiguus* adults have been in May and June, with possibly some captures in July. Larvae in captivity take one year to complete their development (H. Mendel, pers. comm.). It is speculated that the larvae of this species feed on litter beneath the host-plants, although no wild larvae have ever been found.

3.6.4. Habitat requirements

Specimens have been recorded from mixed fen or fen-meadow areas. As with *Cryptocephalus primarius* only very few specimens of this species have been found since it was re-discovered in 1980 (no more than six specimens), mainly by sweeping and therefore, it is difficult to elucidate its habitat requirements. There have been many suggestions as to the food-plant. The adults have been reported to be associated with *Cirsium* spp. growing in damp, shaded hollows (Fowler, 1890). *Betula* spp, *Salix cinerea* and *Rumex* sp. have also been reported as the host-plants of this species on the continent (Mohr, 1966, Hermann, in prep). Recent observations on captive specimens suggest that *C. exiguus* larvae feed on the casings of fallen seeds of *Rumex acetosa* (H. Mendel, pers comm.).

3.6.5. Reasons for decline

Falling water tables due to borehole abstraction and drainage, conversion of sites to arable agriculture and invasion of wet meadow areas by woody shrubs may have contributed to the decline of this species (Hyman & Parsons, 1992). The species to the non-specialist could be mistaken for *C. labiatus*, a common *Cryptocephalus* beetle (Mendel 1998) and it is therefore possible that mis-identification may be partly responsible for the observed rarity in this species.

Tentative recommendations for site management to maintain this species include maintenance of a high water table and propagation of open conditions via rotational grazing. Grazing with large animals may be detrimental to the larvae of this species as a result of trampling. Pashford Poors Fen, the only known current site for this species, is owned and managed by Suffolk Wildlife Trust. The trust has attempted to raise the water level at the site and also graze the wet meadows to control the spread of scrub.

3.7. *Cryptocephalus frontalis* (Marsham 1802)

3.7.1. Description

Cryptocephalus frontalis is another small *Cryptocephalus* species with adults measuring between 2.5 and 3.1 mm in length. This species is almost entirely black with yellow-brown stripes between the elytra and on the lateral margins of each elytron. The legs of this species are yellow-brown.

3.7.2. Distribution

3.7.2.1. UK distribution trends

The known past and present distributions of this species are shown in Figure 3.6 Well over 20 twenty sites for this species have been recorded (Table 3.9). Historic records show that it was distributed from the midlands to the south-east with one record from Cornwall and one record from Wales. *Cryptocephalus frontalis* has been recorded recently from five vice counties (Henderson, 1944; Atty, 1983; Lane and Forsythe, 2000; P. Hodge, pers. comm.)

Table 3.9. Records of *Cryptocephalus frontalis*. Recent records in bold.

Site	Grid Ref	Year	Sources
Nr Gloucester (E. Gloucs.)	SO61	1908	Atty, 1983.
Nr. Stroud (E. Gloucs.)	SO80	1922	Atty, 1983.
Kemerton (Warks.)	**SO93**	**1993**	**M. Cox , pers. comm., 1999**
Nr. Evesham (Worcs.)	SP15	Unknown	Shirt, 1987.
Lighthorne (Warks)	**SP3357**	**1999**	**Lane and Forsythe, 2000.**
Nr. Banbury (Oxon.)	SP4024	Unknown	M. Cox , pers. comm., 1999.
Nr. Oxford (Oxon.)	SP41	Unknown	M. Cox , pers. comm., 1999.
Nr. Oxford (Oxon.)	SP50	Unknown	Shirt, 1987.
Nr. Oxford (Oxon.)	SP5311	1923	Bedwell, 1923.
Nr Saddington resevoir (Leics)	SP69	1943	Henderson, 1943.
Great Glen (Leics)	SP6597	1944	Tozer, 1943.
Kilby-Foxton Canal (Leics)	SP699899	Unknown	Leicestershire Museums, Art Galleries and Records Service.
Nr. Oxford (Oxon.)	SU49	Unknown	M. Cox , pers. comm., 1999.
Nr Helston (Cornwall)	SW72	Unknown	Shirt, 1987.
Nr. Hemel Hempstead (Herts.)	TL10	Unknown	M. Cox , pers. comm., 1999.
Nr. Bedford (Beds.)	TL15	Unknown	M. Cox , pers. comm., 1999.
Nr. Bedford (Cambs.)	TL34	Unknown	M. Cox , pers. comm., 1999.
Nr. Peterborough (Hunts.)	TL38	Unknown	M. Cox , pers. comm., 1999.
Nr. Cambridge (Cambs.)	TL45	Unknown	Shirt, 1987.
Nr. Newmarket (Cambs.)	TL57	Unknown	M. Cox , pers. comm., 1999.
Nr. Chelmsford (Essex)	TL81	Unknown	M. Cox , pers. comm., 1999.
Nr. Thetford (Essex)	TL88	Unknown	M. Cox , pers. comm., 1999.
Ruislip (Msex.)	TQ0887	1917	Harold, 1917.
Nr. Horsham (W. Sussex)	TQ23	Unknown	Shirt, 1987.
Nr. Staines (Msex.)	TQ28	Unknown	Shirt, 1987.
Nr. Epsom (Surrey)	TQ37	Unknown	Hyman and Parsons, 1992.

Harvey's Lane (E. Sussex)	**TQ4714**	**1978 - 2001**	**P. Hodge, pers. comm., 2000 & 2001.**
Nr. Uckfield (E. Sussex)	TQ53	Unknown	P. Hodge, pers. comm., 2000.
Thorndon Park (Essex)	TQ617913	1984; 1985	M. Cox , pers. comm., 1999.
Nr. Canterbury (Kent)	TR16	Unknown	Hyman and Parsons, 1992.
Grosmont (Monmouthshire)	SN3422	1903	J. H. Flint Collection, Leeds Museum, pers obs., 2000.

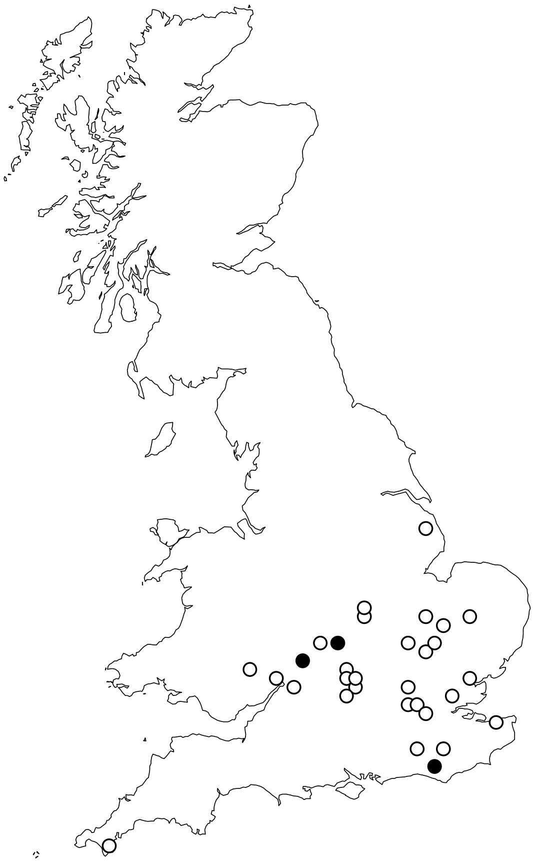

Figure 3.6. Past and present distribution of *Cryptocephalus frontalis*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.7.2.2. European distribution

On the continent this species has been recorded throughout the West-Palaearctic, but it has only ever been caught rarely (Warchalowski, 1991; Burlini, 1955).

3.7.3. Life cycle

Adults of this species have been caught in May, June and July. It is speculated that the larvae of this species feed on litter beneath the host-plants, although no wild larvae have ever been found. Larval development in captivity takes one year (I. Menzies, pers. comm.).

3.7.4. Habitat requirements

Captures of this species have been from mature hedgerows in cultivated land and alongside road verges in East Sussex, (P. Hodge, pers. comm.), Warwickshire (Lane and Forsythe, 2000), East

Kent, South Essex and Oxfordshire (Fowler, 1890; Fowler, 1913). Specimens have also been beaten from *Populus* sp. in Middlesex (Harold, 1917). The Harvey's Lane population site in East Sussex is the only location where numerous individuals of this species have been captured. Observations of captive adults and larvae have shown that one of the food-plants is hawthorn (*Crataegus monogyna*) (I. Menzies, pers. comm.). On the continent it has been associated with *Betula pendula* and *Populus tremula* (Warchalowski, 1991; Burlini, 1955).

3.7.5. Reasons for decline

In the last half a century the decline of this species appears to have been considerable, although the vague nature of many of the older records makes re-surveying impossible. The Harveys Lane population is strong and many individuals can be found each year (P. Hodge, pers. comm.). Old records similarly indicate that in suitable areas this species could be found in large numbers (Harold, 1917; Henderson, 1943). Being highly localised and in a non protected area the remaining healthy population is nonetheless vulnerable to changes in farming practice and possibly to over-collecting. Based on this anecdotal evidence, threats to this species include hedgerow removal and the use of insecticides around hedgerows in cultivated land. Due to the small size of *Cryptocephalus frontalis* and its occurrence in areas that are not designated as reserves it may well have been under-recorded.

Due to the paucity of biological information on this species formulating even tentative recommendations for habitat management is again very difficult. Field observations have linked it to very mature hawthorn hedgerows. Drastic, mechanised winter cutting of the hedgerow in East Sussex does not seem to have been detrimental to the survival of this species (P. Hodge, pers. comm.). Such cutting of hedgerows may even be necessary to maintain a range of vegetation structures and micro-climate profiles.

3.8. *Cryptocephalus biguttatus* (Scopoli 1763)

3.8.1. Description

Adult *Cryptocephalus biguttatus* range from 4.3 mm to 6.0 mm in length and are uniform glossy black except for a spot, variable in size and colour (usually yellow), on the posterior portion of each elytron. The legs of this species are uniformly black.

3.8.2. Distribution

3.8.2.1. UK distribution trends

Few localities have been described for this species (Table 3.10). The known past and present distributions of this species can be seen in Figure 3.7. The vast majority of records have been from the south of England, particularly in and around Surrey (Sharp, 1871; Fowler, 1890; Nicholson, 1921; Allen, 1970a; Jones, 1988; Hyman and Parsons, 1992). There is a disjunct recent record for NE Yorkshire (Hyman and Parsons, 1992). Recently, specimens have been recorded from four vice-counties with sites including Wisley Common in Surrey, Lavington Common in West Sussex and the North Yorkshire Moors. It is also possible that the number of records of *C. biguttatus* may have been exaggerated due to its similarity to one of the many colour forms of the much commoner *C. bipunctatus* (Sharp, 1871).

Table 3.10. Records of *Cryptocephalus biguttatus*. Recent records in bold.

Site	Grid Ref.	Year	Sources
Chartley Moss (Staffs)	SK0028	1896	Shirt, 1987.
Bournemouth (Dorset)	SZ09	1904	Shirt, 1987.
Parley Common (Dorset)	SZ090990	1932	Shirt, 1987.
Parley Heath (Dorset)	SZ0999	1964	M. Cox, pers. comm., 1999.
Wisley Common (Surrey)	TQ0658	**1989-present**	**I. Menzies, pers. comm..2000.**
Lyndhurst (Hamps)	SU20	1912	Shirt, 1987.
The New Forest (Hamps)	SU30	1897	M. Cox, pers. comm., 1999.
Eversley (Hamps)	SU7762	1905	M. Cox, pers. comm., 1999.
Pamber Forest (Hamps)	SU6161	1910	Shirt, 1987.
Lavington Common (W. Sussex)	**SU9519**	**1983-present**	**Hyman and Parsons, 1992.**
Walmer (E. Kent)	TR379500	1942	Shirt, 1987.
Chobham Common (Surrey)	SU9765	Unknown	Shirt, 1987.
Esher Common (Surrey)	TQ1362	1875	M. Cox, pers. comm., 1999.
Esher, Surrey (Surrey)	TQ1464	Unknown	Shirt, 1987.
Wellington College Bog (Berks)	SU832628	1923	Shirt, 1987.
Chat Moss (Lancs)	SJ7096	1908	M. Cox, pers. comm., 1999.
Fen Bogs (NE Yorks)	**SE854975**	**1986**	**Hyman and Parsons, 1992. J.H. Flint Collection, Leeds Museum, pers. obs., 2000**

Figure 3.7 Past and present distribution of *Cryptocephalus biguttatus*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.8.2.2. European distribution

On the continent this species is found throughout the Western Palaearctic where it can be found occasionally in relatively large numbers, but only very locally (Burlini, 1955, Warchalowski, 1991).

3.8.3. Life cycle

Adults of this species have been found through May and June into the beginning of July. No wild larvae have been captured, but it has been shown that captive bred larvae take one or two years to reach maturity (I. Menzies, pers. comm.).

3.8.4. Habitat requirements

All the individuals that have been recorded have been from wet-heathland and bog-land sites (Sharp, 1871; Fowler, 1890; Nicholson, 1921; Allen, 1970a; Jones, 1988; Hyman & Parsons, 1992). Very little basic biological information is known about this species, although, *Erica tetralix* is known to be an adult host-plant of this species (Nicholson, 1921) adults have also been found feeding on *E. tetralix* on the continent (Burlini, 1955; Warchalowski, 1991, D.

Telnov, pers. comm.) and captive larvae have been reared on the adult host-plant (I. Menzies, pers. comm.).

3.8.5. Reasons for decline

The decline of *C. biguttatus* has been relatively marked, although it has only ever been known from a small number of sites. In some of the southern historic locations it was possible to capture 20-30 specimens by visual searching (Nicholson, 1921), but on the whole, it has never been a common species. (Shirt, 1987). Mis-identification of *C. biguttatus* as one of the morphs of the very variably patterned *C. bipunctatus* and vice-versa may have resulted in errors among the historic locations for this species (Sharp, 1871). The observed rarity of *C. biguttatus* may also be compounded by way of the habitat that it utilises. Its only known host-plant, *Erica tetralix*, is a relatively low growing plant that occurs in dense patches. Sampling the inner parts of these patches without disturbing the beetles and forcing them to drop to the ground is difficult. Threats to *C. biguttatus* are thought to include falling water tables and the loss of traditional heath-land management techniques (Hyman & Parsons, 1992).

Due to the lack of biological information managing sites for the maintenance of extant populations is problematic. What is known suggests that high water table levels should be maintained and *E. tetralix* heath should be managed to ensure a variety of successional stages. Wisley Common, owned by the Surrey Wildlife Trust and Lavington Common are both managed in this way. In common with other *Cryptocephalus* species it is probable that *C. biguttatus* is thermophilous and thus micro-habitats may be required which exhibit warm micro-climates. Therefore, a complex *E. tetralix* environment ranging from areas of bare-ground through to mature heath should be managed in areas which are sheltered from wind but open to southern aspects for insolation.

3.9. Cryptocephalus querceti (Suffrian 1848)

3.9.1. Description

This species is slightly smaller than *Cryptocephalus decemmaculatus,* with adults measuring between 2.4 and 3.5 mm in length. The body of the adult is entirely glossy black with completely yellowish legs. The female is very bulky compared to the male.

3.9.2. Distribution

3.9.2.1. UK distribution trends

Very few specimens and localities have ever been recorded for this species (Table 3.11). The known past and present distributions of this species are shown in Figure 3.8 with Donnington Park added relatively recently to the small list of current sites. Of the previously known localities two were also in the midlands and one was in Berkshire (Bedwell, 1926; Johnson, 1965; Lott, pers. comm.; pers. obs.), and there is a single doubtful records from Lancashire. The record of *C. querceti* from Chat Moss (SJ7096) is probably an error as the site is completely unsuitable for this species. However it is suitable for, and indeed once supported, *C. decemmaculatus*. A male *C. decemmaculatus* in its dark form (*var. bothnicus*) would strongly resemble *C. querceti*.

Table 3.11. Records of *Cryptocephalus querceti*. Table 3.3. Recent records in bold.

Site	Grid Ref.	Year	Sources
Windsor Great Park (Berks.)	**SU9473**	**1930 - 2001**	**Shirt, 1987. I. Menzies, pers. comm., 1999, 2000 & 2001. Pers. obs., 1999.**
Donington Park (Leics.)	**SK414269**	**1988**	**M. Cox, pers. comm., 1999.**
Birklands & Bilhaugh (Notts.)	**SK620683**	**1929; 1938; 1965; 1993**	**M. Cox, pers. comm., 1999.**
Langford Moor (Notts.)	SK8555	1911	M. Cox, pers. comm., 1999.
Chat Moss (Lancs.)	SJ7096	Unknown	M. Cox, pers. comm., 1999.

Figure 3.8 Past and present distribution of *Cryptocephalus querceti*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.9.2.2. European distribution

Cryptocephalus querceti is found throughout the West-Palaearctic region, where it is again recorded only rarely and in very small numbers (Warchalowski, 1991).

3.9.3. Life cycle

Adults of this species have been found for only a short period at the end of May and into June. It has been shown that captive bred larvae take one year to reach maturity (I. Menzies, pers. comm.)

3.9.4. Habitat requirements

Almost all of the specimens of this species have been found on ancient oak trees (*Quercus* spp.) in areas of wood-pasture, with a few specimens also recorded on hawthorn (*Crateagus monogyna*) (Bedwell, 1926; Johnson, 1965; D. Lott, pers. comm.; pers. obs.). Adult beetles collected in Windsor Great Park in the summer of 1999 suggest that this species can be relatively abundant in suitable, localised areas. The results of sampling of the ancient oak trees on which it occurs revealed that 93% (n = 13) of the adult beetles found were on the epicormic growth that occurs on the cankerous swellings of some of these old trees. (R. Piper, unpublished data). A 1999 survey of the areas in Sherwood Forest where this species was recently recorded (D. Lott, pers. comm.) did not yield any specimens of *C. querceti*. This site is more woodland than wood-pasture and bracken (*Pteridium aquilinum*) is abundant. Observations of captive adult feeding suggest that tender new oak leaves are important for this species (I. Menzies, pers. comm.). As with other *Cryptocephalus* species the larvae of *C. querceti* appear to be relatively catholic in their tastes, but oak litter, anecdotally, seems to be their preferred food. On the continent this species is thought to be associated with *Betula* sp., *Populus tremula* and *Quercus* sp. Wild larvae of *C. querceti* have been sieved from the litter at the base of ancient oak trees in Sweden (L. Engstrom, pers. comm.).

3.9.5. Reasons for decline

Threats to this species include the removal of old and diseased trees for safety and aesthetic reasons. Over-grazing and browsing of epicormic growth may also be detrimental to the larvae and adults respectively. Large grazing animals trampling the ground beneath the old trees on which adults are known to occur may adversely affect the larvae.

C. querceti is sufficiently similar to *C. labiatus* (particularly the males) to generate a certain amount of under-recording. As this species is almost exclusively associated with ancient oaks it is given an indicator status of Grade 1 in Harding and Rose (1986). Gauging the decline of this species is difficult, as very few sites have ever been known for this species.

The available field observations of this species enable a more thorough understanding of its requirements than for some of the other species in this chapter. The area within Windsor Great Park, part of the Royal Estate, supports a good population of *C. querceti*. Therefore, it appears as though the management of this area has been favourable for the long-term survival of *C. querceti*, i.e. light grazing around the large trees and no cutting or trimming of the trees for aesthetic reasons. The areas within Sherwood Forest, owned by the Forestry Commission, where *C querceti* had been recorded are very different to the Windsor areas and it may be that the more enclosed nature of Sherwood Forest results in it being sub-optimal for *C. querceti.* Bracken litter may also be detrimental to *C. querceti* larvae at this site, but there is no direct evidence to confirm this.

3.10. Cryptocephalus sexpunctatus (Linnaeus 1758)

3.10.1. Description

Cryptocephalus sexpunctatus adults measure between 4.0 and 5.3 mm in length. The type form has three black spots on each elytron (Plate 13), although the pattern is variable. The pronotum is black with a 'T' shaped yellow-orange pattern in the centre. Males have a pair of lateral processes on the 2nd abdominal sternite, while on each side of the female pygidium there is a small tubercle.

3.10.2. Distribution

3.10.2.1. UK distribution trends

Among the *Cryptocephalus* beetles in this study *C. sexpunctatus* seems to have been recorded historically from a relatively large number of sites (Table 3.12). Within the last five years specimens of this species have been recorded only from Stockbridge Down (Hampshire) and Kirkconnell Flow NNR (Kirkcudbrightshire) but Figure 3.9 shows the known past and present distribution of this species in the UK Most of the localities for this beetle were in the south east of England with disjunct records from Scotland.

Table 3.12. Records of *Cryptocephalus sexpunctatus*. Recent records in bold.

Site	Grid Ref	Year	Source
Glen Affric Area (E. Invernesshire)	NH22	1963	M. Cox, pers. comm., 1999.
Nr Dalry (Ayrshire)	NS2949	1867	Sharp, 1867.
East Loathian	NT27	Unknown	M. Cox, pers. comm., 1999.
Kirkcudbrightshire	NX76	Unknown	M. Cox, pers. comm., 1999.
Kirkconnell Flow (Kirkcudbrightshire)	**NX967698 A**	**1995**	**A. Godfrey, pers. comm., 1999.**
Nr Worcester (Worcs.)	SO87	1921	Ashe, 1922.
Colesbourne (E. Gloucs)	SP01	1946	I. Menzies, pers. comm., 1999.
Gulf Scrubs, Colesbourne (E. Gloucs)	SP0214	1945	I. Menzies, pers. comm., 1999.
Ham street (Kent)	TQ6173	1957	M. Cox, pers. comm., 1999.
Stockbridge Down (Hants.)	**SU3834**	**1990-1996**	**I. Menzies, pers. comm., 1999.**
Lord's Wood (Hants.)	SU3916	1887	M. Cox, pers. comm., 1999.
Nr. Southampton (S. Hants.)	SU41	Unknown	M. Cox, pers. comm., 1999.
Nr. Horsham (W. Sussex)	SU91	Unknown	M. Cox, pers. comm., 1999.
Nr. Dorchester (Dorset)	SY88	1900-1970	M. Cox, pers. comm., 1999.
Lime Woods (N. Lincs)	TF094750	1956	M. Cox, pers. comm., 1999.
Scotgrove Wood (N. Lincs)	TF130704	1956	M. Cox, pers. comm., 1999.
Nr Ipswich (S. Suffolk)	TL92	1895	Morley, 1895.
Colchester (N. Essex)	TM0024	1944 -48	M. Cox, pers. comm., 1999.
Nr. Sudbury (S. Suffolk)	TM11	1900-70	M. Cox, pers. comm., 1999.
Nr. Dorking (Surrey)	TQ35	Pre 1900	M. Cox, pers. comm., 1999.
East Malling (Kent)	TQ5715	1947	Shirt, 1987.
Darenth Wood (W. Kent)	TQ5873	1905-47	Shirt, 1987.
Grays Chalk Pit (S. Essex)	TQ6078	1978-86	Shirt, 1987. M. Cox, pers. comm., 1999.
Pilgrims Way, Ryarsh (Kent)	TQ6759	1947	Massee, 1947.
Cobham Park (W. Kent)	TQ6868	Unknown	Maidstone Local Record Centre.
Cobham Woods (W. Kent)	TQ6968	Unknown	Maidstone Local Record Centre.
Orlestone Forest (E. Kent)	TQ9835	1958	M. Cox, pers. comm., 1999.

Figure 3.9. Past and present distribution of *Cryptocephalus sexpunctatus*. [Filled circles = extant populations (positive surveys within last five years); Open circles = putative extinct populations). Some symbols represent more than one population.

3.10.2.2. European distribution

Cryptocephalus sexpunctatus is known to occur over the whole of the western Palaearctic region, with its northern boundary in Norway (Warchalowski, 1991). It is only captured rarely and in small numbers (Warchalowski, 1991).

3.10.3. Life cycle

All of the known records of adults of this species are from May and June. Captive larvae of this species were shown to complete their development in one or two years (Owen, 1996).

3.10.4. Habitat requirements

Large populations of this beetle were recorded in Kent (Massee, 1947; Cox, 1948). During May and June of 1923 and 1947 this species was recorded as very plentiful in Darenth Wood in Kent (Massee, 1947), with many hundreds of specimens collected. However, during intervening years at this site it apparently occurred rather sporadically. Although, historically, large numbers of this species have been recorded, very little is known of its ecology other than its host-plant affinities. The strongest populations of this species seem to have occurred in areas of *Corylus avellana* coppice. *C. avellana* may be the most important food-plant for *C. sexpunctatus* in

Britain, but adult feeding has also been observed on *Populus tremula* and *Salix fragilis*, (Ashe, 1922; Cox, 1948). On the continent it has been recorded on *Betula pendula, Crataegus* sp. and *Quercus* sp. (Koch, 1992). Captive larvae of this species were shown to be able to complete their development on a diet of hazel leaves (Owen, 1996).

3.10.5. Reasons for decline

Due to the paucity of field observations the exact requirements of this species in the wild are difficult to elucidate, making management of sites for this species problematic. In a broad sense the factors causing the decline of this species are loss of broad leaved woodland and neglect of woodland together with conversion to high forest (Hyman & Parsons 1992). On a finer scale it can be argued that the great decrease in coppicing over the last century has precipitated a decline in this species as very large populations were once found in *Corylus avellana* coppice. By the 1980s coppicing was practised in only 2 % of woodlands, most of which were of non-native sweet chestnut (*Castaneus sativa*) in the southern counties (Forestry Commission, 1984). Neglect of coppiced areas within broadleaved woodland could therefore result in the loss of *C. sexpunctatus*. The very strong *Cryptocephalus sexpunctatus* population at Darenth Wood was lost in the late 1940's as a result of a housing development. The large numbers of *C. sexpunctatus* recorded in Darenth Wood in 1923 and 1947 coincides with very cold, long winters in 1922 and 1946. The very cold winter may have severely affected the small mammal population at the site thus removing a source of larval *Cryptocephalus* predation. Therefore, the large *C. sepunctatus* populations observed may have been a result of chance climatic events.

Recent English records for *C. sexpunctatus* have been from Stockbridge Down (Hampshire). *C. avellana* is abundant at this site but there is none of the young coppiced growth in sheltered conditions that seems most suitable for this species, and it appears that no more than five specimens have been found since 1990. Any areas within broadleaved woodland which offer host-plants in the correct warm micro-climates may provide a habitat for *C. sexpunctatus*, but conversely the neglect of woodland rides, glades and scrub maturation could potentially result in the loss of *C. sexpunctatus* populations. As with the other *Cryptocephalus* species the nature of larval development dictates that grazing of sites with large animals may be detrimental, but this has not been confirmed for any of the species.

3.11. Discussion

It is apparent from examining the older entomological literature that very little attention was paid to defining an exact location of capture by historic collectors or if it was then the location was kept secret to prevent competitors from going there. Most often the only location information included is the nearest village, town or city. The vague nature of these records makes it very difficult to re-survey the areas in question and confirm the presence of the relevant species. *C. frontalis* is known to occur reliably at only one site and as almost all of the old records give no discrete location it is impossible to return to the sites in order to re-survey them.

Of the *Cryptocephalus* species described in this chapter the only species that have declined considerably are *C. sexpunctatus* and *C. frontalis.* The others species have never been abundant in the UK. This was once a widespread and locally common insect but now cannot be reliably found anywhere in the UK. The decline in the other species is less marked although *C. exiguus* was once found, locally, in relatively large numbers whereas now it is very hard to locate anywhere. *C. querceti* has perhaps the narrowest range of host affinities as it is almost exclusively found on ancient oak trees. Nonetheless, more sites are known today for this species than were known a century ago. *C. primarius* appears to always have been a sporadically appearing species. The only site where it occurred reliably in significant numbers was Rodborough Common, but the last specimen captured at this site was in 1985. *C. biguttatus* is a much more difficult species to sample than the other species so it very difficult to assess the level of decline in this species.

Although British *Cryptocephalus* beetles occur in a range of habitats (Figure 3.10), scrub transition supports the greatest number of species and also the majority of these are of conservation concern.

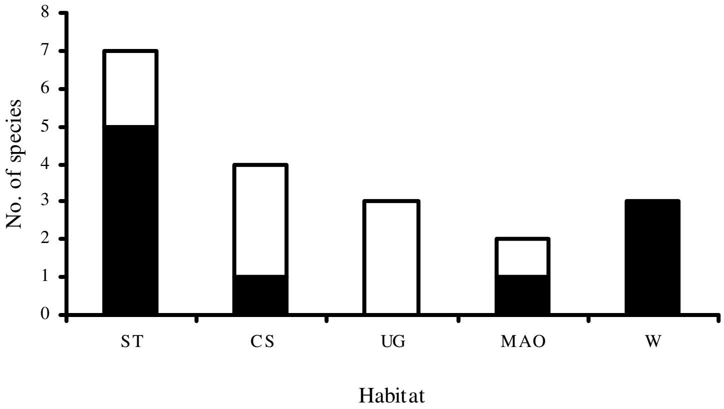

Figure 3.10. Fig. 1. No. of British *Cryptocephalus* species with action plans or priority statements per habitat (black = Species with individual action plans or priority statements; white = other species). ST = scrub transition, CS = calcareous slopes, UG = unimproved grassland, MAO = mature/ancient oaks, W = wetland.

Table 3.13. The habitats and BAP status of British *Cryptocephalus* beetles.

Species	Present Status	Habitat
C. aureolus	Notable B	calcareous slopes
C. biguttatus	Vulnerable	wetland
C. bilineatus	Notable B	unimproved grassland
C. bipunctatus	Notable B	scrub transition / calcareous slopes
C. coryli	Endangered	scrub transition
C. decemmaculatus	Vulnerable	scrub transition on wetland
C. exiguus	Endangered	wetland
C. frontalis	Notable A	scrub transition
C. fulvus	No status	unimproved grassland
C. hypochaeridis	No status	calcareous slopes
C. labiatus	No status	mature / ancient trees
C. moraei	No status	unimproved grassland
C. nitidulus	Endangered	scrub transition
C. parvulus	Notable B	scrub transition
C. primarius	Endangered	calcareous slopes
C. punctiger	Notable A	scrub transition
C. pusillus	No status	mature / ancient oaks
C. querceti	Vulnerable	mature / ancient trees
C. sexpunctatus	Vulnerable	scrub transition
C. violaceus	Extinct	calcareous slopes

Species inhabiting scrub do not require early successional habitats *per se*, merely the relatively warm microclimates associated with them (Thomas, 1983b, 1993; Cherrill & Brown, 1990b; Warren 1994). Coppicing, produces warm microclimates favoured by thermophilic insects (Mitchell & Woodward, 1987) and the near-cessation of this type of woodland management has been implicated in the decline of *Cryptocephalus* species in Britain. For example, *Cryptocephalus sexpunctatus* was once found in considerable numbers on hazel (*Corylus avellana*) coppice (Massee, 1947), but today the species is classed as Vulnerable in Britain and has been recorded from only two sites in the last decade (Hyman & Parsons, 1992). Coppicing was a widespread form of woodland management during the industrial revolution of the 18th to 19th century (Warren & Key, 1989). However, the first national survey in 1905 revealed that coppicing was only practised in 30 % of woodlands (Peterken, 1981). By the 1980s this had declined to 2 % of woodlands, most of which were of non-native sweet chestnut (*Castaneus sativa*) in the southern counties (Forestry Commission, 1984). Coppicing may produce habitats with warm micro-climates, however, species associated with coppiced woodland may encounter a sub-optimal food resource. Certain herbivorous insects have been shown to be unable to cope with the high levels of phenolic herbivore-defence substances present in the young leaves of coppice regrowth (Meyer and Montgomery, 1987).

Rearing larvae has shown that the immature stages of *Cryptocephalus coryli, C. nitidulus* and *C. decemmaculatus* survive particularly well in captivity. *C. decemmaculatus* larvae that were reared with the intention of propagating a captive population were fed, solely, leaf litter from *Salix alba*. *Salix cinerea* was not readily available therefore it was decided to feed the larvae the litter from another *Salix* species. Different willow taxa have been shown to have no effect on the mortality of other chrysomelid species (Orians *et al.*, 1997). The larvae appeared to flourish and they reached full size after only three months, although they were kept satiated until the winter at which time they were acclimatised to prepare for diapause. During the simulated winter the larvae of all the species continued to feed, even at 5 °C. Activity in an insect at this temperature is unusual and it is possible that this behaviour allows the larvae to feed during the autumn and winter even in very cool conditions. This may be especially important if the larvae has not grown enough during the late summer to be able to pupate in the following spring / summer. Being active in the cool conditions of the autumn may also enable the larvae to take advantage of the relative abundance of leaf litter at this time of the year.

A significant proportion of the larvae that were reared did not pupate even though they were fully developed. The reason for this phenomenon is unknown. It is possible that this is an artefact of 'hedge betting' by the previous generation. This theory suggests that to overcome the detrimental effects on the population of a scenario such as a poor summer not all of the larvae will pupate in one particular year. Some of the larvae will continue feeding and metamorphose the following season therefore bypassing the possible poor environmental conditions of one season in favour of the next. Leaf litter contains less nitrogen and water than fresh leaves (Scriber and Slansky, 1981) and invertebrates that feed on this type of vegetable matter may be expected to have a protracted development compared to counterparts feeding on fresh vegetation.

Preferences for warm transitional habitats may predispose *Cryptocephalus* and other thermophilic species to being uncommon because, whether anthropogenic (e.g. as the result of coppicing) or natural (e.g. rabbit activity), scrub transition is an ephemeral habitat (Thomas, 1993). Furthermore, although these early to mid successional and open anthropogenic habitats have existed for millennia they have become severely fragmented during the last century (Department of the Environment, 1994; Rackham, 1995). However, dispersal ability in *Cryptocephalus* is limited (see Chapter 7) and this suggests that habitat patch location may be a limiting factor. Studies of the population genetic structure of several *Cryptocephalus* species have shown that small distances and apparently trivial barriers to dispersal can impeded gene flow (see Chapter 8). Butterflies associated with this ephemeral habitat have been shown to be surprisingly sedentary and are also declining in Britain (Thomas, 1991).

It is likely that the decline of *Cryptocephalus* beetles in Britain is compounded by the failure of conservation bodies to recognise the importance of the scrub habitat on which many of them depend. The term scrub encompasses a diversity of habitats that have in common a dominance of shrubs (Hopkins, 1996). Scrub is therefore not treated as a discrete habitat. As such, the demise of such habitat is difficult to document compared to more distinct biotypes such as wetlands, which have experienced an 80% loss in the last 2000 years (Merritt, 1994; Rackham, 1995). Furthermore, scrub habitats are often considered undesirable in conservation strategies for species with other habitat preferences. For example, habitat management for grassland butterfly species and heath-dwelling reptiles involves scrub clearance (UK Biodiversity Steering Group, 1999). Invading scrub, with open pockets where the microclimate is relatively warm appears to be more suitable for *Cryptocephalus* beetles than dense scrub.

In the case of some other thermophilic insects in Northern Europe rarity has been attributed to populations being on the northern limits of their species' distribution (Thomas & Morris 1994). Butterfly populations near the edge of species ranges have been shown to experience much greater fluctuations than those further south, and are thus more prone to stochastic local extinction in unfavourable years (Thomas, *et al.*, 1994). This may apply to *Cryptocephalus primarius* which, in continental Europe, occurs only in the south-west. (Warchalowski, 1991) Although it has been postulated that sedentary and specalised invertebrate species can exhibit unusually rapid range expansion in marginal areas due to putative climate warming no range expansion has been observed in any *Cryptocephalus* species. (Thomas, 1993; Thomas *et al.*, 1999; Thomas, 2000). In Britain *C. primarius* has only been found on south-facing slopes in association with *Helianthemum nummularium* flowers, the petals of which may act as parabolic reflectors producing a hot spot in the centre of the flower (Kevan, 1975).

The decline of *Cryptocephalus* is attributable to a suite of factors including a predisposition to rarity because of limited dispersal ability and use of a patchy and ephemeral resource (scrub) that is being increasingly fragmented or, in the case of coppicing, absent. Many sites have been given varying levels of protection in the hope of maintaining their insect faunas, but the threats that are posed to insect species are still largely based around habitat loss. The stonghold of *Cryptocephalus sexpunctatus* was lost thanks to a housing development and countless other sites for the other rare *Cryptocephalus* species will have disappeared as a result of habitat loss, such as *C. exiguus* at Freshney Bog, *C. coryli, C. nitidulus*, *C. punctiger* at Darenth Wood and *C. nitidulus* at Wychwood Forest. The old threats, however, are now likely to be compounded by improper site management strategies. The conservation of these beetles requires that the significance of scrub as a habitat needs to be recognised and that it is managed within areas where it is normally considered detrimental. This management would have to be complex allowing vegetation transitions combined with periodic clearances of high woodland and of grasslands that are being invaded. If the habitat requirements of a species with very exacting requirements such as the rare *Cryptocephalus* beetles are not understood then routine management may be detrimental.

A factor contributing to the decline of these *Cryptocephalus* species may have been over-collecting. Collecting would have started in Victorian times and appears to have continued regularly until the 1940's, although it still occurs today. Notes left by deceased collectors often describe the collection of a series of specimens of a particular species from a single location even though at the time the species was known to be rare (Kidson-Taylor, 1904; 1906; 1909; Donisthorpe, 1938). Even though this collecting would only have been perpetrated by a handful of individuals its effect may have been very significant indeed. Records in the literature show that some areas were widely regarded as good hunting grounds for certain rare species (Kidson-Taylor, 1909). Knowledge of a certain area was disseminated amongst the entomological fraternity and several collectors would have visited the same sites year after year to obtain their series. Often, if the species in question appeared in apparently large enough numbers hundreds were taken and were exchanged with associates at a later date (Massee, 1947). The effect of over-collecting on a relatively small, isolated *Cryptocephalus* population could have been catastrophic and it is quite likely that several populations have succumbed to extinction as a result of stochastic influences augmented by over-collection. A prime potential example is the population of *C. sexpunctatus* at Darenth Wood (over-collecting here would have been compounded by habitat loss due to a housing development). This population may have seemed very strong in 1923 and 1947 to the collector but heavy collecting could have had a severe impact.

Chapter 4. A novel technique for relocating concealed insects

4.1. Introduction

An understanding of the population dynamics of individuals requires knowledge of spatial behaviour (Turchin, 1991). Gathering information on the spatial behaviour of many smaller organisms such as insects is problematic because observing them in the field without disturbing their natural behaviour and habitat is sometimes very difficult. This problem is compounded by the small size, crypsis, and rarity of many insect species.

Various methods have been used to detect and record micro-habitat preferences of ground dwelling insects in the field. These include pitfall trapping (Rijnsdorp, 1980; Best *et al.*, 1981), radio-active marking (Southwood, 1978; Baars, 1979), harmonic radar (Mascanzoni & Wallin, 1986; Lovei *et al.*, 1997) and radiotelemetry (Riley, 1989; Pride & Swift, 1992). Of the above methods harmonic radar has perhaps shown the most promise for the detection of tagged individuals (Mascanzoni and Wallin, 1986; Roland, *et al.*, 1996). This method is particularly useful for organisms that are relatively vagile, however, the resolving power of harmonic radar does not lend itself to the study of relatively sedentary ground-dwelling animals. This method is also extremely costly, and the size of the tags used in harmonic radar studies are often a problem. Although lightweight, the diode tags used must have a trailing aerial (Mascanzoni & Wallin, 1986), which is a particular disadvantage for studies of small litter-dwelling insects where it is likely to be a hindrance to natural movement.

The novel technique detailed here involves the use of metallic tags and commercial metal detection equipment. It does not have the detection range of harmonic radar but is a much cheaper system that uses a smaller, more discreet tagging technique. In field experiments, the technique has proven to be effective in relocating released beetle larvae living in concealed situations. It was used to determine the mobility, micro-habitat preferences, and overwintering survivorship of leaf beetle larvae of the chrysomelid *Cryptocephalus coryli* (Linnaeus). *Cryptocephalus* larvae inhabit cases made of their own faeces that they carry around in the leaf litter. The cryptic cases of the larvae, their small size, and the habitat in which they reside make it very difficult to locate larvae using conventional techniques.

Cryptocephlalus coryli is known from only two U.K. sites and is listed as RDB1 (endangered) (Hyman & Parsons, 1994). In common with other members of the genus, eggs are covered in faeces by the female and dropped to the ground beneath the host plant. Once hatched, the larva adds to the egg case to eventually form the characteristic larval case. The larvae are the overwintering stage for the genus and feed on leaf litter. There is no clear-cut diapause. The biodiversity action plan for this species (UKBG, 1999) has the target of the re-introduction of this species to three sites by 2005. For such introductions to be successful, a thorough understanding of mortality and micro-habitat preferences of the larvae is essential.

4.2. Materials and methods

A detection system was employed that was based on the principle of the pulse field induction loop (Pulse Technologies, Oxford, U.K.). The device was designed originally to locate small amounts (< 2 mm) of non-ferrous and ferrous metal in fabrics. The metal detector consists of one small, hand-held unit (720 g), which for field use is connected to a 12 v lead acid gel battery (Yuasa, Westmont, USA). The tags used to label the insects were a strip (mean = 1 ± S.D. 0.2 mm × mean = 3 ± S.D. 0.2 mm and mean = 0.35 mg ± S.D. 0.07 mg) of stainless steel, that was taken from the security labels that are attached to goods to deter shoplifters. Different sized tags were tested and it was found that the device had a maximum detection range of about 7 cm. One small strip of metal was attached to each of the cases using a small drop of epoxy resin adhesive (Bostik, Leicester, U.K.). Laboratory reared *C. coryli* larvae were then marked individually with a disc of acetate sheet (0.9 mm diameter) on which a unique code was printed (font size 2) using a laser printer. The disc was bored from the sheet using a modified mechanical pencil and attached to the case of the larvae with epoxy resin adhesive as before. Once the insect was detected in the field the code on the disc could be read using a portable microscope (Specwell Tokyo, Japan) and the insect quickly returned to the place of capture. The use of the acetate labels allowed the behaviour and fate of individual insects to be monitored. The range of the equipment in this trial was never more than 3 cm. In initial tests, detection was found to be possible through any type of litter/soil, and moisture did not seem to impede the locating of tagged individuals. Further tests of the relocating technique were applied to the third instar (mean = 0.030 g ± S.D. 0.0038 g including case, n20) and last (fifth) instar (mean = 0.092 g ± S.D. 0.0033 g including case, n = 20) larvae of *C. coryli*. The mass of the larvae was recorded before and after tagging and for third instar larvae the tag represented 3.26 ± S.D. 0.48% of larval body weight while for last instar larvae the tags represented 1.18 ± S.D. 0.36% of their body weight. To test the effect of the tags on the mobility of the larvae, a 1 × 1 m box was filled with leaf litter to a depth of 4 cm. Twenty tagged larvae and 20 untagged larvae were allowed to disperse for 24 h (20 °C, 12 h dark, 12 h light). The distances moved by the larvae away from the release point were recorded.

Field tests were carried out using 40 tagged larvae released in October 1999 at Kirkby Moor U.K. (54° 15’ N 3° 8.6’ W)**.** Prior to release, the larvae were acclimatised by placing them in successively cooler incubators (20, 13, 8 and 5 °C). Ten larvae were placed beneath each of four *Betula pendula* trees, the main host plant used by this species at the site. Over the first 48 h, the larvae were relocated in the morning and the evening and the distance moved from the release point was recorded. For the rest of the test period, the larvae were retraced once a month until March 2000. During each visit, the micro-habitat in which the larvae were found in was recorded, together with evidence of predation. Larvae were recorded as still alive if the head capsule was visible at the aperture end of the case.

4.3. Results

During laboratory tests it was found that tagged larvae moved an average of 7.1 (± 7.59) cm over a 24 h period. Untagged larvae moved 7.6 cm (± 7.9) cm in the same time. A T test showed that there was no significant effect of tagging on movement through the leaf litter (T = -0.12, *P* = NS). In the field, the first 48 h monitoring of the released larvae revealed a nocturnal pattern of activity (Figure 4.1)

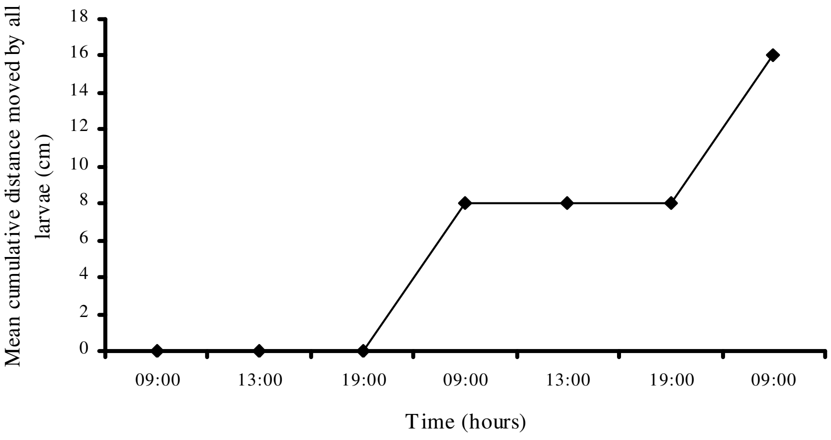

Figure 4.1. Timing of movement of *Cryptocephalus coryli* larvae over a 48 hour period.

corresponding with observations on captive larvae, where the majority of feeding appears to take place overnight. The micro-habitats to which the larvae of *C. coryli* had relocated are shown in Figure 4.2.

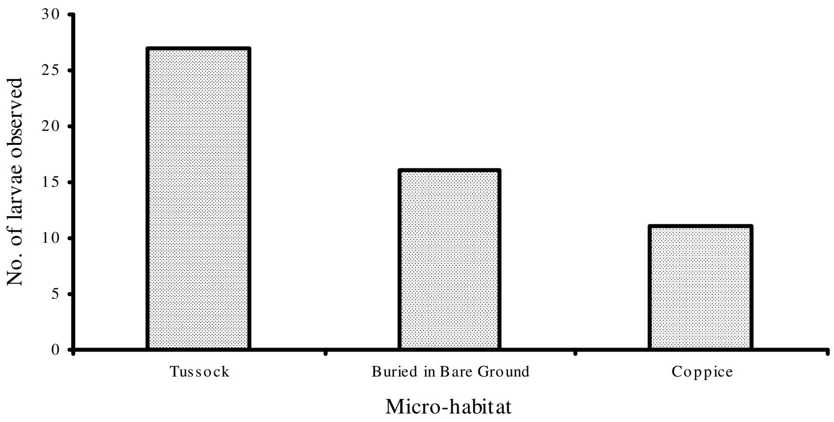

Figure 4.2. Micro-habitat selection by *Cryptocephalus coryli* larvae (based on observations made during entire study period).

Larvae were either partly buried in soil, secreted within small grass tussocks or in coppice stools. 82% of the observations of larvae being partly buried in bare ground concerned mature last-instar larvae, pointing to a change in micro-habitat prior to pupation (Figure 4.3) and possibly the need for a small-scale mosaic of ground characters for successful development in this species.

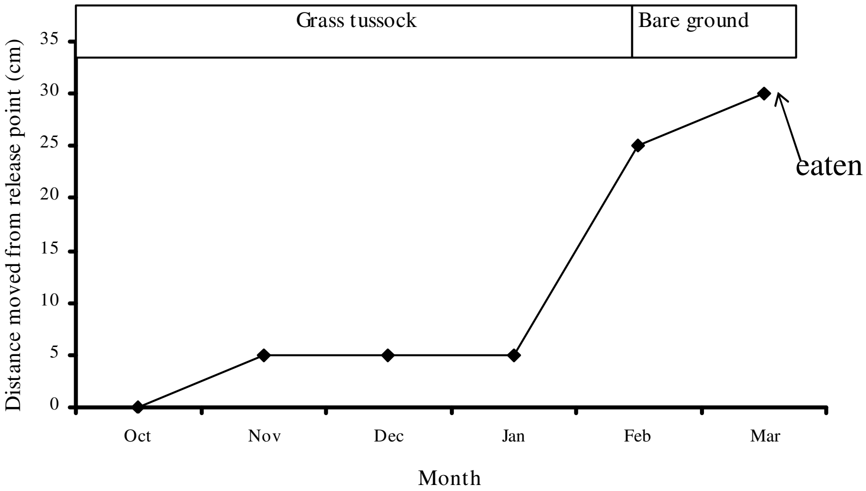

Figure 4.3. Micro-habitat selection of a single *Cryptocephalus coryli* larvae over a 5 month period.

Individual marking enabled the micro-habitat selection and mortality of specific larvae to be studied (Figure 4.3). During the study, many empty, damaged larval cases were found. These cases had been chewed or gnawed open and the larvae had been removed cleanly from inside, probably by a small mammal. At the end of the experiment fully 87.5% of the relocated larvae had been eaten (Figure 4.4).

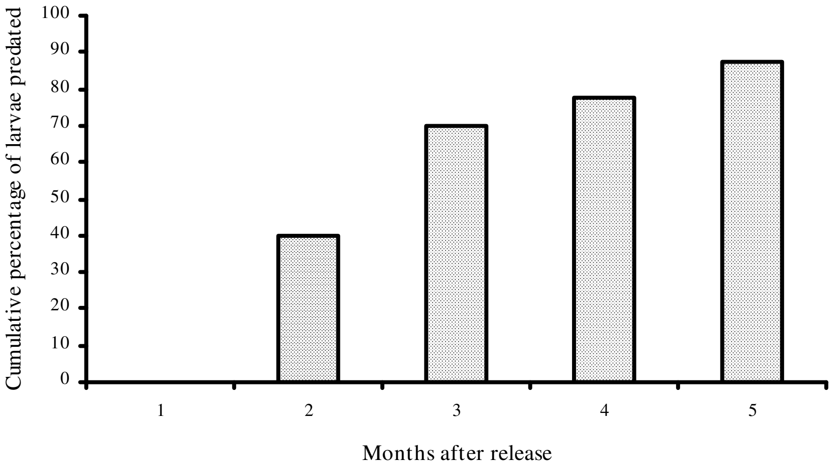

Figure 4.4. Cumulative predation on *Cryptocephalus coryli* larvae over a five month period. (Total No. of larvae eaten = 32).

The technique enabled 90% of the released larvae to be relocated after a period of 5 months. During this time, the metal tags showed only minor corrosion. Only one of the tags had come free from the larval cases, this may have been a result of the action of the predator as it removed the larva from its case.

4.4. Discussion

The field tests showed that metal detection is an efficient method for relocating relatively immobile larvae in semi-concealed locations. The technique enabled both behavioural and ecological aspects of *C. coryli* larvae to be understood in their natural environment.

The range of the detection system is small but is ample for the relocation of insect larvae that do not disperse very far. The technique enables tagged individuals to be found quickly with minimal habitat disturbance. With more sensitive equipment the detection range could be increased and the tag sized reduced. The system is many times cheaper than an alternative detector based on the harmonic radar principle [harmonic radar hardware (Recco, Lidingo, Sweden) costs ~ £15 000, whereas a handheld metal detector (Pulse Technologies) is ~ £400]. Furthermore, harmonic radar can have difficulty pinpointing separate signals from a group of released animals if they remain in close proximity to the release point, and water and humidity have also been shown to attenuate harmonic radar signals (Lovei *et al.*, 1997). Some organisms can also generate false signals that confuse the operator of the harmonic radar equipment (Lovei, *et al.*, 1997). No such problems were encountered using the metal detector.

The use of a metal detector and metal tags would be useful for describing the habitat use and ecology of other small terrestrial invertebrates that are relatively sedentary and cryptic. For example, this method could be used to determine pupation sites of many leaf beetles whose larvae move away from the host plant and construct a pupal chamber in the top layer of the soil. The tag would be shed with the ecdysed cuticle of the last instar larvae and deposited within the pupal chamber. The distance moved away from the host plant could be described along with the micro-habitats chosen by the larvae. Presently, recapturing released larvae of a cryptic nature usually entails destructive sampling of the habitat (Nicholls & Pullin, 2000). The over-wintering strategies of adult insects on or in the ground beneath their host-plants could also be studied. Adult insects could also be relocated in cryptic situations such as the fissures in tree bark. Finally, in principle this technique could be applied to any situation where individuals are otherwise difficult to locate but are present relatively close to the surface.

Chapter 5. The food and habitat preferences of adult and larval *Cryptocephalus* pot beetles: how compatible are they?

5.1. Introduction

Understanding the ecological requirements of a species is crucial for its conservation (Bedick *et al.,* 1999) and recovery plans often founder due to a lack of basic biological information (Tear *et al.,* 1993; 1995). In particular, sympathetic management of a habitat that supports a rare species can only be carried out if detailed ecological information exists (New *et al.,* 1995). Understanding the habitat and food preferences of larvae and adults are two major facets of this ecological information and there is a wealth of data on the micro-habitat and host-plant preferences of immature and adult insects. The link between oviposition preference and offspring performance is crucial in the understanding of plant-insect interactions, reflecting the generally greater mobility of the adult stages (Craig *et al*., 2000). Female insects are assumed to maximise their fitness by ovipositing on high quality hosts (Scheirs *et al.,* 2000), leading to the suggestion that females should oviposit where their larvae have the greatest chance of survival (Courtney & Kibota, 1990). This *naïve adaptationist* theory has nonetheless been supported in some studies (Price *et al*., 1990; Ohgushi, 1995). Alternative theories have needed to be put forward to explain the frequently poor correlation between oviposition preference and larval performance (Thompson, 1988; Courtney & Kibota, 1990). It has recently been shown that some female insects will maximise their fitness by selecting high-quality hosts for feeding, thus increasing their fecundity at the cost of increased larval performance (Scheirs *et al*., 2000). This preference-performance relationship leads to the implication that some herbivorous insects are ‘bad’ mothers for their own selfish gain (Mayhew, 2001). Studies of oviposition preference and larval performance have concentrated on species where the females evaluate their oviposition site, such as leaf mining flies (Valladares & Lawton, 1990; Scheirs *et al.,* 2000). However, in the pot beetle genus *Cryptocephalus* the females show no obvious oviposition preferences. This unusual situation results in adult habitat preferences being potentially disjunct from the habitat requirements of the larvae (Donisthorpe, 1938). The integrity of a population at any one site can then depend on a handful of host trees that have the coincidental juxta-position of habitat that is suitable for both adults and larvae. Due to the very different habitat requirements of *Cryptocephalus* adults and larvae, preservation and enhancment of their populations depend on management that takes the requirements of both stadia into consideration.

The objectives of this work were to elucidate the habitat and feeding preferences of adult beetles, characterise suitable and unsuitable host-trees and investigate the performance of larvae on different types of leaf litter.

5.2. Habitat preferences

5.2.1 Materials and Methods

Headley Warren (Plates 16 and 17) and Kirkby Moor (area A, Plate 25) (*Cryptocephalus coryli*); Headley Warren (area A) and The White Downs (area A, Plate 22) (*C. nitidulus*) and Wybunbury Moss (*C. decemmaculatus*) were the sites where adults could be reliably found and were visited over two successive field seasons (1999 and 2000). Systematic sampling using visual searching and beating of foliage with a long stick (2 m) into a beating tray elucidated the distribution of adult beetles within the sites. The location of a captured adult was recorded together with its sex, host-plant, height of capture and aspect on the tree (divided into quarters, N, S, E and W). At each site, trees that adults were never found on (n =10) and adjacent trees that regularly played host to adults (n =10) were compared in terms of their physical characteristics (height, whether coppiced or not). Ground level characteristics associated with each bush were also examined, with $50cm^2$ quadrats placed beneath each tree and the proportional cover of grasses, herbs, moss, bare ground and leaf litter recorded. Four quadrats were located in N, S, E and W aspects around each bush. Maximum sward height beneath each of these trees was also measured.

The trees were also examined in terms of two microclimatic variables: wind speed and temperature. Both were measured from ground level to 2.5 m above ground level using Testo 425 and Testo 625 instruments. The measurements were taken as close to the leaf surface as possible in situations where adults would be found basking. The temperature probe (Testo 625) was modified with the addition of a foil shield around the sensor so that the temperature in the shade was recorded. These micro-climatic variables were measured in the middle of June at the same time of day (12 noon) for a period of five days. Each recorded measurement was actually the mean of values recorded over a 20 second period that was calculated by the probes. The use of data loggers was not an option in the research as the microclimate around many trees had to be measured and the trees were also very scattered over a large area. This would have entailed many sensors and the data generated would not have suited the needs of this research.

5.2.2. Results

5.2.2.3. Adult host plant preferences

Kirkby Moor differs from Headley Warren in having no *Corylus avellana*, but possesses relatively more *Crataegus monogyna* than Headey Warren. *Cryptocephalus coryli* adults were predominantly captured on *Betula pendula* at both sites (Figure 5.1). Few specimens were captured on the host-plant that gives this beetle its trivial name (*Corylus avellana*) and only one specimen, a female, was observed on *Crataegus monogyna.* Feeding in the wild was only rarely seen and involved adults feeding on *B. pendula* leaves and leaf petioles. The commonest trees at Headley Warren were *B. pendula* in the Downs Field and *C. avellana* in the Flying Bomb Field. *Crataegus monogyna* is relatively uncommon at Headley Warren.

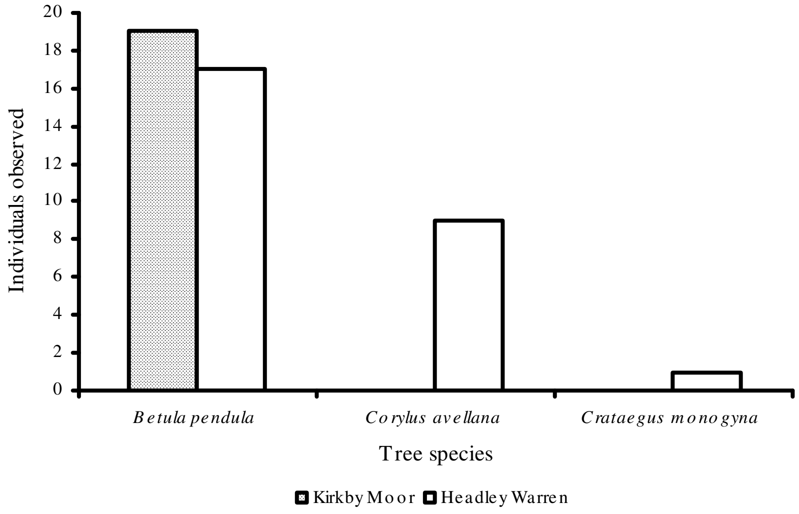

Figure 5.1. Incidence of *Cryptocephalus coryli* adults on three tree species.

B. pendula is also the commonest scrub species on the White Downs, although *Crataegus monogyna* and *C. avellana* are relatively abundant at this site. *Cryptocephalus nitidulus* adults were observed on a total of four tree species there and at Headley Warren (Figure 5.2). All four of these species are found at Headley Warren, but *Acer campestris* is not found in *C. nitidulus* habitat on the White Downs. The largest numbers of individuals were observed on *Betula pendula*, while the observations of adults on the field maple (*Acer campestre*) can be viewed as incidental as these trees were located between several *B. pendula* and *Corylus avellana* trees along the edge of a coppiced wood. The observations of adults on *C. monogyna* yielded some interesting results, as 20 (86.9%) of the beetles observed on this tree species were female (Figure 5.3). In contrast, on *B. pendula* the ratio of males to females was approximately two to one, and females were also in a slight minority on the other tree species (Figure 5.3). There was a significant difference in the sex ratio observed on the two tree species (χ^2 (d.f. = 1) = 0.0013, $P = 0.001$).

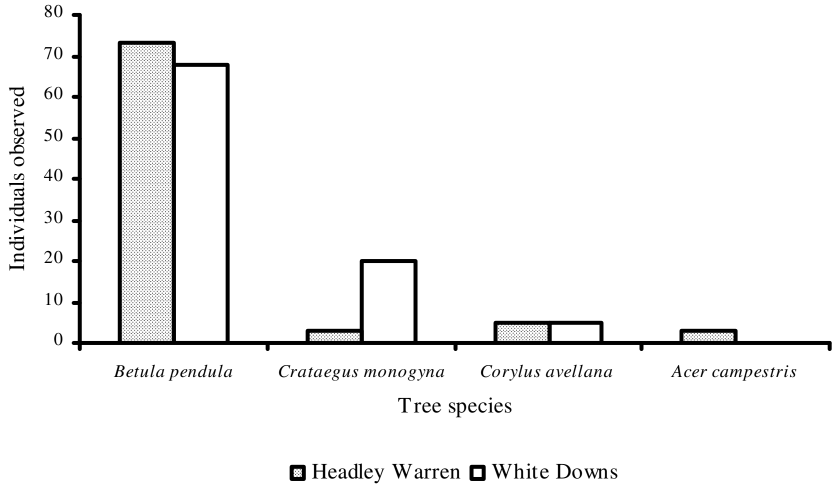

Figure 5.2. Incidence of *Cryptocephalus nitidulus* adults on four tree species.

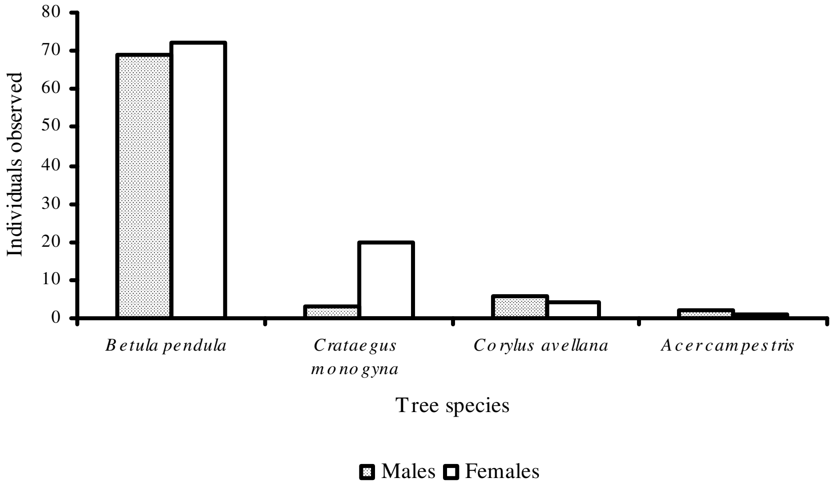

Figure 5.3. Incidence of male and female *Cryptocephalus nitidulus* adults on four tree species

Cryptocephalus decemmaculatus is found around the inner part of Wybunbury Moss. *Betula pubescens* is the most common type of tree at the site with hundreds of individuals, whereas only 13 *Salix cinerea*, and only three or four *Betula pendula* trees are present in this part of the Moss. The largest numbers of *C. decemmaculatus* individuals were observed perching on *B. pubescens* and *S. cinerea* with no adults observed on *Frangula alnus* or *Pinus sylvestris,* the other trees found in this area (Figure 5.4).

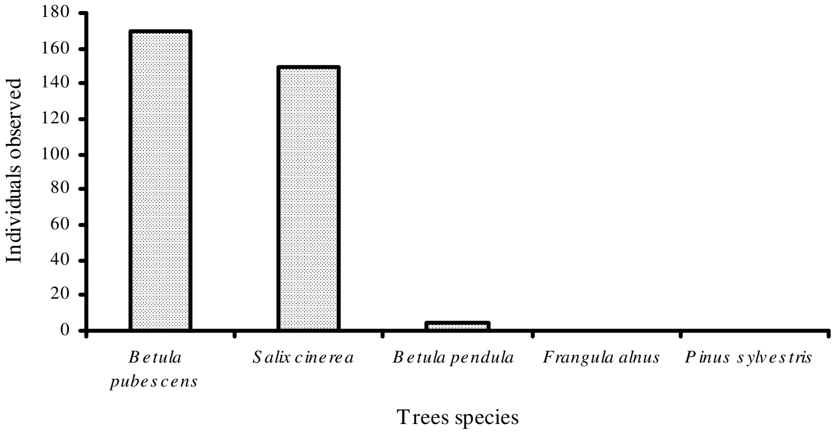

Figure 5.4. Incidence of *Cryptocephalus decemmaculatus* adults on five tree species.

In June of 1999 every single tree within areas A, B and C was searched once. A mean number of 11 beetles could be seen on each of the *S. cinerea* trees (Figure 5.5) whereas over the same period a mean of only three *Cryptocephalus decemmaculatus* adults could be seen on any one of the occupied *B. pubescens* trees.

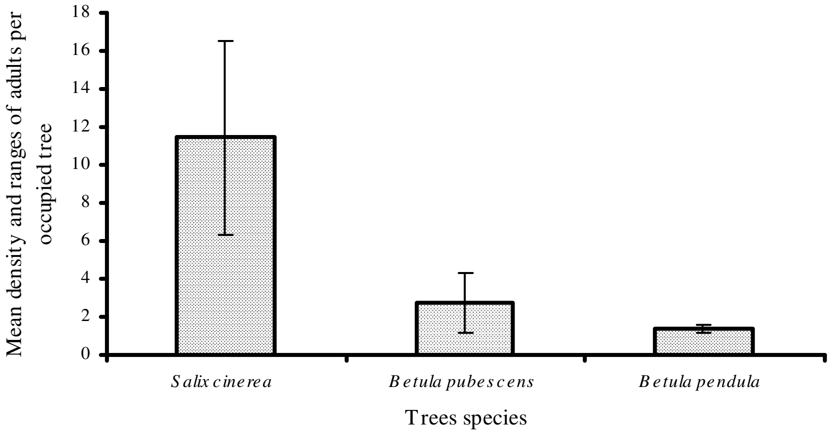

Figure 5.5. Density of *Cryptocephalus decemmaculatus* adults on three tree species. *Salix cinerea n* = 13, *Betula pubescens n* = 62, *B. pendula n* = 3 (means ± S.D.).

5.2.2.4. Adult height and aspect preferences

Of all the *Cryptocephalus coryli* beetles that were observed over the two field seasons, 44 (96%) were seen in south facing aspects. The majority of adults were recorded at heights between 1.01 and 1.5 m (Figure 5.6). The *Betula pendula* trees at Headley Warren exhibited a browse line that started from about 0.5 m. This browse line meant that adult beetles could not perch lower than about 0.5 m, whereas perches were available down to ground level at Kirkby

Moor. There was no significant difference in the median height of capture between the two sites [Kirkby Moor (*n* = 26), mean = 1.45 m S.D .± 0.78 m, median = 1.43 m; Headley Warren (*n* = 20), mean = 1.55 m S.D .± 0.79 m, median = 1.4 m; Mann-Whitney Z = -0.362, *P* = 0.717].There was also no difference between the height at which males and females were observed [males (*n* = 24), mean 1.52 m S.D. ± 0.78 m, median = 1.37 m; females (*n* = 22), mean = 1.45 m S.D .± 0.89 m, median = 1.45 m; Mann-Whitney Z = -0.42, *P* = 0.68].

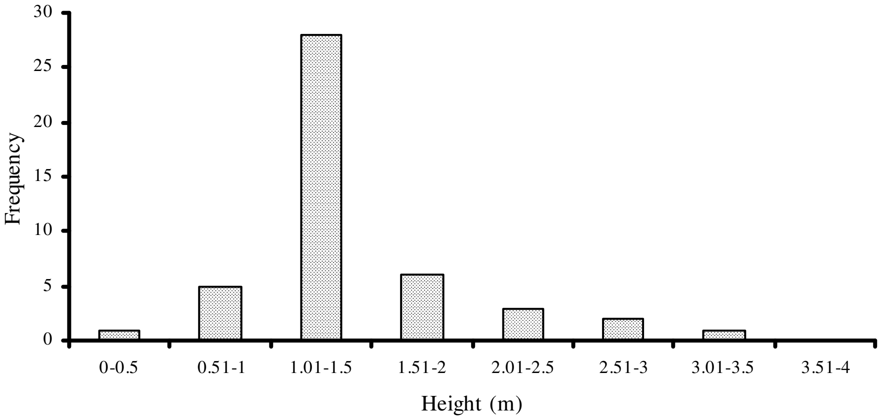

Figure 5.6. Heights of capture of *Cryptocephalus coryli* adults (data from Headley Warren and Kirkby Moor with all tree species combined)

One hundred and seventy four (98.3%) of the *Cryptocephalus nitidulus* adults observed over the two field seasons were observed in southern aspects on the trees. The greatest numbers of *C. nitidulus* beetles were similarly found on foliage between 1.01 and 2 m above the ground (Figure 5.7). Occupied trees were routinely large (>6 m) sampling the tops of these trees was difficult and some beetles may have been missed. A decrease in the number of beetles found beyond 2 m can nonetheless be seen. There was no significant difference in the median height of capture between Headley Warren and the White Downs [Headley Warren (*n* = 36), 1.83 m ± S.D. 0.97 m, median = 1.90 m; White Downs (*n* = 141), 1.79 m ± S.D. 0.88 m, median = 1.95 m; Mann-Whitney Z = -0.653, *P* = 0.865]. There was also no significant difference in the median height at which males and females were observed [males (*n* =113), 1.94 m ± S.D. 0.46 m, median = 1.93 m; females (*n* = 64), 1.87 m ± S.D. 0.57 m, median = 1.9 m; Mann-Whitney Z = -0.772, *P* = 0.44].

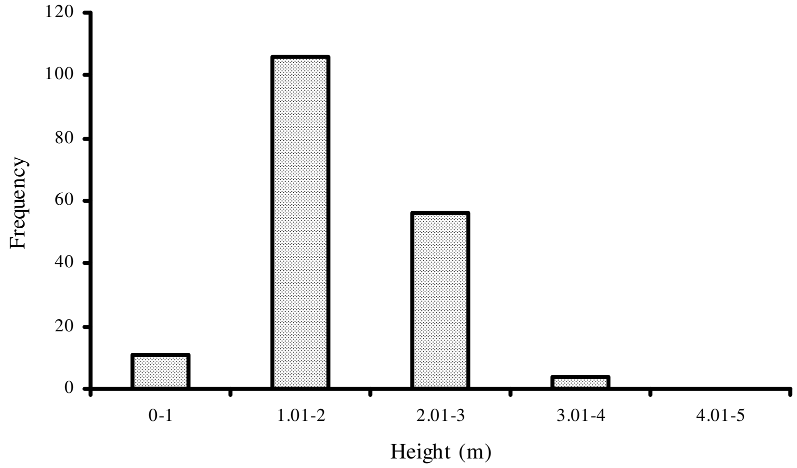

Figure 5.7. Heights of capture of *Cryptocephalus nitidulus* adults (Headley Warren and White Downs and all three tree species combined)

Of all the adult *Cryptocephalus decemmaculatus* beetles that were observed on the trees over the two field seasons only 9 (2.5%) were found in aspects other than south facing ones. Most of the adult *C. decemmaculatus* beetles were observed between a height of 0.41 and 1.2 m (Figure 5.8). This reflects the opportunities available, as there are very few trees on the central part of Wybunbury Moss that are taller than 2 m furthermore the tall, dense ground vegetation beneath the host-plants prevents the adult beetles from perching very low on the host plants. There was no significant difference in the median height at which males and females were observed on their host-plants [males (*n* = 356), mean = 0.76 m ± S.D. 0.36 m, median = 1.15 m; females (*n* = 268), mean = 0.78 m ± S.D. 0.38 m, median = 1.05 m; Mann-Whitney Z = -0.88, *P* = 0.93].

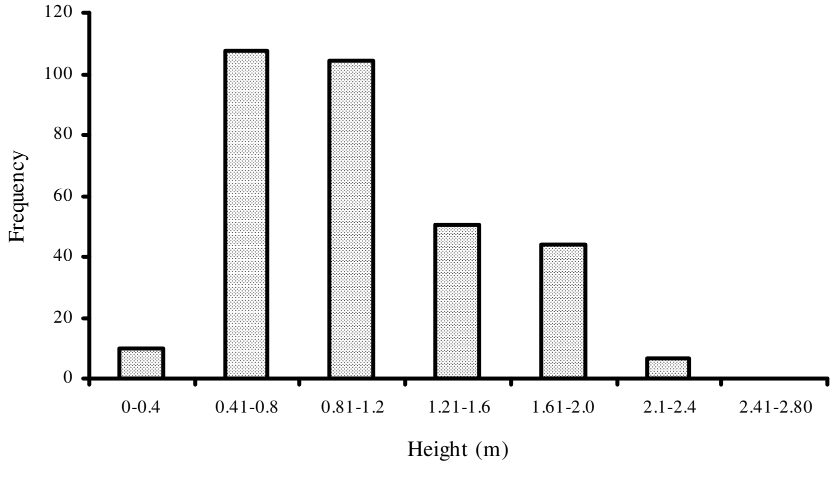

Figure 5.8. Heights of capture of *Cryptocephalus decemmaculatus* adults (all tree species and 1999 and 2000 observations combined).

5.2.2.5. Adult microclimate preferences

At Kirkby Moor, air temperatures were recorded at appropriate heights and aspects around *Betula pendula* trees that were utilised by adult *Cryptocephalus coryli* (n =10) and around adjacent trees of similar size on which adult beetles were never seen (n =10). The trees in the utilised group were on average more than 4°C warmer than adjacent trees in the non-utilised group (Figure 5.9). The air temperature around the utilised trees at the height at which most adults were mainly observed (1.01 to 1.5 m) was mean = 25.3 °C ± S.D. 1.87 °C, which was significantly higher [F (1, 18) = 107.13, $P < 0.001$] than the temperatures around non-utilised trees at this height (mean = 18.6 °C ± S.D. 0.85 °C).

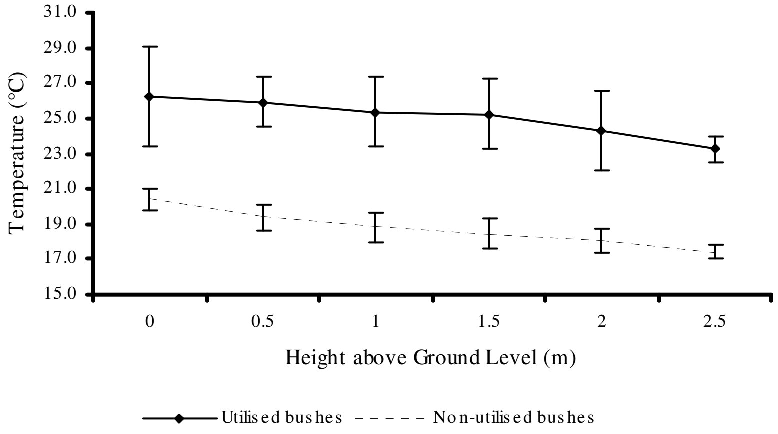

Figure 5.9. Temperatures around utilised and non-utilised host-plants of *Cryptocephalus coryli* (means ± S.D.).

The slightly decreasing temperature with increasing height shown in Figure 5.9 is paralleled by increasing air velocity (Figure 5.10). The air velocity around utilised trees at a height of 1.1-1.5 m was mean = 0.32 m/s ± S.D. 0.23 m/s, which was significantly lower [F (1, 18) = 22.14, *P* < 0.001] than the air velocity around non-utilised trees at the same height (mean = 1.02 m/s ± S.D. 0.41 m/s).

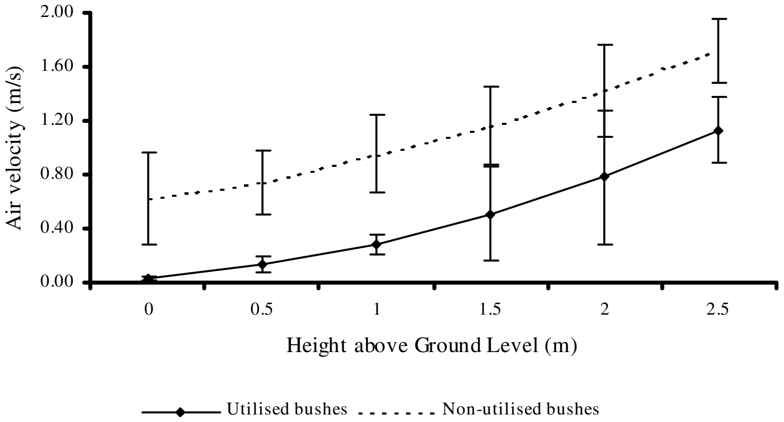

Figure 5.10. Air velocity around utilised and non-utilised host-plants of *Cryptocephalus coryli* (means ± S.D.).

The temperature around trees utilised by *Cryptocephalus nitidulus* at the White Downs was about 4 °C warmer than the temperature around adjacent non-utilised trees (Figure 5.11). The air temperature around trees at which most adult beetles were found (1.01–3 m) was mean = 23.6 °C ± S.D. 1.8 °C, significantly higher [F (1, 18) = 7.52, *P* < 0.001] than temperatures at the same height around non-utilised trees (mean = 19.2 °C ± S.D. 2.3 °C).

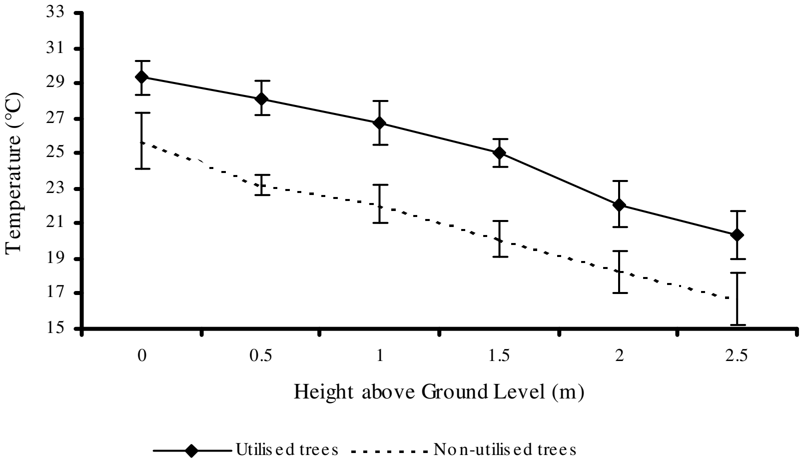

Figure 5.11. Temperatures around utilised and non-utilised host-plants of *Cryptocephalus nitidulus* at the White Downs (means ± S.D.).

As expected, air velocity (wind speed) was again inversely related to temperature. (Figure 5.12). The air velocity around utilised trees at the height at which most adults was found (1.01–3 m) was mean= 0.44 m/s ± S.D. 0.06 m/s, significantly lower [F (1, 18) = 12.38, $P = < 0.002$] than the wind speed at the same height around non-utilised trees (mean = 0.62 m/s ± S.D. 0.13 m/s).

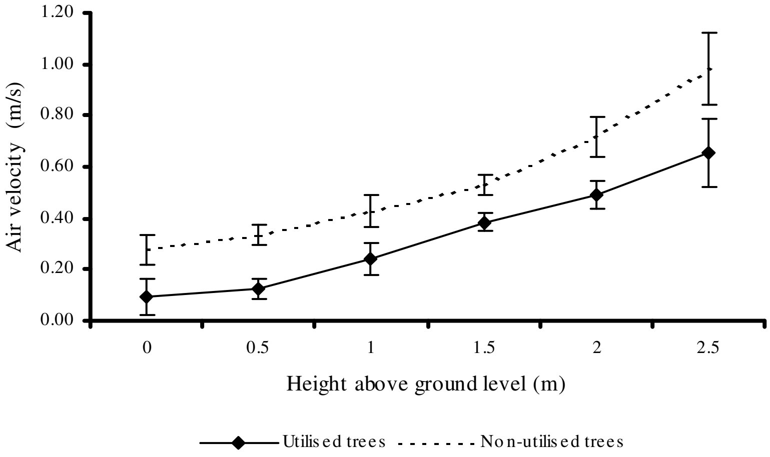

Figure 5.12. Air velocity around utilised and non-utilised host-plants of *Cryptocephalus nitidulus* at the White Downs (means ± S.D.).

The difference between trees utilised and non-utilised by *Cryptocephalus decemmaculatus* trees in terms of air temperature was relatively large (Figure 5.13), with host trees having extremely high air temperatures on the days when recordings were made (Figure 5.13). The air temperature around the utilised trees at the height at which most adults were observed (0.41-1.2 m) was mean = 29.2 °C ± S.D. 0.36 °C, which was significantly higher [F (1, 18) = 243.14, P = < 0.001] than the temperature around non-utilised trees (mean = 24.8 °C ± S.D. 0.91 °C).

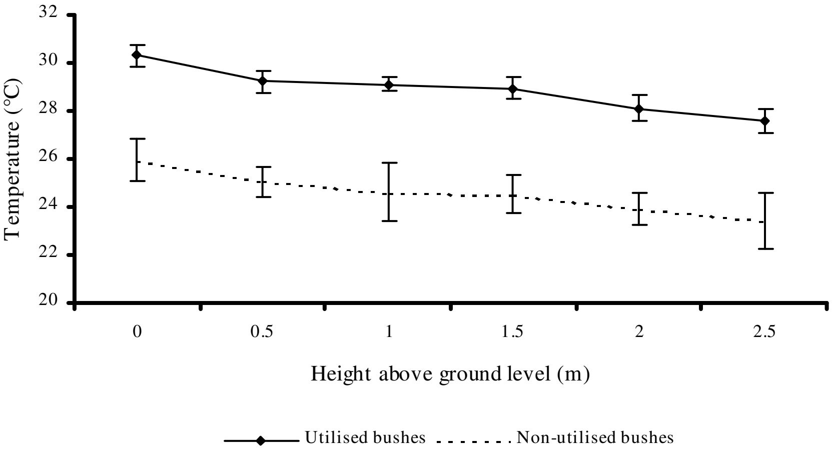

Figure 5.13. Temperature around utilised and non-utilised host-plants of *Cryptocephalus decemmaculatus* (means ± S.D.).

At the height at which most adult *C. decemmaculatus* were observed (0.41-1.2 m) the air velocity around utilised trees was mean = 0.23 m/s ± 0.14 m/s (Figure 5.14). This was significantly lower [F (1, 18) = 243.14, $P < 0.001$] than the air velocity at the same height around non-utilised trees (mean = 0.70 m/s ± 0.32 m/s).

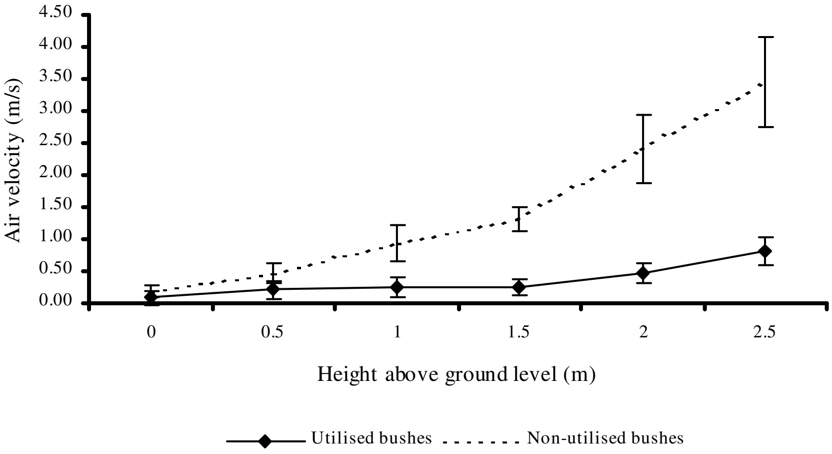

Figure 5.14. Air velocity around utilised and non-utilised host-plants of *Cryptocephalus decemmaculatus* (means ± S.D.).

5.2.2.6. Ground cover characteristics related to adult preferences

Table 5.1 summarises the ground cover characteristics beneath trees at Kirkby Moor. There was a high proportion of grass cover beneath trees both utilised and non-utilised by *Cryptocephalus coryli* adults. Neither grass cover or sward height varied significantly between the two groups of trees. The percentage herb cover was significantly higher [F (1,18) = 5.77, *P* = 0.021] beneath utilised trees whereas there was a significantly higher [F (1,18) = 12.49, *P* = 0.001] percentage cover of moss beneath utilised trees. The percentage cover of bare ground [F (1,18) = 15.65 *P* = <0.001] and leaf litter [F (1,18) = 4.95 *P* = 0.032] were also significantly higher beneath utilised trees.

Table 5.1. Summary of ground cover (means) beneath *Cryptocephalus coryli* utilised (*n* =10) and adjacent non-utilised (*n* =10) *Betula pendula* trees.

	Max. sward height (cm)	Moss (%)	Grass (%)	Bare ground (%)	Herbs (%)	Leaf litter (%)
Non-utilised trees	4.5	1.7	67.9	3.1	14.9	8.3
Utilised trees	2.2	5.7	45.5	14.7	25.5	14.1

Trees utilised by *Cryptocephalus nitidulus* on the White Downs were characterised (Table 5.2) by significantly lower sward heights [F (1,18) = 78.16 *P* = <0.001], significantly greater moss cover [F (1,18) = 30.11 *P* = <0.001], significantly greater bare ground cover [F (1,18) = 5.41 *P* = 0.037], significantly greater herb cover [F (1,18) = 6.69 *P* = 0.023] and significantly less grass cover [F (1,18) = 26.52 *P* = <0.00]. Percentage leaf litter cover did not vary between the two groups of trees.

Table 5.2. Summary of ground cover (means) beneath *Cryptocephalus nitidulus* utilised (*n* = 10) and adjacent non-utilised (*n* = 10) host-trees.

	Max. sward height (cm)	Moss (%)	Grass (%)	Bare ground (%)	Herbs (%)	Leaf litter (%)
Non-utilised trees	3.8	6.0	64.0	6.0	2.3	16.0
Utilised trees	0.85	24.5	20.5	22.5	8.3	25.5

Trees utilised by *Cryptocephalus decemmaculatus* at Wybunbury Moss (Table 5.3) were characterised by significantly greater moss cover [F (1,18) = 13.42 *P* = 0.003] and significantly less herb cover [F (1,18) = 15.29 *P* = 0.002]. Maximum sward height, grass cover, bare ground cover and herb cover did not vary significantly between the two types of trees.

Table 5.3. Summary of ground cover (means) beneath *Cryptocephalus decemmaculatus* utilised (*n* = 10) and adjacent non-utilised (*n* = 10) host-trees.

	Max. sward height (cm)	Moss (%)	Grass (%)	Bare ground (%)	Herbs (%)	Leaf litter (%)
Non-utilised trees	1.7	86	5.3	0.3	8.4	14.1
Utilised trees	1.6	90.9	5.3	0	4.6	27.8

Binary logistic regressions (SPSS version 10.1) were used to analyse the differences between host trees that were regularly used by the adults and those that were not in terms of their ground cover characteristics. *Cryptocephalus coryli* adult preferences for different trees seems to be most related to percentage moss cover (Table 5.4). This variable was used to produce a classification that projected an overall correct group membership of 92.5% (Table 5.7). Other significant variables were percentage herb cover, followed by percentage grass cover and sward height (marginally). The variables of bare ground and leaf litter were of no significance and were not selected for use in succeeding steps of the binary logistic regression.

Table 5.4. The relative significance of ground variables beneath *Betula pendula* trees related to their utilisation by adult *Cryptocephalus coryli* adults (forward conditional binary logistic regression output).

Variable	B	Standard Error	Degrees of Freedom	Significance
Sward Height	0.553	0.287	1	0.0540
% Moss Cover	7.137	1.807	1	<0.0001
% Grass Cover	-3.621	1.554	1	0.0200
% Herb Cover	-3.186	1.142	1	0.0050
Constant	3.718	2.174	1	0.0870

Cryptocephalus nitidulus adult preferences were most related to percentage bare ground cover (Table 5.5). Percentage herb cover was the penultimate variable to be removed from the analysis, but it was not significant (Table 5.5). The other measured variables were omitted during earlier stages of the process.

Table 5.5. The relative significance of ground variables beneath *Betula pendula* trees influencing their utilisation by adult *Cryptocephalus nitidulus* adults (forward conditional binary logistic regression output).

Variable	B	Standard Error	Degrees of Freedom	Significance
% Bare ground	38.41677	7654.046	1	0.01
% Herb Cover	130.1169	15683.68	1	0.99
Constant	-146.2422	16384.72	1	0.99

The model produced using the variable of percentage bare ground cover projected an overall correct group membership of 95% (Table 5.7).

Cryptocephalus decemmaculatus adult preference for different trees was most significantly related to percentage herb cover (Table 5.6) and this variable was used in the model to produce an overall correct group membership of 84.2% (Table 5.7). Other significant variables were percentage bare ground, followed by percentage moss cover. The variables of sward height, percentage grass cover and percentage cover of leaf litter were of no significance and were not selected for use in succeeding steps of the process. The trees utilised by the beetles were therefore characterised by having lower herb percentage cover, no bare ground and more moss than the trees that were ignored.

Table 5.6. The relative significance of ground variables beneath host-trees influencing their utilisation by adult *Cryptocephalus decemmaculatus* adults (forward conditional binary logistic regression output).

Variables	B	Standard Error	Degrees of Freedom	Significance
% Moss cover	-1.206	0.482	1	0.012
% Bare ground cover	-5.191	1.951	1	0.008
% Herb cover	-2.572	0.929	1	0.006
Constant	10.929	3.781	1	0.004

Table 5.7. Final binary logistic regression classification of *Cryptocephalus coryli, C. nitidulus* and *C. decemmaculatus* utilised and non-utilised host-trees showing % accuracy of predicted group membership.

Species	Non-utilised trees		Utilised trees		Overall %
	Correctly classified	Incorrectly classified	Correctly classified	Incorrectly classified	
C. coryli	**18**	**2**	**19**	**1**	**92.5**
C. nitidulus	**20**	**0**	**18**	**2**	**95.0**
C. decemmaculatus	**16**	**4**	**17**	**3**	**84.2**

5.3. Adult Feeding preferences

5.3.1. Materials and methods

Wild caught *Cryptocephalus coryli* adults from Headley Warren and Kirkby Moor were maintained in the shade, in the field, in the cages shown in Figure 5.15. The core of Oasis, used to provide a source of moisture, was re-hydrated approximately every two days.

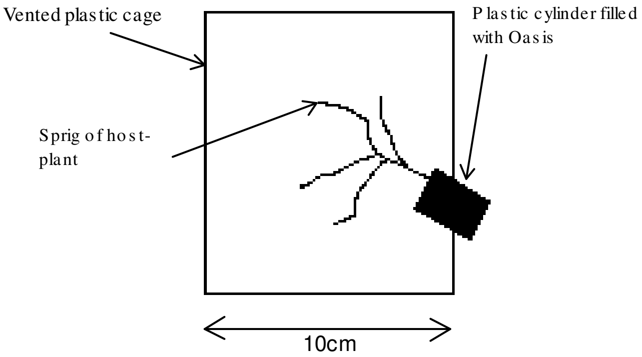

Figure 5.15. Cage used to maintain adult *Cryptocephalus* beetles.

Only gravid female beetles were used in the feeding trials, as demonstrated by their prior oviposition in captivity. They had ceased faeces production forty-eight hours before the experiment, indicating that faeces accumulated from previous feeding episodes had all been voided. ‘Starvation’ tests were conducted by offering the beetles foliage of one host-plant at a time. *Cryptocephalus coryli* adults from Headley Warren would have been exposed to *Betula pendula* (uncoppiced, young and mature coppiced trees) and *Corylus avellana* prior to the experiments whereas only *B. pendula* (uncoppiced, young and medium coppiced trees) was available to them at Kirkby Moor. The *B. pendula* trees used for the comparison with *C. avellana* were non coppiced, whereas, only coppiced *C. avellana* was available (in Lincolnshire coppiced *C. avellana* foliage was taken from woodland adjacent to the Kirkby Moor site). During prior field studies *Cryptocephalus nitidulus* adults were observed perching on the foliage of *Betula pendula, Corylus avellana* and *Crataegus monogyna*. During prior field studies *Cryptocephalus decemmaculatus* adults were observed perching on the foliage of *Salix cinerea*, *Betula pubescens* and *B. pendula*. A single host-plant leaf was taken from one of ten trees of each of these species for each of the experiments. Leaves were chosen that were of a similar age, from similarly aged trees that were between three and five metres in height. The chosen leaves were growing on south facing aspects on the trees and showed no signs of feeding damage. Each beetle was placed in a feeding chamber with the relevant leaves and allowed to eat in shaded conditions in the field for 48 hours. The faeces of the beetles were then collected and placed in airtight, labelled glass tubes. The tubes were taken back to the laboratory where the contents were placed on a watch glass and dried in an oven until they reached a constant mass.

5.3.2. Results

Adult *Cryptocephalus coryli* from both populations produced significantly more faecal material on a diet of uncoppiced *Betula pendula* than on coppiced *Corylus avellana* (Figure 5.16) [Headley Warren; *Corylus avellana* (*n* = 10), mean = 0.0031 g ± S.D. 0.0016 g, median = 0.0027 g. *Betula pendula* (*n* = 10), mean = 0.0102 g ± S.D. 0.0026 g, median = 0.0096 g Mann-Whitney Z = -4.103, *P* = < 0.001. Kirkby Moor; *Corylus avellana* (*n* = 10), mean = 0.0032 g ± S.D. 0.0021 g, median = 0.0022 g. *Betula pendula* (*n* = 10), mean = 0.0090 g ± S.D. 0.0020 g, median = 0.0087 g; Mann-Whitney Z = -4.132, *P* = <0.001]. The amount of faecal material produced by the beetles from the two populations when feeding on *C. avellana* was very similar, even though *C. avellana* is absent at Kirkby Moor.

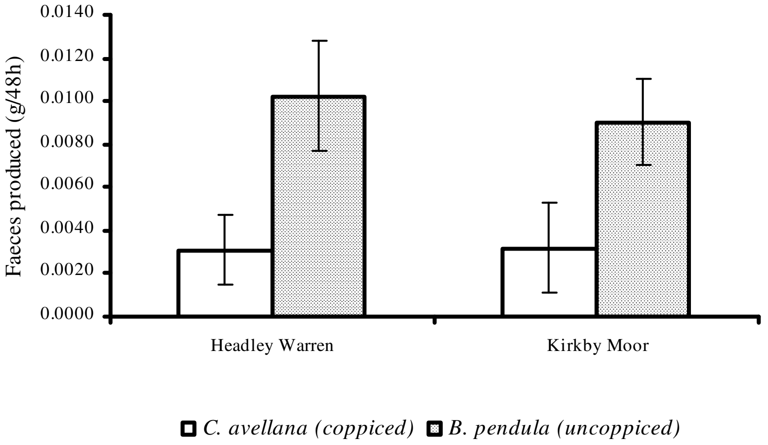

Figure 5.16. Starvation feeding tests of *Cryptocephalus coryli* adult females from two populations using the foliage of *Corylus avellana* and *Betula pendula* (*n* = 10 beetles per tree species). Means ± S.D.

Feeding experiments were also carried out using *Betula pendula* leaves from coppiced and un-coppiced rootstocks of apparently similar ages (Figure 5.17). Coppiced and uncoppiced foliage were available at both the sites. Adults from both populations produced far more faecal material when feeding on foliage from un-coppiced than coppiced *B. pendula* (Figure 5.17) compared to when they were feeding on foliage from coppiced *B. pendula* [Headley Warren; Uncoppiced *B. pendula* (*n* = 10), mean = 0.0122 g ± S.D. 0.0024 g, median = 0.0120 g; Coppiced *B. pendula* (*n* = 10), mean = 0.0040 g ± S.D. 0.0018 g, median = 0.0044 g Mann-Whitney Z = -4.158, *P* = 0.000. Kirkby Moor; Uncoppiced *B. pendula* (*n* = 10), mean = 0.0139 g ± S.D. 0.0048 g, median = 0.0131 g; Coppiced *B. pendula* (*n* = 10), mean = 0.0054 g ± S.D. 0.0016 g, median = 0.0059 g, Mann-Whitney Z = -4.157, *P* = <0.001]. The amounts of faeces produced when feeding on uncoppiced *B. pendula* were about the same as the comparison with *C. avellana.*

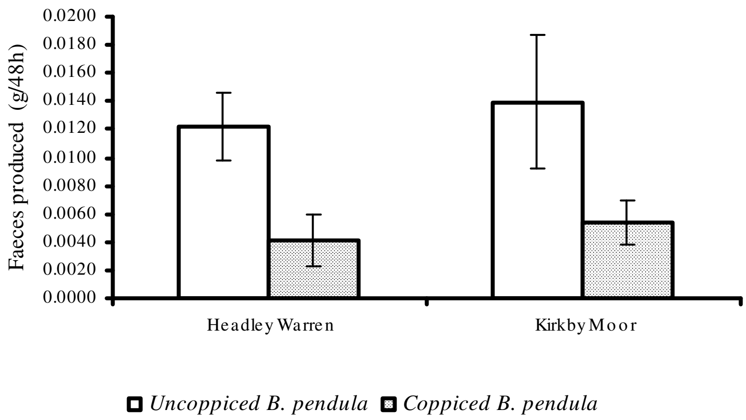

Figure 5.17. Starvation feeding test of *Cryptocephalus coryli* adult females from two populations using the foliage of coppiced and un-coppiced *Betula pendula* (*n* = 10 beetles per treatment). Means ± S.D.

Coppice age also had an effect on adult *Cryptocephalus coryli* faecal production (Figure 5.18). Young un-coppiced plants were defined as saplings, whereas young coppiced plants were *Betula pendula* trees that had only recently been coppiced and therefore produced a profusion of new growth from the cut trunk. Medium age coppiced *B. pendula* were trees that exhibited evidence of coppicing, but not in the previous winter. Mature coppiced *B. pendula* were large trees that had been coppiced, perhaps once, in their lifetime. Uncoppiced trees were selected to be of a similar height to those in the three coppiced age groups. This experiment was only carried out at Headley Warren, where *B. pendula* trees that fitted the above criteria were abundant.

More faeces were produced when the beetles were feeding on un-coppiced *B. pendula* sapling foliage than on leaves from young, recently coppiced trees (Figure 5.18). This trend was the same for medium age *B. pendula* although the difference between un-coppiced and coppiced was less marked. However, the trend was reversed in mature trees, where the amount of faeces produced by adults feeding on *B. pendula* from mature coppiced stock was higher than the amount of faeces produced by adults feeding on *B. pendula* from mature non-coppiced trees.

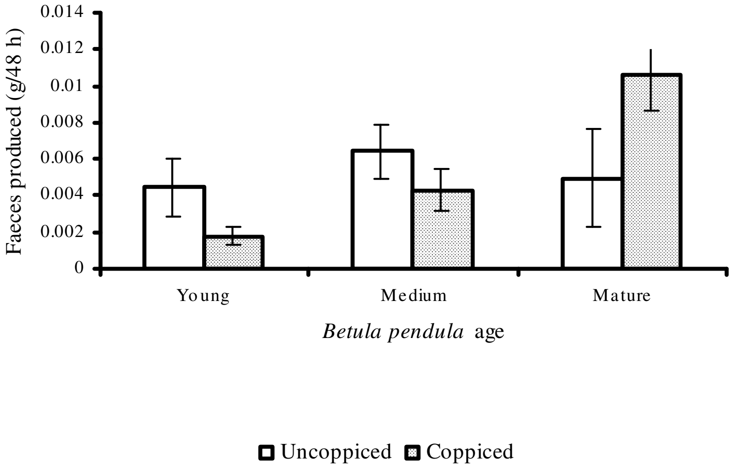

Figure 5.18. Starvation feeding tests of *Cryptocephalus coryli* adult females (*n* = 6 beetles per treatment) from two populations using the foliage of coppiced and un-coppiced *Betula pendula* from a range of ages. Means ± S.D.

A one way ANOVA followed by *post-hoc* testing (LSD test) showed that the palatability of uncoppiced leaves from medium aged parent plants was significantly higher than with leaves from uncoppiced young or mature parent plants [F (2, 14) = 3.89, $P = < 0.05$]. There was also a significant difference [F (2, 14) = 45.12, $P = < 0.001$] in the palatability of coppiced leaves, with those from young or medium age trees less palatable than those from mature trees (Figure 5.18). As a consequence of this interaction between tree age and coppicing effects uncoppiced leaves of saplings were more suitable than leaves from the coppiced trees whereas on mature trees the situation was reversed.

In feeding tests the adults of *Cryptocephalus nitidulus* have an equal preference for the foliage of *Betula pendula* and *Crataegus monogyna* (Figure 5.19).

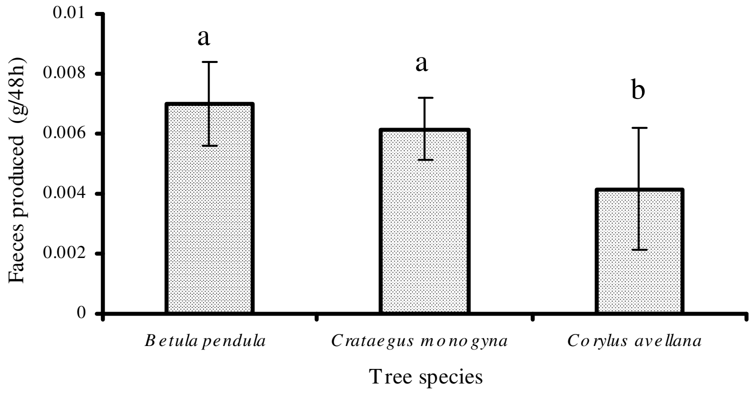

Figure 5.19. Starvation feeding tests of *Cryptocephalus nitidulus* adult females (*n* = 10 beetles per treatment) using the foliage of three host-trees (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Significantly different amounts of faeces were produced by adult *Cryptocephalus nitidulus* beetles feeding on the different types of foliage [F (2, 27) = 8.805, *P* = 0.001]. *Post-hoc* testing showed that the mass of faeces produced by adults feeding on *Betula pendula* was not significantly different to that produced when feeding on *Crataegus monogyna* foliage, but both were significantly higher than when they were on a diet of *Corylus avellana.*

The female biased sex ratio among the *Cryptocephalus nitidulus* found on *Crataegus monogyna* in the field led to starvation tests comparing sexual food preferences on *C. monogyna* using beetles. Females produced 0.009 g S.D. ± 0.0016 g of faeces whereas males produced 0.0036 g S.D. ± 0.0010 g over the same three day period, about one third the amount produced by females. The type of feeding damage produced by the two sexes was also different, with the females preferring to strip the *C. monogyna* sprigs of their bark, and even the thorns of the sprigs were heavily stripped. The males only ate the leaves and the petioles of the *C. monogyna* sprigs.

Foliage from *Salix cinerea*, *Betula pubescens* and *B. pendula* collected at Wybunbury Moss was used in the first starvation feeding experiment using *Cryptocephalus decemmaculatus* adults (Figure 5.20). Analysis (ANOVA single factor and *post-hoc* testing) of the amount of faeces produced by adults feeding on different types of foliage showed a highly significant [F (2, 57) = 1009.6, *P* = <0.001] preference for the foliage of *S. cinerea.* There was no significant difference in the amount of faeces produced by adults feeding on *B. pubescens* compared to those adults feeding on *B. pendula.*

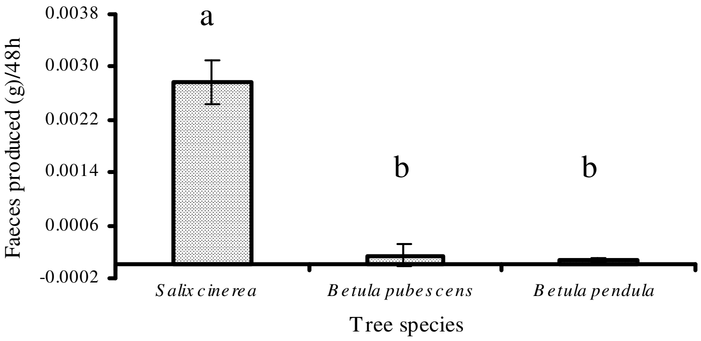

Figure 5.20. Starvation feeding test using *Cryptocephalus decemmaculatus* (*n* = 10 beetles per treatment) adult females feeding on the foliage of three host species (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Foliage of non-regrowth origin was not used in the experiment, as it was not readily available to *C. decemmaculatus* adults at the only English site for this species. Adults preferred the regrowth foliage from young *Salix cinerea* trees to regrowth from older *S.cinerea* or *Betula pubescens* trees (Figure 5.21). There was a significant difference between groups in the mass of faeces produced [F (3, 76) = 63.76 , *P* = <0.001]. *Post-hoc* testing showed that when adults were feeding on young *S. cinerea* tree regrowth the amount of faeces produced was significantly higher than in the other treatments

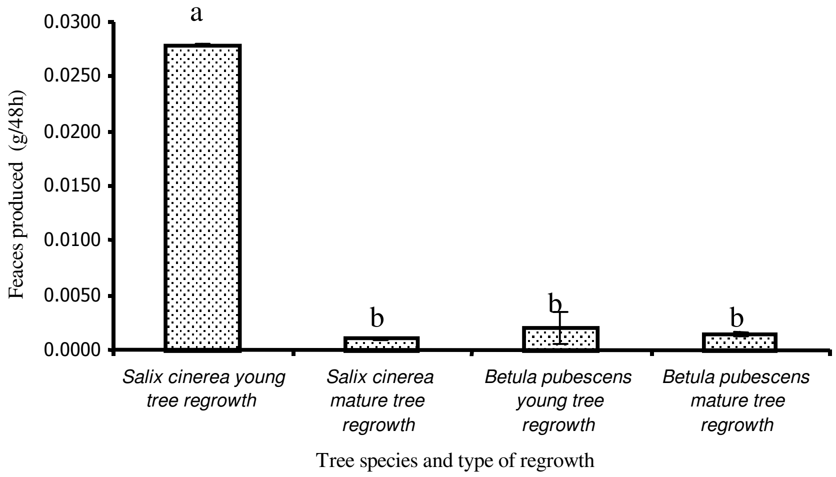

Figure 5.21. Starvation feeding test of *Cryptocephalus decemmaculatus* adult females (*n* = 6 beetles per treatment) using the foliage of coppiced *Betula pubescens* and *Salix cinere*a (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

5.4. Impact of host plants on fecundity

5.4.1 Materials and methods

The preference in the field for *Crataegus monogyna* shown by female *Cryptocephalus nitidulus* prompted further investigation of their fecundity when fed *Betula pendula* or *C. monogyna*. Twenty females were starved for 48 hours to void the digestive tract of foliage ingested before they were captured. Later, ten were fed *B. pendula* and ten were fed *C. monogyna* leafy stems. The females were allowed to feed and oviposit for 72 hours. After this time any eggs were removed from the cages and counted.

5.4.2 Results

Female *Cryptocephalus nitidulus* on *Crataegus monogyna* produced a mean number of 51.0 eggs ± S.D. 9.5 eggs whereas the females fed *Betula pendula* produced less than half as many eggs (mean = 19.0 eggs ± S.D. 3.3 eggs) [*C. monogyna* (*n* = 10), mean = 51.0 eggs ± S.D. = 9.5 eggs, median = 50 eggs; *Betula pendula* (*n* = 10), mean = 19.0 eggs ± S.D. 3.3 eggs , median = 19 eggs, Mann-Whitney Z = -2.89, *P* = 0.004]. No measurements were made of the eggs themselves although it appeared that the egg cases of the females feeding on *C. monogyna* were bulkier and were formed from relatively more feaces.

5.5. Larval performance and feeding preferences

5.5.1. Materials and methods

Captive bred mated females of *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* were maintained in the cages shown in Figure 5.22 during the late summer of 2000.

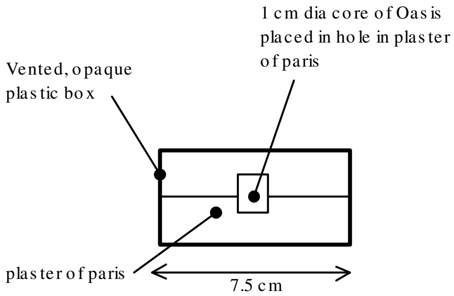

Figure 5.22. Container for the captive rearing of *Cryptocephalus* larvae.

The eggs from the females of each species were bulked together and then selected at random for the experiments and placed in one of four experimental containers. These containers were the same as the one shown in Figure 5.17, although they were partitioned to produce five separate compartments and thus five pseudo-replicates of each treatment. 60 eggs were placed in each compartment so that each container contained 300 eggs. Before the eggs hatched, leaf litter of the type that would be available to wild larvae was collected from the relevant sites for each species. For *C. coryli* and *C. nitidulus* litter was taken from Headley Warren and divided into *Betula pendula*, *Corylus avellana* and *Crataegus monogyna* litter. For *C. decemmaculatus* larvae*,* litter taken from Wybunbury Moss was divided into *Salix cinerea* and *Betula pubescens*. *Salix alba* litter was also used as *C. decemmaculatus* larvae had already been found to readily eat it. A mixed litter was also prepared for each species that contained all of the aforementioned components in equal proportions, together with remnants of other plants (mainly herbs) that occur at the sites.

Before feeding trials commenced the collected and sorted litter was placed in a freezer at -80°C for 72 hours to rid the leaves of mites that can be detrimental to captive *Cryptocephalus* larvae. The food for the larvae in the petri dishes was replenished when the supply of leaf litter had almost been consumed. The small core of oasis in the centre of the petri dishes was re-hydrated approximately every two days. The larvae were maintained until they reached their last instar. At this point five of the larvae were taken from each pseudo-replicate and weighed. The remaining contents of the petri dishes were then sieved and the unhatched eggs and dead larvae were sorted. First instar mortality was distinguished from later deaths by sorting through these dead larvae to find cases that had hatched, but did not show the distinctive split and repair of the case that indicates ecdysis.

5.5.2. Results

Between about 30 and 50% of the *Cryptocephalus coryli* larvae died during their first instar. Variation among 1st instar mortality on the range of diets was significant [F (3,16) = 7.57 *P* = 0.002]. Of the four diets that were used in the trial the highest 1st instar mortality was seen when they were fed *Corylus avellana*, closely followed by *Crataegus monogyna* (Figure 5.23). Mortality in 1st instar larvae was significantly lower when they were reared on a diet of *Betula pendula* litter or a mixed litter diet which contained *B. pendula* litter .

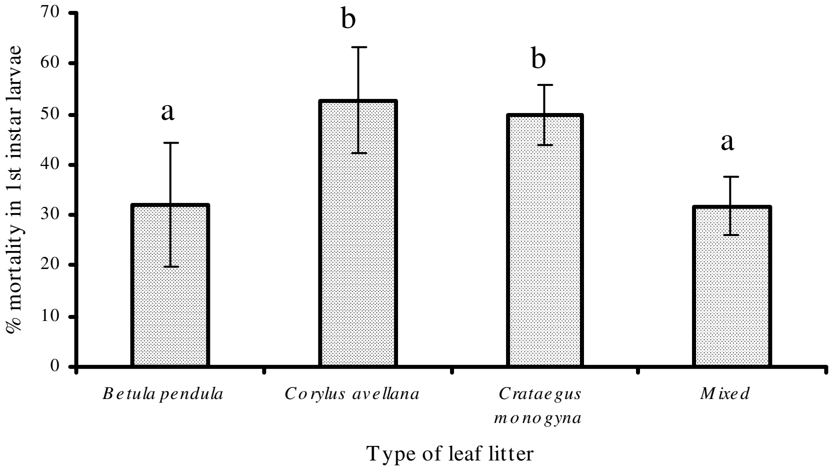

Figure 5.23. Mortality in 1st instar *Cryptocephalus coryli* larvae reared on four litter treatments (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Mortality rates among 1st instar *Cryptocephalus nitidulus* larvae was comparable to those recorded for *C. coryli*. There was significant between group variation in the *Cryptocephalus nitidulus* larvae reared on the different litter treatments [F (3,16) = 4.94, *P* = 0.013] with larvae reared on *Crataegus monogyna* litter exhibiting significantly higher levels of 1st instar mortality than the other larvae (Figure 5.24). The levels of mortality in the other three groups were not significantly different to one another.

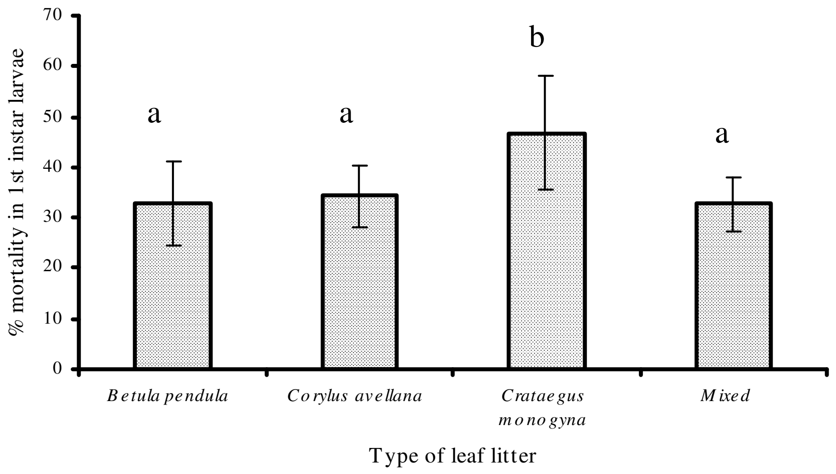

Figure 5.24. Mortality in 1st instar *Cryptocephalus nitidulus* larvae reared on four litter treatments. (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Mortalities amongst 1st instar *Cryptocephalus decemmaculatus* larvae were around 40% or more. There was significant between group variation [F (3,16) = 3.44, *P* = 0.042] in the mortality of the larvae reared in the four treatments, with 1st instar mortality significantly higher in larvae reared on *Betula pubescens* compared to the other types of litter (Figure 5.25).

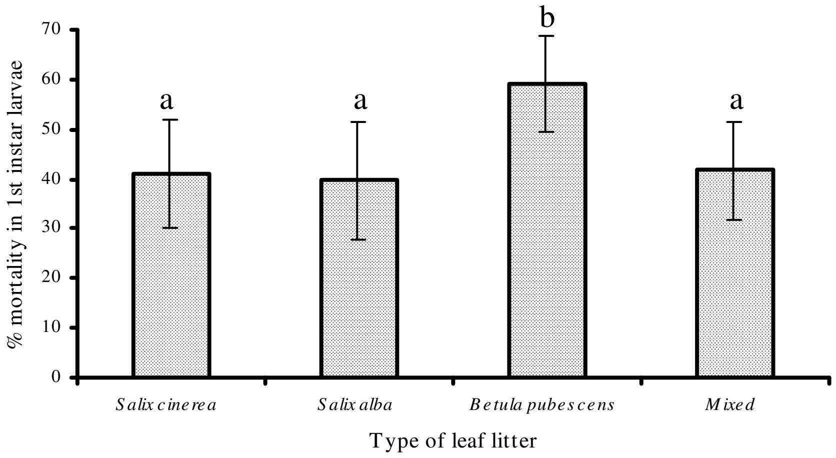

Figure 5.25. Mortality in 1st instar *Cryptocephalus decemmaculatus* larvae reared on four litter treatments (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Between group variation in the mass of final instar *Cryptocephalus coryli* larvae was significant [F (3, 96) = 1132.02, *P* = <0.001]. Larvae were significantly heavier (final instar mass) when they were reared on a diet of *Betula pendula* litter or a diet of mixed litter containing *B. pendula* (Figure 5.26). Final instar larvae reared on *Crataegus monogyna* litter were significantly lighter than those reared on *Corylus avellana* litter.

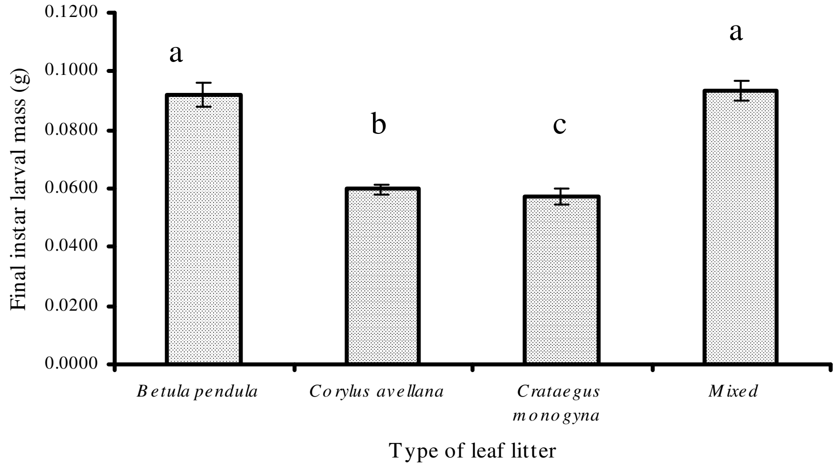

Figure 5.26. Mass of final instar *Cryptocephalus coryli* larvae reared on four litter treatments (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Between-group variation among final instar mass of *Cryptocephalus nitidulus* larvae was significant [F (3, 96) = 567.41, *P* = <0.001]. Larval mass was significantly higher in larvae feeding on *Betula pendula* and a mixed litter diet containing *B. pendula* (Figure 5.27), whereas larval performance was lowest on *Crataegus monogyna.*

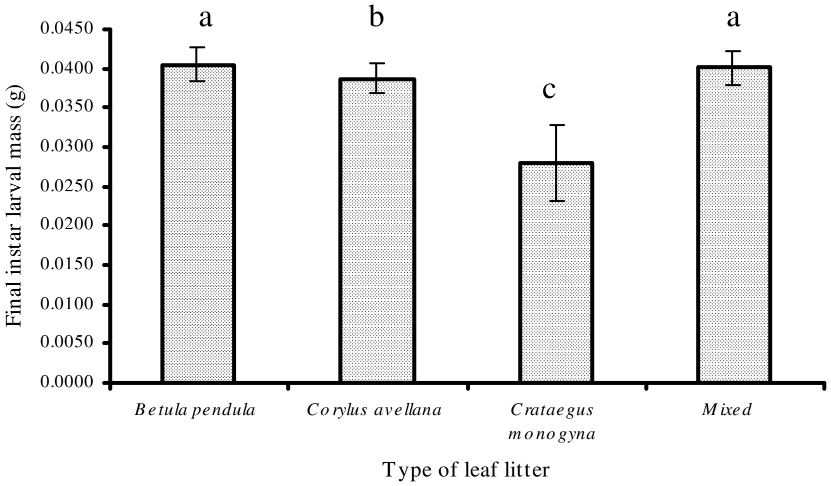

Figure 5.27. Mass of final instar *Cryptocephalus nitidulus* larvae reared on four litter treatments (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

Between group variation in the mass of final instar *Cryptocephalus decemmaculatus* larvae was also significant The mass of final instar larvae reared on a *Salix alba* litter diet and a mixed litter diet containing *S. alba* was significantly higher than if they were reared on the other litters (Figure 5.28). The mass of larvae reared on *B. pendula* litter was also significantly less than if they were reared on *S. cinerea* litter. [F (3, 96) = 13.91, *P* = <0.001].

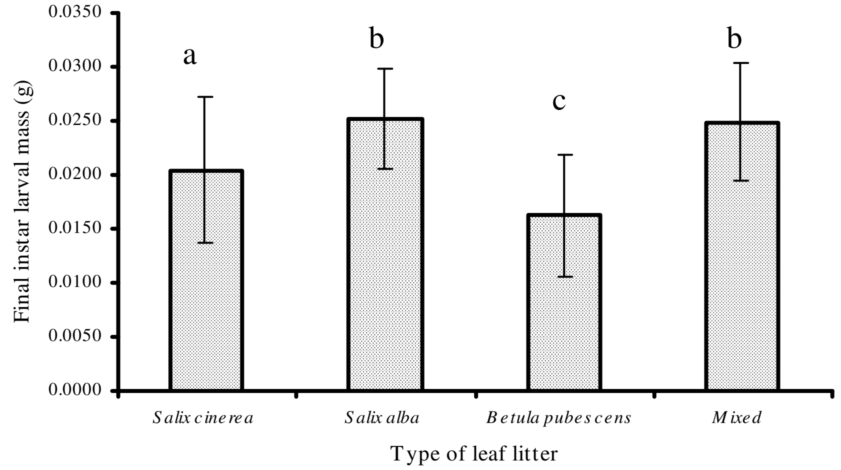

Figure 5.28. Mass of final instar *Cryptocephalus decemmaculatus* larvae reared on four litter treatments (means ± S.D.). Bars with different letters were significantly different in LSD tests following ANOVA.

5.6. Discussion

During two years of intensive fieldwork very few adult specimens of *Cryptocephalus coryli* were observed. *C. nitidulus* was found in relatively large numbers on one small part of the White Downs, whereas *C. decemmaculatus* was abundant at its one known English site. The beetles that were observed provide insights into the ecological requirements of these species.

Cryptocephalus beetles and their relatives are generally thought to be thermophilic (Erber, 1988). The results of this study suggest that *C. coryli*, *C. nitidulus* and *C. decemmaculatus* are no exceptions. The vast majority of the adult beetles observed were found perching in southern aspects on their host-plants. The plants they select exist in areas that are open to the sun, but sheltered from prevailing winds by windbreaks of taller vegetation. The presence of these windbreaks ensures that the temperatures there are much higher than in nearby areas that are not utilised by the adults. Wind speed in these sheltered areas was also lower.

While the heights of the plants they select obviously limits their choice, the majority of adults were captured relatively low down on their host-trees, *C. nitidulus* adults could nonetheless be found relatively high on their host-trees, suggesting less thermophilic tendencies than *C. coryli* and *C. decemmaculatus.* Utilising the lower parts of the host-trees enabled the adults to take advantage of the higher temperatures and lower air velocities that occured there. Moving higher up the host-trees would not only result in a cooling effect, as the higher air velocities would also increase the beetles' rate of water loss via evaporation (May, 1985). The consequent increased loss of latent heat during vaporisation would also cool the insects. The longevity of adult female chrysomelids may be increased by higher temperatures (Stewart *et al.*, 1999), therefore, it would be beneficial for a female especially to actively seek out warmer microclimates. Egg production, feeding rate and movement will also increase at warm temperatures.

The sheltered and warm situations of the trees utilised by adult *Cryptocephalus* beetles and the heights at which they bask buffers the adults against unfavourable microclimatic conditions. Teneral adults of some beetles have been shown to be very sensitive to water loss through their relatively permeable cuticle (Willmer *et al.,* 1996). During this teneral phase adults aggregate and seek out humidity buffered microclimates and feed on young leaves that have relatively high water content (Willmer *et al.,* 1996). Aggregation, the eating of young leaves and sheltering in apical meristems were observed in teneral *C. decemmaculatus* adults. The permeability of a mature adult's cuticle has been shown to be up to three times less than a teneral adult (Withers, 1992; Hadley, 1994) which frees mature adults, to a certain extent from the constraints of water loss

Cryptocephalus coryli, historically, has been associated with Hazel (*Corylus avellana*) a link that gave the beetle its trivial name. Despite this, only small numbers of beetles were seen on this plant and feeding experiments confirmed that *B. pendula* is the preferred host of this species. *Betula pendula* leaves may be very similar to *Crataegus monogyna* leaves in terms of mechanical defence, in that neither has leaves with protective hairs. *Corylus avellana* leaves on the other hand are clothed in downy hairs that may deter some herbivores (Soetens *et al.,* 1991). *B. pendula* leaves contain many chemicals that are thought to deter herbivores (Palo, 1984), but the leaf chemistry of *C. avellana* and *Crataegus monogyna* is poorly known. Teneral adults were often seen feeding on very young, growing leaves. The protein and nitrogen content of foliage is usually highest in young, growing tissues in spring and because they are softer they may be easier to eat (Obermaier & Zwolfer, 1999).

Cryptocephalus nitidulus females feeding on *Crataegus monogyna* chose to eat not only the foliage, but also stripped the bark of the hawthorn sprigs. It is likely that this food is very fibrous due to the high lignin content, therefore providing greater amounts of faeces with which to cover the eggs. The eggs produced by females feeding on *C. monogyna* were not only produced in profusion, but also had a relatively larger case than the eggs produced by the females feeding on the *B. pendula*. The larger cases may provide the eggs and first instar larvae with better protection from desiccation, consequently *C. monogyna* seems to be an excellent resource for adult *C. nitidulus* but not for the larvae.

The commonest tree in the inner part of Wybunbury Moss is the downy Birch (*B. pubescens*). Sallow (*S. cinerea*) plants in situations and of a size suitable for the adult beetles are very scarce at the site. *Cryptocephalus decemmaculatus* adults were observed on both species. The density of teneral adults, in particular, on these trees was very high. One small *S. cinerea* tree at Wybunbury Moss had as many as 40 individuals basking or partially secreted in the furled leaves of the meristems at any one time over a period of around seven days in early June (See Plate 23). *Salix* species are often preferred to *Betula* species by herbivorous insects (Kennedy and Southwood, 1984). This preference may be due to differences in the defensive tactics of the plants or a higher ability of insect herbivores to detoxify and excrete *Salix* secondary metabolites (Palo, 1984). The leaf chemistry of *B. pubescens* and *B. pendula* is similar (Palo, 1984), but *B. pubescens* contains higher quantities of mono- and sesquiterpenes that have been shown to have feeding deterrent and toxic properties to insects and other invertebrates (Rice *et al*., 1978; Langenheim *et al*., 1980). *B. pubescens* leaves are also densely covered in trichomes, which provide a mechanical feeding deterrant.

Coppicing was shown to affect the feeding preferences of *Cryptocephalus coryli* and *C. decemmaculatus* adults. The effects of coppicing on leaf chemistry have been studied in some tree species. Certain lepidopteran larvae have been shown to be unable to cope with the high levels of phenolics present in the young leaves of coppice re-growth (Meyer & Montgomery, 1987). The foliage of newly coppiced *B. pendula* and *S. cinerea* trees is very lush, especially if the coppice re-growth is from a large cut trunk with an extensive rootstock. The leaves on trees are also much larger than on an uncoppiced tree of a similar size. When mature coppiced *B. pendula* trees were compared to mature non-coppiced trees it was found that *C. coryli* preferred foliage from the former. In terms of appearance the leaves of these two types of *B. pendula* are very similar, but it appears that their leaf chemistry may be different. Coppicing may therefore produce habitats with suitable warm microclimates, but the trees may be a sub-optimal food resource unless there is an age range of coppiced host-plants available. Further study is needed to elucidate the effect of coppicing on leaf chemistry and the role that it plays in influencing feeding in herbivorous insects such as *Cryptocephalus* spp.

The ground cover beneath trees that were not utilised by adult *Cryptocephalus* beetles was generally different to that beneath trees that were utilised. A greater proportion of bare ground or moss cover was closely associated with adult utilisation. Dense cover beneath *Cryptocephalus coryli* and *C. nitidulus* host trees might be detrimental to larvae. It may result in conditions that are too cool and damp for the larvae. Secondly, dense vegetation beneath the host-trees may provide better cover for the small mammals that were shown to eat these larvae. Several *Cryptocephalus* species require a substrate to burrow into before pupation (Masutti, 1960; Erber, 1988) and the presence of moss or bare ground may provide larvae with a substrate that is easier to burrow into before they pupate. Many larvae were found in this situation during experimental releases (see Chapter 6). Moss, due to its absorptive qualities may also buffer the humidity in larval microclimates. Levels of humidity have been shown to be critical for the termination of diapause in chrysomelids, and sequences of wetting events followed by periods of dryness produce high hatch rates of eggs and pupae (Nahrung and Merritt, 1999). Mosses will also represent one of the few types of fresh vegetation available to the larvae before pupation in the early spring. The presence of such vegetation has been shown to be important in successful pupation in *Cryptocephalus pini* (Masutti, 1960).

Tree preferences of adults results in non random ground flora for the larvae, but without experimental studies, whether these are better or worse for larval development cannot be determined. There are nonetheless indications that the differences might be significant.

It has been shown that a significant proportion of chrysomelid adults often remain close to the place of their larval development (Alyokhin and Ferro, 1999). Emerging *Cryptocephalus* adults appear to climb their nearest tree. This may well be the tree that their mother oviposited from, and will lead to the aggregation of beetles on trees where larval development has been successful. Consequently, successive generations of beetle will develop beneath the tree and lay some of their eggs from its branches until it eventually becomes unattractive to adults or the ground surface changes. A consequence of this is that the integrity of *Cryptocephalus* populations at any one site is frequently dependent on an extremely limited number of trees that happen to provide optimal or near optimal conditions for the adults and larvae. Three such trees exist at Wybunbury Moss (see Plate 23), one tree at Headley Warren (see Plate 14) and several trees on one small section of the White Downs (see Plate 22).

Several *Cryptocephalus* species have been shown to feed on a very wide spectrum of leaf litters including the litter of gymnosperms (Steinhausen, 1996) and the *Cryptocephalus* larvae in this study appeared to feed voraciously on all litter types offered in the experiments. Differential mortality and performance of the larvae nonetheless showed that even though their tastes appeared to be relatively catholic, growth and survivorship were severely reduced on certain litter types. Although all of the litter types were devoured with similar vigour the observed differences in mortality and larval mass indicate that the quality of the food ingested was variable. Interestingly, it has been shown that fresh leaves of the herb species growing beneath trees utilised by adults are unpalatable to *C. coryli* larvae and therefore the litter is critical (Owen, 1999). In terms of the *Cryptocephalus* species in this study do adult feeding preferences correspond with larval performance? They mainly do, so the trees they prefer will tend to have ‘good’ litter below

Cryptocephalus nitidulus larval performance suggests that *Crataegus monogyna* litter provide a sub-optimal diet, yet females lay more eggs if they feed on this plant. This observation could represent a conflict between the ‘interests’ of females and offspring. It is in the female’s interests to produce as many successful larvae as possible. It is in the interests of the larvae to be deposited in a habitat that offers optimal conditions to complete their development, although there are several examples of females preferentially ovipositing in conditions that are sub-optimal for offspring (Bernays and Graham, 1988; Rank, 1994; Berdegue, *et al.,* 1998). While the ground beneath a *C. monogyna* tree may have a predominance of *C. monogyna* litter, wind-blown litter from other trees nearby will also be found under any given tree. This litter mix will give developing *C. nitidulus* larvae a choice, although, it remains to be seen if the catholic tastes of *Cryptocephalus* larvae in captivity is present in the field, when a choice between different leaves will often be available. An ideal habitat for both females and larvae may contain a mixture of both tree species.

To conclude, it appears that *Cryptocephalus coryli, C. nitidulus* and *C. decemmaculatus* adults are very thermophilic, with the only extant populations in this country to be found in south facing situations. The temperature is much higher and wind speed much lower in these pockets than in adjacent non utilised areas. Optimal habitats for these species contain host-plants that are not only suitable for adults but also possess ground characteristics that are optimal for the larvae. The juxta-position of good adult host-plants in suitable conditions with optimal larval habitat below them is rare, producing a handful of ‘beetle trees’ at each site that can support high densities of adult beetles. *Cryptocephalus* larvae are not able to disperse great distances (see Chapter 7) and teneral adults have been shown to be unable to fly in many beetles (Willmer *et al.* 1996). Therefore, teneral adults are likely to be found and will reach maturity on or very near to the tree from which they were laid as eggs. These ‘beetle trees’ grow in the very dynamic ecotone between woodland and grassland, heathland or bog land and cannot remain suitable for adults and larvae for a long period of time. The dynamic nature of this habitat means that the beetles have to switch locations periodically, which is not easy for them as they are not very vagile.

Chapter 6. Life in the litter: Larval overwintering in three species of *Cryptocephalus* 'pot' beetle.

6.1. Introduction

Studying the insect fauna of leaf litter presents several problems to the ecologist. Most techniques that are used in the study of leaf litter provide absolute population estimates (Mason, 1970; Speight, 1973; Southwood, 1978). Other techniques such as berlese funnels, etc. are behavioural based (Macfayden, 1961). Trapping techniques such as pit-falls rely on the animal taking the action that leads to enumeration (Luff, 1975; Southwood, 1978). All these techniques involve a great deal of disturbance to the leaf litter habitat. Studying one particular species in the leaf litter is very difficult due to the problems associated with finding relatively small numbers of individuals in such a very cryptic habitat. Many of the insects in this habitat are also cryptically coloured. Most of the studies on leaf litter insects have focused on biotic interactions and faunal diversity (Okajima & Urushihara 1992; Reddy *et al.*, 1992; Carcamo *et al.,* 2001; Sharon *et al*., 2001; Rieske & Buss, 2001). To date there is a dearth of literature focused on the ecology of individual leaf litter species.

An important determinant of the viability of rare insect species in northern latitudes is the period of winter hibernation (Nicholls & Pullin, 2000). Over-wintering survival has been the focus of many studies, principally with lepidopteran larvae (Webb & Pullin, 1996; Webb & Pullin, 1998; Joy & Pullin, 1999; Nicholls & Pullin, 2000; Tanhuanpaa *et al.,* 1999). In contrast, very little research has been undertaken on the over-wintering survival of beetles other than those of economic significance. Some studies have focused on the micro-habitat preferences of chrysomelid larvae that over-winter at the base of their host-plants (Spring & Kok, 1999), but literature detailing with the effects of predation on coleopteran larvae that spend all or part of their time in leaf litter appears to be non-existent. Determining the survival of larvae over this relatively long, but inactive winter period is often particularly difficult due to many insects taking refuge in microhabitats which render their detection and recovery difficult. This problem is compounded by many immature insects being particularly cryptic.

Marking of individuals provides a means of monitoring over-wintering success in the leaf litter, but recovery of released individuals using visual searching can be destructive and consequently does not allow repeat sampling. In an attempt to remedy this problem a novel technique was employed using the attachment of metal tags that can be found with a metal detector. This allows efficient recovery of released insect larvae without destruction of their habitat (see

Chapter 4). This enabled *in situ* observation of individual insects that spend the winter period in the leaf litter.

Cryptocephalus (Coleoptera, Chrysomelidae) adults feed on leaves and petals and are generally oligophagous, though a few species have more restricted host ranges (Erber, 1988). Their larvae are found in leaf litter and eat mainly dried and decaying leaves (Lesage, 1985), although fresh plant material may also be required before pupation (Masutti, 1960). Adults are generally thermophilic and capable of flight and can be found sitting in exposed positions on leaves. Females oviposit from such perches, covering each egg in faeces to form an egg case that is dropped onto the ground below. Once hatched, larvae carry the egg case and continue to add to it to form a larval case, hence the name ‘pot beetles’ (Erber, 1988). Over-wintering in northern latitudes takes place in the larval stage with pupation and adult emergence in the spring (Steinhausen, 1994). UK species are often univoltine, but some require more than one year to complete their development (Owen, 1996, 1999; Pers. Obs.).

The larvae and adults of *Cryptocephalus* beetles live in different habitats and this has interesting implications for the “*mother knows best*” hypothesis that has been the subject of recent studies (Mayhew, 1997; Scheirs, 2000; Mayhew, 2001). Overwintering larvae of three *Cryptocephalus* species of conservation concern in the UK were studied. *Cryptocephalus coryli* is a RDB1 species that is currently restricted to three known sites in England. Adults can be found mainly on *Betula pendula* growing in heathland or downland. *C. decemmaculatus* (RDB2) adults are found mostly on *Salix* species growing in wet areas. It is currently known from just one English site and one Scottish site. *C. nitidulus* (RDB1) is restricted to three sites, all in England, where adults can be seen mostly on *Betula pendula* growing in heathland or downland. These three species along with three other *Cryptocephalus* species are BAP priority species (UKBG, 1999) and each species now has a Biodiversity Action Plan or priority statement. Each plan highlights the need for the establishment of new populations and the enhancement of current populations. Both of these goals require an understanding of the ecological requirements of the larval stages if they are to be successful.

The aims of this study were as follows:

1. Monitor the survival of released *Cryptocephalus* larvae during the over-wintering period and determine their sources of mortality
2. Determine whether predation is related to ground cover characteristics.
3. Determine whether larvae fare better beneath the trees where adults would normally oviposit or if adult habitat preferences are sub-optimal for larval survivorship.

4. On the basis of the above provide guidelines on how to improve the chances of success of larvae released as part of the re-establishment programmes outlined in the action plans for these species, and to facilitate management of sites where they occur.

6.2. Materials and methods

6.2.1. Study sites

Experimental introductions of final instar *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* larvae were conducted at four sites during the autumn and winter of 2000. *C. coryli* larvae were released at two sites in Lincolnshire that lie within the historical distribution of this species, while *C. decemmaculatus* and *C. nitidulus* larvae were released at sites which currently support the respective species. Eight hundred and thirty larvae were released in total (Table 7.1).

6.2.2. Larval releases

Larvae of the three *Cryptocephalus* species were reared from eggs laid in captivity on a diet of adult host-plant leaf litter (see Chapter 5). Final instar larvae of *Cryptocephalus coryli*, *C. nitidulus* and *C. decemmaculatus* were tagged with small strips of metal (Plate 29) as described in Chapter 4 and acclimatised prior to release by placing them in progressively cooler incubators (20, 13, 8 and 5° C; with four days at each temperature). The larvae were transported to the release sites in a cool box. The tags used to label the larvae were 1 mm ± S.D. 0.2 mm × 3 mm ± S.D. 0.2 mm and 0.35 mg ± S.D. 0.07 mg. The tags represented mean = 1.18 % ± S.D. 0.36% of final instar (n = 10) larval body weight (*Cryptocephalus coryli*), mean = 3.26% ± S.D. 0.48% (*C. nitidulus*) and mean = 4.17% ± S.D. 0.48% (*C. decemmaculatus*). Ten larvae were placed beneath each host-plant within a radius of 50cm of the trunk. Table 6.1 shows the number of larvae released at the sites.

Cryptocephalus decemmaculatus and *C. nitidulus* larvae were each released beneath trees in one of three different habitats. The first of these were trees in habitats already utilised regularly by adult beetles, namely areas of scrub in south facing sheltered conditions (Table 6.1 A). The second type were trees in habitats that appeared suitable for adult beetles, but regular surveying had shown that they were not being utilised (Table 6.1 B). The third type was beneath trees not utilised by adults in habitats they do not occupy, i.e. beneath a dense canopy or recently cleared plantation (Table 6.1 C). *C. coryli* larvae were released in 'B' and 'C' type sites in November of 2000 and recovered approximately monthly until May 2001. *C. decemmaculatus* and *C. nitidulus* larvae were released in January of 2001, but Foot and Mouth Disease restrictions meant that larvae were only relocated once (*C. decemmaculatus*) or twice (*C. nitidulus*).

Table 6.1. Total numbers of larvae released per study site. Each tree chosen at each site had ten larvae released beneath (A, B and C for sites indicate the following: A = releases beneath trees in habitats already utilised by adults, B = releases beneath trees in habitats that appear suitable for adults, but not utilised by them and C = releases beneath host plants not utilised by adults, in habitats they do not occupy.

Species	Site	No. of larvae released	Origins of larvae	Release (R) and monitoring (M) dates
C. coryli	Laughton Forest 1 (Lincs.). **B**.	80	Kirkby Moor	R = 20/11/2000 M1 = 05/12/2000 M2 = 25/01/2001 M3 = 23/05/2001
	Laughton Forest 2 (Lincs.). **C**.	70	Kirkby Moor	R = 20/11/2000 M1 = 05/12/2000 M2 = 25/01/2001 M3 = 23/05/2001
	Whisby (Lincs.). **B**.	180	Kirkby Moor	R = 14/11/2000 M1 = 24/11/2000 M2 = 16/01/2001 M3 = 08/05/2001
C. decemmaculatus	Wybunbury Moss (Cheshire). **A**.	100	Wybunbury Moss	R = 22/11/2000 M1 = 28/05/2001
	Wybunbury Moss (Cheshire). **B**.	100	Wybunbury Moss	R = 22/11/2000 M1 = 28/05/2001
	Wybunbury Moss (Cheshire). **C**.	100	Wybunbury Moss	R = 22/11/2000 M1 = 01/04/2001
C. nitidulus	White Downs (Surrey). **A**.	100	White Downs	R = 24/11/2000 M1 = 23/01/2001 M2 = 04/01/2001
	White Downs (Surrey). **B**.	50	White Downs	R = 22/11/2000 M1 = 23/01/2001 M2 = 04/01/2001
	White Downs (Surrey). **C**.	50	White Downs	R = 22/11/2000 M1 = 23/01/2001 M2 = 04/01/2001

6.2.3. Cryptocephalus coryli releases in Laughton Forest

Larvae reared from eggs laid by females caught on *Betula pendula* at Kirkby Moor were released at Laughton Forest (TF8698), approximately 50 km from Kirkby Moor (TF2262). Forest Enterprise operations are currently reclaiming parts of the site as heathland. Two areas were used for the study (situated 90 m apart at their closest point). The first, Area 1 (Plate 30), was a site with *Betula pendula* scrub and appeared similar to the habitat currently occupied by *C. coryli* at Kirkby Moor. There was a diverse ground cover in this area with many *Molinia caerulea* tussocks, mosses and herbaceous species. Area 2 (Plate 31) was a recently partially-cleared area with very little ground vegetation apart from isolated grass tussocks. This area would not be utilised by *C. coryli* adults because it is too early in the vegetation succession and lacks the small birch trees from which they oviposit.

6.2.4. Cryptocephalus coryli releases in Whisby Pits Nature Reserve

Larvae originating from females caught at Kirkby Moor were released at Whisby Pits Nature Reserve (SK9067), which is about 35 km from Kirkby Moor. The Lincolnshire Trust for Nature Conservation owns this site. The area chosen for the releases was a relatively uniform section of

Betula pendula scrub on a sand/gravel surface with diverse ground vegetation consisting of grasses and many herbaceous plant species (Plate 32). The area, which is a reclaimed gravel extraction site, was chosen because of its superficial similarity to other localities that support this species, in particular the presence of a complex *B. pendula* scrub in south-facing, sheltered conditions.

6.2.5. Cryptocephalus decemmaculatus releases in Wybunbury Moss

This site (SJ6950) is a type of quaking bog or "Schwingmoor" of which there are only two surviving in England (Plate 33). It is a National Nature Reserve that is owned and managed by English Nature and covers an area of approximately 20 hectares. The inner region of the site is essentially a floating mat of *Sphagnum* moss with water up to 12 metres deep underneath. *Cryptocephalus decemmaculatus* is found around the perimeter of this *Sphagnum* lawn on *Salix cinerea and Betula pubescens* bushes growing in south-facing aspects.

6.2.6. Cryptocephalus nitidulus releases in the White Downs

The three release sites for *Cryptocephalus nitidulus* larvae were spread over a 1.9 km section of the White Downs (TQ1249) (Plates 34 and 35), which is owned and managed by the National Trust. The White Downs is an extensive area of calcareous grassland with large swathes being invaded by *Betula pendula, Corylus avellana, Craetagus monogyna, Viburnum lantana* and *Ligustrum vulgare*.

6.2.7. Recovery of larvae

The larvae were recovered by using a sensitive hand-held metal detector (Pulse Technologies, Oxford, UK) that was swept over the release area. Recovering released *Cryptocephalus decemmaculatus* larvae also entailed the use of a magnet due to their small size (<6 mm). Once detected with the metal detector the magnet was employed to pull the larvae from the moss where they were sheltering. The microhabitats in which the larvae were found were recorded, together with their condition and if necessary, likely causes of death. Larvae were readily recorded as being still alive as the head capsule was visible at the aperture end of the case.

6.2.8. Ground cover

Ground cover characteristics were recorded for each local area where larvae were released. A 50 cm^2 quadrat was placed to the N, S, E and West around the release point and the percentage cover of grasses, mosses, herbs, bare ground and leaf litter were estimated visually. Leaf litter was recorded first and then removed if it was obscuring the ground flora. Maximum sward height was measured with a 30 cm ruler.

6.2.9. Predation

Cryptocephalus coryli larvae were found to suffer frequent predation. In order to establish the species of predator, mammal trapping was carried out at the Laughton Forest site at the end of May 2001. 110 mammal traps (a mixture of Longworth traps and Sherman traps) were set out (Figure 6.1) to sample the small mammal faunas in the two areas of Laughton Forest where the larvae had been released in November 2000 and in the area between them. 25 pitfall traps were also placed in each area to sample for surface-active, predatory invertebrates (Figure 6.1).

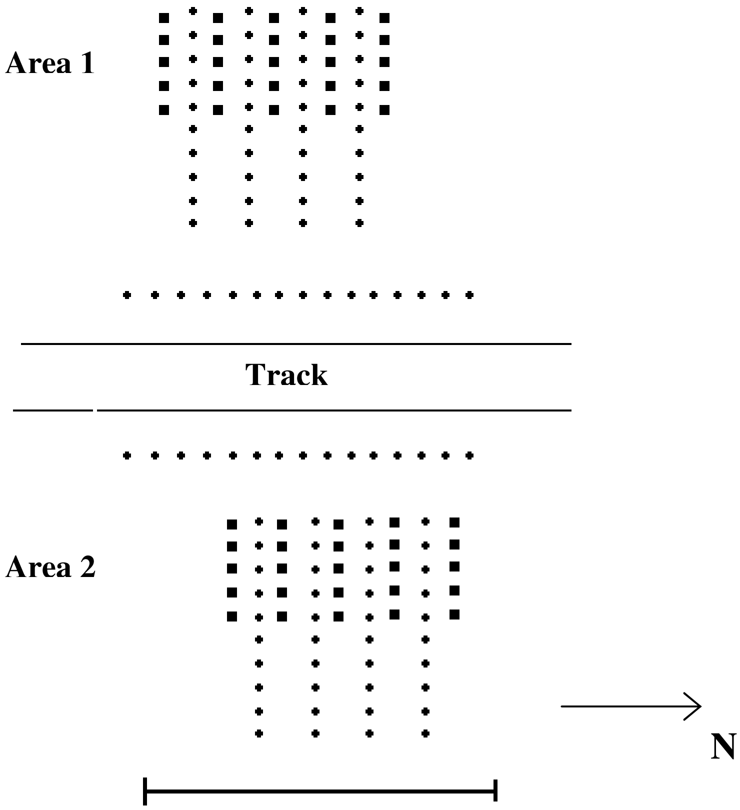

Figure 6.1. Layout of mammal traps and pitfall traps at Laughton Forest site. Round symbols = mammal traps; square symbols = pitfall traps. Scale bar = 50m.

Feeding damage to *Cryptocephalus coryli* larval cases caused by different species of predators was characterised by placing single calliphorid maggots in empty *C. coryli* larval cases. The maggots were killed beforehand by placing them in boiling water. Twenty-five of these cases were then placed, singly, in some of the mammal traps along with corn and calliphorid pupae. Mammal traps were set during the evening and checked the following morning on five occasions. Cutting fur from their hindquarters marked the captured mammals. If a trap with a mammal had included a *C. coryli* case then the case was recovered. Pitfall traps were also checked every morning over five days and the contents identified and then released in the field. Four *Carabus problematicus* (Carabidae) beetles were taken back to the laboratory and maintained in suitable conditions together with *C. coryli* cases, each filled with a maggot as before, for two weeks.

6.3. Results

6.3.1. Cryptocephalus coryli

The numbers of recovered larvae at the three release sites was generally high (Table 6.2) and was always over 50% of the larvae remaining to be found. There was no significant difference [F (2, 30) = 0.820, *P* = 0.450] in the total number of recovered larvae at the three sites. Recapture rates at Whisby were higher for recaptures 1 and 3 than in 2, perhaps because recapture 2 took place during the coldest months of the year, when larvae would have been inactive. Recaptures at the Laughton Forest site showed the same pattern, with the lowest recaptures rate again during recapture 2 (Table 6.2).

Table 6.2. Total numbers of *Cryptocephalus coryli* larvae that were recovered during each recapture episode at the Whisby and Laughton Forest sites.

	Laughton Forest 1			**Laughton Forest 2**			**Whisby**		
	Recapture 1 (Release + 15 days)	**Recapture 2 (Release + 70 days)**	**Recapture 3 (Release + 180 days)**	**Recapture 1 (Release + 15 days)**	**Recapture 2 (Release + 70 days)**	**Recapture 3 (Release + 180 days)**	**Recapture 1 (Release + 10 days)**	**Recapture 2 (Release + 65 days)**	**Recapture 3 (Release + 175 days)**
Unrecovered	20	11	5	20	36	30	72	76	17
Recovered	60	36	17	50	29	15	108	77	90
Alive	27	11	2	45	9	8	81	31	26
Dead	4	4	2	3	10	3	3	7	19
Predated	29	21	13	2	10	4	24	39	45

Of the three release sites, the rate of predation was highest in Laughton Forest Area 1 (Figure 6.2), where after a period of 180 days almost 80% of the released larvae had been predated. In comparison, by this time, only about 23% of released larvae had been predated in Area 2 of the Laughton Forest site and 60% at the Whisby site.

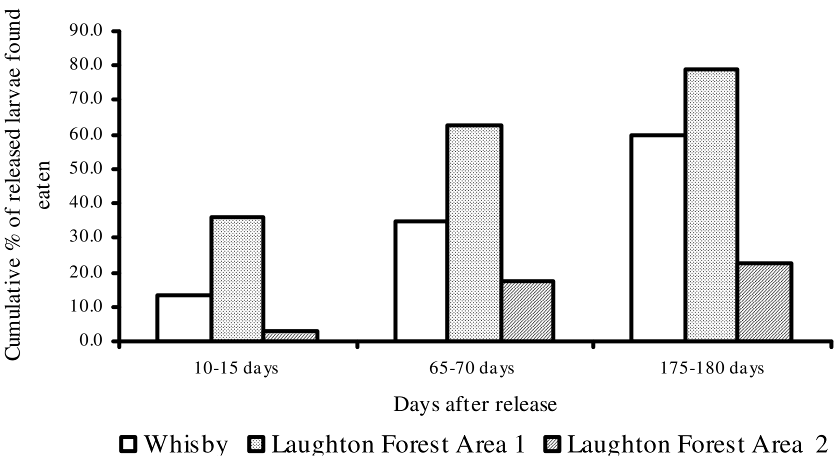

Figure 6.2. Predation in overwintering *Cryptocephalus coryli* larvae.

There was a significant difference between the final numbers of predated larvae that were recovered from the three sites [F (2, 30) = 13.51, *P* = <0.001]. Damage to the larval cases ranged from a small hole in the posterior end of the case to almost complete fragmentation. On eight occasions only the metal tag fitted to the larval case was located. These loose tags were assumed to be artefacts of predation as a persistent predator would have been able to dislodge them.

Post-hoc testing (LSD test) of the same data showed that by the end of the experiment the number predated at Whisby was significantly higher (*P* = <0.001) than the predation seen at Laughton Forest Area 2. This was also the case for Laughton Forest Area 1 compared to Laughton Forest Area 2 (*P* = <0.001). The number of larvae predated at Whisby was not significantly different to that at Laughton Forest Area 1.

Area 2 of the Laughton Forest site had the highest level of larval mortality due to factors other than predation by the end of the experimental period (22.9%) (Figure 6.3). The lowest (16.1%) was seen in Area 1 of the Laughton Forest site. This reflects the numbers of larvae that have not been eaten. When the numbers rather than proportions of larvae dying through causes other than predation are compared, there was no significant difference [F (2, 30) = 0.845, *P* = 0.439] between the final numbers of recovered, dead larvae from the Whisby site and the Laughton Forest Areas 1 and 2. How these larvae perished is not clear. In some cases fungal hyphae were seen to be protruding from the case aperture, but it was very difficult to tell whether they were saprophytic or entomophagous. All other instances of larval death concerned cases, which appeared to be empty, but upon opening they yielded a decayed or desiccated larva in the bottom of the case.

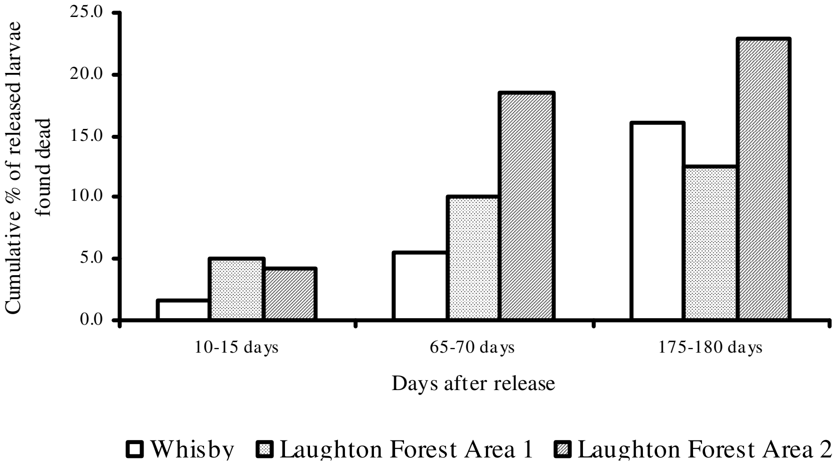

Figure 6.3. Mortality other than predation in overwintering *Cryptocephalus coryli* larvae.

Area 1 within Laughton Forest showed the greatest overall losses of larvae (Figure 6.4). The maximum possible number of remaining larvae at this site (assuming that all non-recovered larvae were alive) was seven of an original 80 released of which two (28.6%) were confirmed alive on the last sample date. The maximum number of larvae left at Area 2 within Laughton Forest was 38 out of 70 of which eight (21.1%) were confirmed alive on the last sample date. A maximum of 43 (from an original 180) larvae were left at the Whisby site of which 26 (60.4%) were confirmed alive on the last sample date.

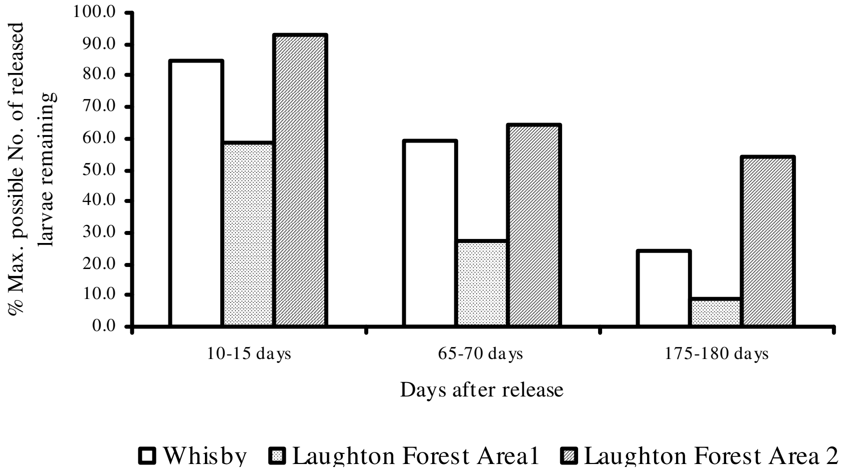

Figure 6.4. Losses of released *Cryptocephalus coryli* larvae due to predation and other mortality factors

The recovery of the larvae also enabled their microhabitat preferences to be observed. During the course of the study mature larvae were found partly buried in the substrate with the posterior end of the case sticking out from this small burrow. This behaviour was interpreted as the full-grown larvae preparing for pupation. If the three sites are combined then one, three and 19 larvae were found in this position in bare ground or dense moss during recaptures one, two and three respectively.

After five days of mammal trapping in Laughton Forest the only species recorded was the Wood Mouse (*Apodemus sylvaticus*). Area 1 yielded nine Wood Mice, but none were found in Area 2. Two and three mice were caught in Transects A and B respectively.

Eight of the traps that were baited with *C. coryli* larval cases contained a Wood Mouse. The cases showed the same type of damage as larval cases predated in the field (Plate 36). They had been chewed open and the maggot removed from the inside.

The only large carabid that was found using the pitfall traps was a single specimen of *Carabus problematicus* in Area 1. Four hungry *C. problematicus* offered baited *C. coryli* cases did not attempt to break into them.

A summary of ground cover characteristics beneath the release trees at the three sites is shown in Table 6.3. There was no significant difference between the sites in terms of maximum sward height [ANOVA, F (2, 30) = 2.805, *P* = 0.079], grass [F (2, 30) = 0.043, *P* = 0.958] and herbs

[F (2, 30) = 0.703, *P* = 0.504]. Percentage moss cover between the sites was significantly different [F (2, 30) = 43.293, *P* = <0.001], as was bare ground [F (2, 30) = 57.213, *P* = <0.001] and leaf litter [F (2, 30) = 5.594, *P* = 0.010]. Most of these significant differences resulted from Laughton Forest area 2 and the other sites, which were much more similar in terms of ground cover characteristics.

Table 6.3. Summary of ground cover data beneath release trees at the Whisby, Laughton Forest 1 and Laughton Forest 2 release sites. Letters after values indicate results of *post-hoc* tests (LSD method following ANOVA). Values for each variable with similar letters were not significantly different.

	Sward height (cm)	Moss (%)	Grass (%)	Bare ground (%)	Herbs (%)	Leaf litter (%)
Whisby	0.99 (± S.D. 0.31) a	80.8 (± S.D. 19.9) a	4.64 (±S.D. 6.48) a	11 (± S.D. 17.0) a	4.1 (± S.D. 3.3) a	20.0 (± S.D. 23.0) a
Laughton Forest Area 1	1.3 (± S.D. 0.5) a	86.4 (± S.D. 11.5) a	4.58 (± S.D. 3.8) a	6.6 (± S.D. 11.1) a	2.4 (± S.D. 1.1) a	10.3 (± S.D. 8.4) a
Laughton Forest Area 2	0.85 (± S.D. 0.5) a	6.65 (±S.D. 12.5) b	4.2 (± S.D. 5.3) a	88 (± S.D. 17.5) b	1.5 (± S.D. 1.4) a	45.8 (± S.D. 27.9) b

The majority of release trees at Whisby and all the release trees at Laughton Forest Area 1 had very little bare ground, whereas the situation was reversed in Area 2 of Laughton Forest (Figure 6.5). As the proportion of bare ground increases cumulative predation decreases (Figure 6.5) suggesting that this maybe an important factor influencing the predation of *Cryptocephalus coryli* larvae.

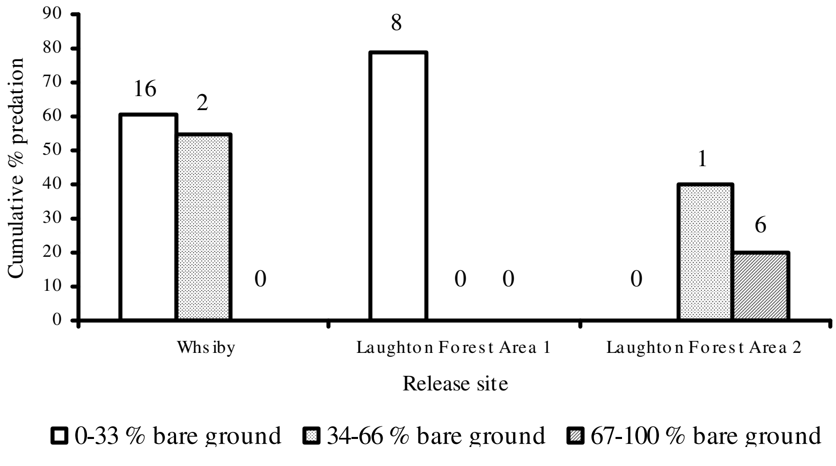

Figure 6.5. Summary of the relationship between bare ground and predation at the three release sites for *Cryptocephalus coryli*. Values above bars refers to the number of release trees within each bare ground cover class.

A binary logistic regression (SPSS version 10.1) was used to determine the relative effects of the measured ground cover characteristics beneath individual trees on predation of released larvae. Data from the three sites were combined. Bare ground percentage cover was the most significant of the measured variables (Table 6.4). Predation was lowest below trees that had the greatest proportion of bare ground. Leaf litter percentage cover was also significant but not selected for use in succeeding steps of the regression. Percentage bare ground cover was used to produce a classification that projected an overall correct group membership of 66%. (Table 6.5). This suggests that the regression model based on ground cover was only a poor predictor of larval predation. Herb, moss and grass percentage cover were of no significance and were not selected for use the in the forward conditional binary logistic regression.

Table 6.4. The relative significance of ground cover variables at larval release sites related to the final level of predated *Cryptocephalus coryli* larvae (forward conditional binary logistic regression output).

Variable	B	Standard Error	Degrees of Freedom	Significance
% Bare Ground Cover	.040	.010	1	<0.001
% Leaf Litter Cover	-.043	.019	1	0.022
Constant	-.358	.143	1	0.012

Table 6.5. Final binary logistic regression classification of confirmed and non-confirmed predated *Cryptocephalus coryli* and *C. nitidulus* larvae related to ground cover characteristics showing % accuracy of predicted group membership.

Species	Confirmed eaten		Not eaten		Overall % correct
	Correctly classified	Incorrectly classified	Correctly classified	Incorrectly classified	
C. coryli	**156**	**15**	**56**	**94**	**66.0**
C. nitidulus	**65**	**36**	**64**	**35**	**64.5**

6.3.3. Cryptocephalus nitidulus

Due to foot and mouth restrictions it was only possible to carry out two recaptures for released *C. nitidulus* larvae. During the first recapture (release + 53 days) the greatest proportion (61%) of larvae were found beneath trees in ‘A’ type release sites. These were trees in habitats already utilised by adults. 27 (54%) of released larvae were recovered from beneath trees in ‘B’ type release sites. These were trees in habitats that appeared suitable but were never seen to be utilised by adult beetles. The lowest proportion of recaptures (46%) was made in ‘C’ type release sites. Adults were never seen on the trees in ‘C’ type habitats. The proportion of recovered larvae during recapture 2 (release + 121 days) was 83.8, 83.3 and 78.8% in release site types ‘A’, ‘B’ and ‘C’ respectively, so the differences between sites had narrowed.

In ‘A’ type release sites the level of observed predation was at its lowest (Figure 6.6). After a period of 121 days 35% of the larvae in ‘A’ type release sites had been eaten. After the same period of time in ‘B’ type release sites 68% of the total number of released larvae had been eaten, whereas 64% of released larvae had been eaten in ‘C’ type release sites.

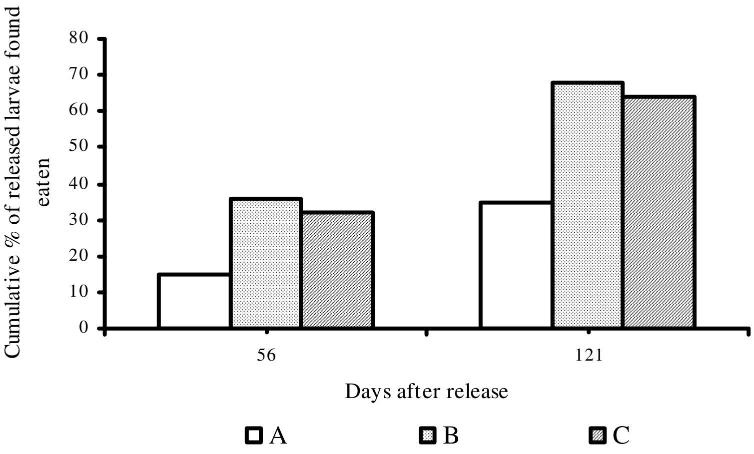

Figure 6.6. Predation in overwintering *Cryptocephalus nitidulus* larvae. A = trees in habitats already utilised by adults, B = trees in habitats that appear suitable for adults, but not utilised by them and C = trees not utilised by adults, in habitats they do not occupy.

There was a significant difference [F (2, 17) = 10.70, P = 0.001] between the final numbers of recovered, predated larvae from White Downs A, B and C. *Post-hoc* testing of the same data showed that final level of predation at White Downs A and White Downs B were significantly different from one another (P = 0.01). This was also the case for White Downs A and White Downs C (P = 0.03). The final levels of predation at White Downs B and C were not significantly different to one another.

Of the 100 larvae released in ‘A’ type release sites 21% had died for reasons other than predation after 121 days. This compares to 6% and 4% in ‘B’ and ‘C’ type release sites respectively (Figure 6.7). A small number of the recovered cases which were found to be empty did shows signs of fungal activity, however, the majority of the dead larvae appeared to have simply desiccated.

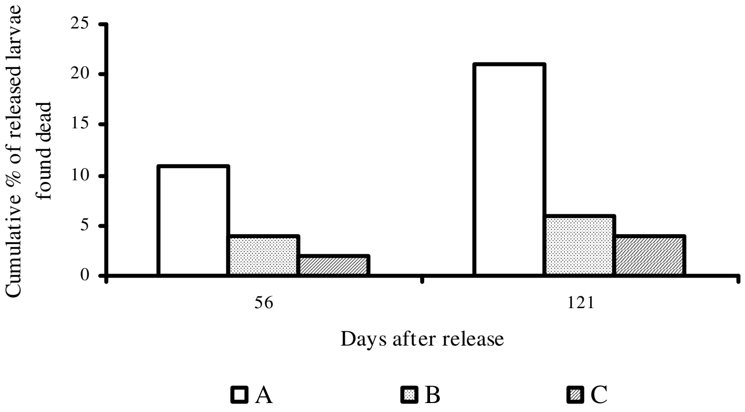

Figure 6.7. Mortality from sources other than predation in overwintering *Cryptocephalus nitidulus* larvae. A = trees in habitats already utilised by adults, B = trees in habitats that appear suitable for adults, but not utilised by them and C = trees not utilised by adults, in habitats they do not occupy.

There was a significant difference [F (2, 17) = 6.34, *P* = 0.009] between the final numbers of recovered, dead larvae from the A, B and C type release sites. *Post-hoc* testing of the same data showed that the final numbers of dead larvae recovered from 'A' type release sites were significantly higher than the numbers of larvae recovered from 'B' and 'C' type release sites (*P* = 0.015 and *P* = 0.007 respectively), which were not significantly different.

After a period of 121 days the maximum possible number of released larvae remaining was in 'A' type release sites (44%). This compares to proportions of 26% and 32% in 'B' and 'C' type release sites respectively (Figure 6.8).

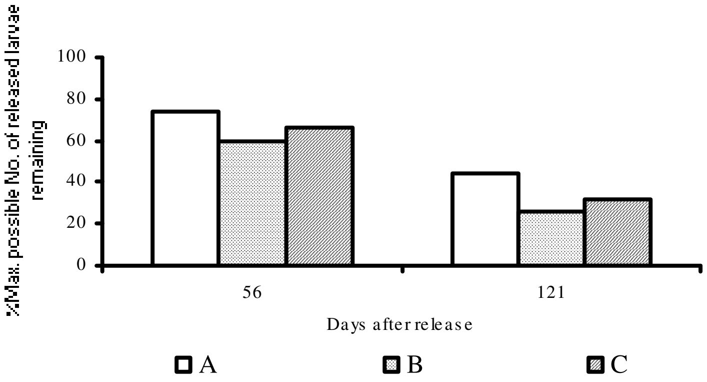

Figure 6.8. Loss of released *Cryptocephalus nitidulus* larvae due to predation and other mortality factors. A = trees in habitats already utilised by adults, B = trees in habitats that appear suitable for adults, but not utilised by them and C = trees not utilised by adults, in habitats they do not occupy.

Observations of released larvae and wild caught larvae provided no obvious indication of habitat preferences made by mature larvae of the sort that were observed in mature *Cryptocephalus coryli* larvae. Of the very few recaptured, intact and sealed larval cases that were found (*n* = 4) all were found lying, relatively exposed, on the soil surface. There was no evidence of burrowing.

A summary of ground cover characteristics beneath the release trees is shown in Table 7.6. There was a significant difference between the sites in terms of maximum sward height [ANOVA, F (2, 18) = 47.870, *P* = <0.001], moss [F (2,18) = 4.829, *P* = 0.021], grass [F (2, 18) = 17.354, *P* = <0.001] and herbs [F (2, 18) = 7.119, *P* = 0.005]. Percentage bare ground cover and leaf litter cover between the sites were not significantly different.

Table 6.6. Summary of ground cover data beneath release trees at the White Downs release sites. Letters after values indicate results of *post-hoc* tests (LSD method following ANOVA). Values for each variable with similar letters were not significantly different.

	Sward height (cm)	Moss (%)	Grass (%)	Bare ground (%)	Herbs (%)	Leaf litter (%)
White Downs A	0.85 (± S.D. 0.47) a	24.5 (± S.D. 7.25) a	20.5 (± S.D. 15.7) a	22.5 (± S.D. 15.5) a	8.33 (± S.D. 3.54) a	26.0 (± S.D. 12.0) a
White Downs B	1.8 (± S.D. 0.45) b	32.5 (± S.D. 20.6) a	21 (± S.D. 12.4) a	18.0 (± S.D. 14.4) a	4 (± S.D. 1.41) b	32.0 (± S.D. 16.0) a
White Downs C	3.8 (± S.D. 0.84) c	6.0 (± S.D. 2.24) b	64 (± S.D. 14.7) b	6.0 (± S.D. 2.24) a	2.32 (± S.D. 2.45) c	16.0 (± S.D. 11.0) a

A binary logistic regression (SPSS version 10.1) was used to determine the relative effects of the measured ground cover characteristics on the predation of released larvae. Sward height was the most significant of the measured variables (Table 6.7). This variable was used to produce a classification table (Table 6.5). The model that was produced projected an overall correct group membership of only 64.5% (Table 6.5) suggesting poor predictive qualities of the binary logistic regression model relating sward height to larval predation. Of the other ground cover variables leaf litter percentage cover was the closest to being significant (*P* = 0.08). Moss, grass, herbs and bare ground percentage cover were much less significant (*P* = >0.13).

Table 6.7. The relative significance of ground cover variables at larval release sites related to the final level of predated *Cryptocephalus nitidulus* larvae (forward conditional binary logistic regression output).

Variable	B	Standard Error	Degrees of Freedom	Significance
Sward Height	-.395	.118	1	.001
Constant	.690	.252	1	.006

6.3.2. Cryptocephalus decemmaculatus

Due to foot and mouth restrictions the number of recapture episodes was limited to one. 128 days after their release in November 2000 49, 53 and 51 *Cryptocephalus decemmaculatus* larvae were found in release site types 'A', 'B' and 'C' at Wybunbury Moss. The number of released larvae that were recaptured was relatively low compared to the *Cryptocephalus coryli* recaptures, and the number of recaptures among the three types of release sites also appeared to be relatively similar.

The highest levels of predation (47.2%) were seen in the 'B' type release sites (Figure 6.9) compared with 41.7% in type 'A' release sites and 46.7% in type 'C' release sites (Figure 6.9).

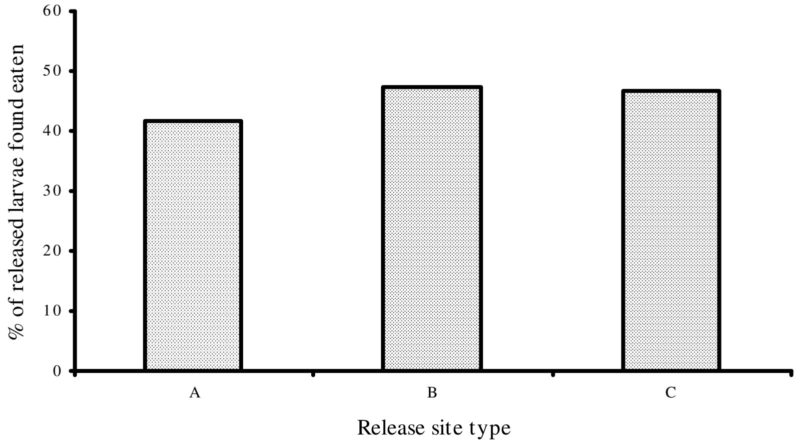

Figure 6.9. Observed predation in overwintering *Cryptocephalus decemmaculatus* larvae in three types of release site (A = trees in habitats already utilised by adults, B = trees in habitats that appear suitable for adults, but not utilised by them and C = trees not utilised by adults, in habitats they do not occupy).

Type 'C' sites were beneath trees that were completely unsuitable for adult female beetles and generally sites beneath a tall, dense canopy. There was no significant difference [F (2, 27) = 0.093, *P* = 0.911] between the final numbers of recovered, predated larvae from Wybunbury release site types 'A', 'B' and 'C'.

The numbers of larvae that were found dead after a period of 128 days were very similar in release site types ‘A’ and ‘B’ (Figure 6.10). In ‘C’ type release sites the proportion of recaptured larvae found to be dead was much higher (21%). Fungal activity in the empty cases was only apparent in larvae released in sites ‘A’ and ‘B’. Desiccation seemed to be the main cause of mortality other than predation in ‘C’ type release sites.

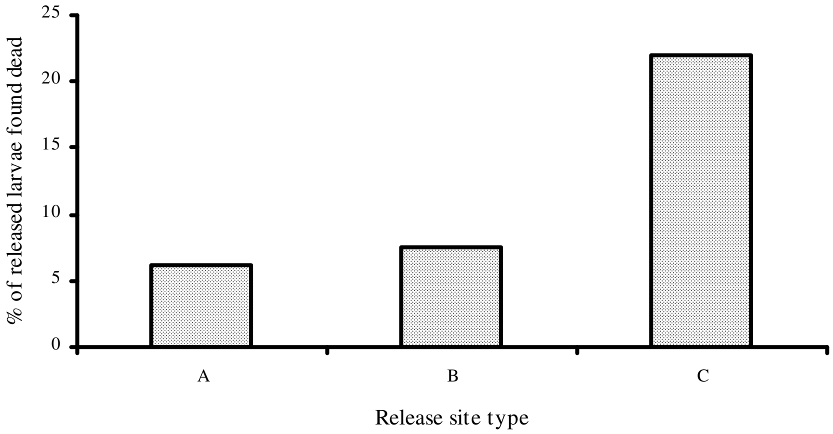

Figure 6.10. Mortality other than predation in overwintering *Cryptocephalus decemmaculatus* larvae in three types of release site. A = trees in habitats already utilised by adults, B = trees in habitats that appear suitable for adults, but not utilised by them and C = trees not utilised by adults, in habitats they do not occupy.

There was no significant difference [F (2, 27) = 0.208, *P* = 0.814] between the final numbers of recovered, dead larvae from the ‘A’, ‘B’ and ‘C’ type release sites

After a period of 128 days the maximum possible proportion of larvae remaining in ‘A’ type release sites was 55 (Figure 6.11). The maximum possible number of larvae remaining in ‘B’ type release sites was 49. Of the total number of recaptured larvae (153) only very few were alive (3.9%). Three of these larvae had sealed up their cases in preparation for pupation while the other three were still active. No observations of parasitism were recorded in the recaptured *C. decemmaculatus* larvae.

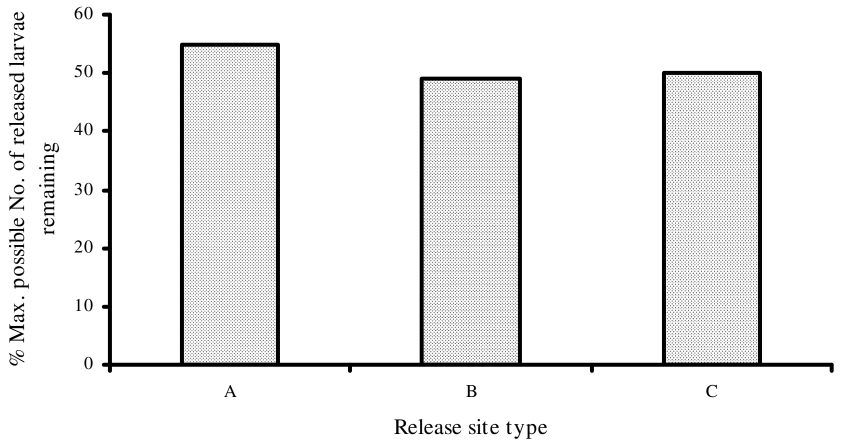

Figure 6.11. Losses of released *Cryptocephalus decemmaculatus* larvae due to predation and other causal mortality factors. A = habitat utilised by adult beetles; B = apparently suitable habitat but not utilised by adult beetles; C= habitat not suitable for adult beetles.

Due to the difficulty encountered in recapturing the released *Cryptocephalus decemmaculatus* larvae it was very difficult to make observations regarding their microhabitat preferences. Only very few intact sealed cases were recovered which compounds the difficulties in defining any habitat preference change that takes place before pupation.

A summary of ground cover characteristics beneath the release trees is shown in Table 6.8. There was a significant difference between the sites in terms of maximum sward height [ANOVA, F (2, 27) = 20.482, *P* = <0.001], grass cover [F (2,27) = 7.966, *P* = 0.002], bare ground [F (2, 27) = 3.237, *P* = <0.05], herbs [F (2, 27) = 3.486, *P* = 0.045] and leaf litter [F (2, 27) = 55.12, *P* = <0.001]. Percentage moss cover between the sites was not significantly different. The vegetation in site C accounted for most of this variation (Table 6.8).

Table 6.8. Summary of ground cover data beneath release trees at the Wybunbury Moss release sites. Letters after values indicate results of *post-hoc* tests (LSD method following ANOVA). Values with same letters were not significantly different.

	Sward height (cm)	Moss (%)	Grass (%)	Bare ground (%)	Herbs (%)	Leaf litter (%)
Wybunbury Moss A	1.6 (± S.D. 0.5) a	90.9 (± S.D. 6.0) a	5.3 (± S.D. 2.6) a	0 a	4.6 (± S.D. 6.5) a	27.8 (± S.D. 19.9) a
Wybunbury Moss B	1.7 (± S.D. 0.5) a	86.0 (± S.D. 6.9) a	5.3 (± S.D. 3.0) a	0.3 (± S.D. 1.0) a	8.4 (± S.D. 8.6) a	14.1 (± S.D. 8.8) a
Wybunbury Moss C	0.4 (± S.D. 0.5) b	82.1 (± S.D. 24.5) a	1.1 (± S.D. 1.5) b	14.5 (± S.D. 25.2) b	1.3 (± S.D. 1.6) b	88.6 (± S.D. 8.4) b

A binary logistic regression (SPSS version 10.1) was used to determine the relative effects of the measured ground cover characteristics on the predation of released larvae. None of the measured ground cover variables were of significance (P = >0.4) in terms of predicting group membership of eaten and uneaten larvae.

6.4. Discussion

The proportion of released larvae recovered during the course of this study was very high compared to similar research focusing on the over-wintering of other insect larvae (Nicholls & Pullin, 2000). There are several reasons why not all the released larvae were recovered. Although many larval cases that were recovered exhibited evidence of predation, the larval cases that were not recovered may have been moved to a safe place by a predator. Small mammals have been shown to pick up a food item and carry it to a safe place before consuming it (Hanski, 1992). Other non-recovered larvae may have been out of the range of the detection equipment. This would be especially true for release sites where the ground was very uneven, with a lot of rabbit activity producing narrow, deep divots, which would make larval detection very difficult. It is also possible that non-recaptured larvae may have lost their metal tag, although, the recovery of a loose metal tag was interpreted as an artefact of predation. Recovery of released *Cryptocephalus decemmaculatus* larvae was lower than the recovery of *C. coryli* and *C. nitidulus* larvae. This may have been due to the inherent differences of the *C. decemmaculatus* site compared to the *C. coryli* and *C. nitidulus* sites. The Wybunbury site is very mossy site, and released larvae could descend up to 20cms through the moss to the peat surface.

The number of recovered *C. coryli* larvae appeared to be at its lowest during recapture 2. This would have been the coldest period during the study and suggests that the released larvae may seek out warmer micro-climates deeper in litter or in rabbit scrapes during the coldest months.

The observations made concerning predation provided insights into the mortality factors affecting over-wintering *Cryptocephalus* larvae. The only small mammal captured during the trapping exercise at the Laughton Forest site was the wood mouse (*Apodemus sylvaticus*). Wood mice are known to feed on insect larvae and pupae during the winter and early summer (Watts, 1968; Green, 1979; Hansson, 1985). The experiment undertaken here has shown that they will break through a *C. coryli* larval case to eat the bait within damaging the cases in the same way as predated larval cases that were recovered using the metal detector. Many more wood mice were caught in Area 1 than Area 2 or transects A and B. Area 1 is essentially dense birch scrub with a lot of low level cover, fallen timber and coppiced stools that would provide a lot of refuges for foraging and nesting wood mice (Wilson, 1992, Fitzgibbon, 1997). Area 2, in contrast, is a recently cleared area with a bare, homogenous ground cover. Wood mice seemed to be absent from this area. This could be due to the area being more open which would leave the mice vulnerable to predation and perhaps lead to their avoidance. Transects A and B were placed in locations bordering the two study areas. Transect B was very overgrown and appeared to represent good mouse habitat. The low number of mice encountered here may be as a result of too much ground cover that may impede movement over the ground. Predation of released *C. coryli* larvae in Area 2 was apparent but very low. Refuges in close proximity to this area may enable mice to forage in this area as long as cover is near by. It has been suggested in other studies that vertebrate predators of insect pre-pupae or pupae must be generalists (Tanhuanpaa. *et al,* 1999) as these immature insect stages are only available for a relatively short time compared to the length of the vertebrates life cycle.

Also, it has been suggested that vertebrate predators are responsible for most mortalities in post-diapause larvae (Duffey, 1968; Webb & Pullin, 1996) whilst invertebrate natural enemies are to blame for most mortality in pre-diapause larvae (Webb and Pullin, 1996). No direct evidence of invertebrate predation was observed, although these releases only concerned more mature larvae. Invertebrate predation may be partially responsible for the predation observed in released *C. decemmaculatus* larvae as this is the smallest and probably most vulnerable species of the three species studied. *Carabus* species are considered to rely on soft-bodied invertebrates (earthworms and slugs) for their food (Jung, 1940; Scherney, 1959a). A fully-grown *C. nitidulus* or a half grown *C. coryli* larvae would therefore appear to be protected inside its hard case from these predatory beetles.

Although not detected in this study, it is possible that Shrews could consume *Cryptocephalus* larvae, especially *C. decemmaculatus* at the Wybunbury site. Both the Water shrew (*Neomys fodiens*) and the Common shrew (*Sorex araneus*) are known from this site (T. Coleshaw, pers. comm.; Pers. obs.). Shrew species have been shown to regulate some insect herbivore populations (Buckner, 1969; Hanski, 1992). It is also possible that Bank voles (*Clethrionomys glareolus*) may be partially responsible for *Crypocephalus* larval predation in some areas as they have been shown to feed on insect larvae and pupae during the winter and early summer (Corbet & Harris, 1991).

Analysis of the numbers of dead larvae (other than those predated) that were recovered showed that only *Cryptocephalus nitidulus* showed any significant difference between the different types of release site. More dead *C. nitidulus* larvae were recovered from ‘A’ type release sites. These were sites where adult beetles were regularly found. The high level of larval death at these release sites may have been due to the lack of ground vegetation. Although the very sparse ground cover may reduce small mammal predation, larvae in these conditions may have been more vulnerable to harsh climatic conditions. The effect of adverse climatic conditions may be buffered by ground vegetation. A certain amount of ground cover will provide insulation from very cold conditions and refuge from very heavy rains that may result in larvae being displaced into unsuitable microhabitats, especially on the very steep escarpements of the White Downs. Vegetation may also buffer larvae against the detrimental effects of desiccation. Some of the dead larvae that were recovered exhibited fungal activity, however, there is no evidence to suggest that these fungi are pathogenic and they may simply be saprophytic.

During this study only recaptured *Cryptocephalus coryli* yielded information regarding microhabitat preferences. The observation of post diapause larvae seeking out patches of bare earth into which they partially bury themselves suggests that they are facilitating their escape, as adults, from the larval case. The posterior part of the case remains unburied and the eclosed adult within chews a cap from the case and escapes. Only circumstantial evidence is available to support the idea that this behaviour may make this stage of the beetle more vulnerable to predation. It is interesting to note that many of the recovered cases of predated, fully developed larvae exhibited damage to the posterior end of the case, which is the part of the case above the ground surface and therefore possibly more vulnerable to predators. However, it may simply be the case that the larva is more easily extracted by the predator from this end of the case. Further work would be needed to investigate this. Only very few mature, sealed *Cryptocephalus decemmaculatus* and *C. nitidulus* larvae were recovered. In the case of *C. decemmaculatus* this may be due to the difficulty in recapturing them. Due to this small sample size it is difficult to define the habitat preferences of mature larvae of these two species. The few sealed *C. nitidulus* cases that were recaptured were found on the ground surface, there was no evidence of burrowing. 'A' type sites for the release of *C. nitidulus* larvae had many narrow fissures in the soil which were wide enough to accommodate fully grown *C. nitidulus* larvae, therefore it is a possibility that mature larvae may seek refuge in such microhabitats.

Very little movement of larvae was seen during the study and this could be due to inactivity induced by the cold weather. Later instars larvae may also be more sedentary than early instars, especially first instar larvae. First instar larvae have been seen to be very mobile in captivity (Pers. obs.), but their dispersal ability in the wild remains to be seen. Monitoring young larvae would be technically difficult, but would surely yield some interesting results.

Another factor that could influence the over-wintering success of *Cryptocephalus* larvae would be flooding. This factor would be particularly relevant to *C. decemmaculatus* larvae. It was impossible to elucidate from this study if the larvae of this species sought drier refuges during the wetter months or are able to tolerate dry conditions. Damp conditions must be a pre-requisite for the survival of this species at a particular site. All known sites for this species, both historic and present are very wet (Stott, 1929; Allen 1960d; Allen 1970a). Other studies have shown that overwintering insect larvae can tolerate flooding and even submergence (LeJeune *et al*. 1955; Webb & Pullin, 1998). It is possible, however, that the presence of moss in areas which appear to be conducive to *C. decemmaculatus* survival limits flooding and submergence of larvae due to its absorbent qualities while maintaining high humidity. ‘C’ type release sites for this species exhibited the highest level of mortality other than predation. This mortality apparently seemed to be as a result of desiccation. These sites were generally drier with no moss beneath a tall dense canopy. This observation lends support to *C. decemmaculatus* requiring humid conditions.

Analysis of the ground cover variables in relation to larval predation showed that *Cryptocephalus coryli* larvae were more likely to be predated if there was less bare ground and leaf litter. Leaf litter coverage could be viewed as being very closely related to bare ground cover. A sward of vegetation may mean that fallen leaves never reach the soil and are more prone to being displaced by wind whilst balanced on the sward. Open ground will encourage a covering of leaf litter. Also, habitat with a high percentage cover of bare ground does not represent optimal foraging habitat for small mammals, i.e. *Apodemus sylvaticus* that have been shown to feed on *C. coryli* larvae. These habitats will be open, rendering the small mammals vulnerable to predation. The level of predation of *C. coryli* larvae was very low in Area 2 of the Laughton Forest site (Plate 31), which had a great deal of bare ground. The interaction between ground cover characteristics, larval predation and mammal activity is reflected in *Cryptocephalus nitidulus*. Larvae of this species were more likely to be predated in release sites with a taller sward. A tall sward would again provide small mammals with cover. *C. nitidulus* no longer exists in Stainton’s field of Headley Warren, where a tall sward of *Brachypodium sylvaticum* has developed. The *C. nitidulus* population in the neighbouring Downs field where the sward is very short is strong: anecdotal evidence that sward height is a crucial factor in the suitability of a particular site for *C. nitidulus*. The evidence suggests that *C. coryli* adults oviposit in areas that are not optimal for larval development. *C. coryli* and *C. nitidulus* share very similar habitat requirements as larvae, however, the larval habitat of *Cryptocephalus decemmaculatus* is very different. There was no obvious link between the measured ground cover variables and the levels of predation at different release sites. *Cryptocephalus decemmaculatus* larvae were as likely to be predated in areas that adults never occurred in, i.e. dense woodland, than in areas where adults regularly occurred. This may be because the full spectrum of habitats in the inner portion of Wybunbury Moss is relatively homogenous in terms of ground cover characteristics. This suggests that wherever females oviposit the chances of the developing larvae being eaten are approximately equal. Moss at the site was ubiquitous and it may be this is crucial for larval development.

Habitat types currently used by *Cryptocephalus coryli* appear to be sub-optimal for larvae, suggesting that female oviposition preference is in conflict with optimal larval performance. The *naïve adaptionist* hypothesis (Courtney & Kibota, 1990) argues that: “female phytophagous insects should oviposit where their offspring have the greatest probability of survival”. This hypothesis has been supported in some studies (Price, 1991; Ohgushi, 1995) but rejected in others (Thompson, 1988; Courtney & Kibota, 1990, Craig *et al.,* 2000). It appears that gravid *Cryptocephalus* females oviposit from host trees, which fulfil their habitat requirements, i.e. small trees in warm, sheltered areas. The female makes no selection of the discrete oviposition site; the eggs are simply dropped onto the ground from the host plant. This behaviour can be in conflict with larval survival. Habitats that are optimal for adult survival can apparently be sub-optimal for the larvae. The areas into which the eggs are oviposited may be very good habitat for predators, as is shown in the contrasting predation seen in the *C. coryli* release sites, Laughton Forest Area 1 and Area 2. Extant populations of the three *Cryptocephalus* species studied here suggest that the long term survival of populations may be dependant on the coincidental occurrence of suitable host trees on ground suitable for larval development. The problems that this coincidental arrangement produces for the long-term survival of these rare *Cryptocephalus* species is compounded by the very nature of the habitat on which they depend. All three species studied here depend on woody invasive species encroaching into suitably warm areas of heathland, downland or wetland. This very dynamic process may facilitate the coincidental occurrence of good adult habitat with good larval habitat. Without management, however, the progressing, suitable front of the scrub transition will produce a mosaic of habitats that offer differing levels of adult and larval suitability where the juxta-position of habitat suitable for adults and larvae is very rare indeed.

The goal of establishing new populations of these species may only be a success if recipient habitats can be found that optimally support both larvae and adults and can be managed in such a way to perpetuate the occurrence of good adult habitat and good larval habitat.

The results of this study also suggest that to establish a population of any of the *Cryptocephalus* species at a recipient site using larvae alone would require many more individuals than were used in this study. The combined effects of predation and other mortality factors result in a very small percentage of released larvae reaching adulthood. This could be partially overcome by rearing adults in captivity, it would still remain to be seen, however, if an introduction of adults reared from a small founder population could propagate itself. Reintroduction of the large copper butterfly to the UK in 1927 has entailed regular population re-enforcements up to the present. To date no re-establishment of this butterfly has resulted in a self-sustaining population (Webb & Pullin, 1996).

Captive rearing is, increasingly, being suggested as an invaluable tool for the conservation of endangered invertebrates with their re-introduction as the ultimate goal. (Pyle, 1988; Morton, 1991; Pearce-Kelly, 1994; Pearce-Kelly *et al.*, 1998). The field of captive breeding is a contentious area with widely differing views regarding the gravity of inbreeding as a result of captive rearing from a small number of founders. Many authors regard inbreeding as a serious hazard (Frankham, 1995a; Snyder *et al.*, 1996) whereas others suggest that inbreeding can remove lethal genes that would otherwise persist in the population (Templeton & Read, 1983, 1984; Pray & Goodnight, 1995). Captive breeding in preparation for an introduction can also lead to the species in question becoming less genetically variable and characteristics may be selected for that are related to their tolerance of confined spaces. This phenomena has been documented in a wide range of taxa (Frankham, 1995; Latter & Mulley, 1995; Lachance & Mangan, 1990; Ralls & Ballou, 1986). Recent studies suggest that if fitness is to be maintained in the captive environment then large individual populations should be maintained or migration between smaller populations should be sustained. Thirdly, individuals should be selected that prosper under inbreeding (Backus, 1995; Bryant, *et al.,* 2000). Alternatively, if the goal is to maintain current fitness as well as genetic variability for future adaptability then captive populations of a large size should be maintained (Bryant, *et al.,* 2000).

To enhance the success of introductions or augment present populations of the *Cryptocephalus* species studied here measures may be needed to control the predation by small mammals. An alternative to controlling predation would be to release larvae in prepared areas that are suitable for adult beetles, but also suitable for larval development because small mammal activity is minimal. The average density of the only small mammal recorded in this study (*Apodemus sylvaticus*) is seven individuals per hectare (Montgomery, 1989). After a good autumn seed crop, however, this density can be as high as 200 per hectare (Harris, *et al.*, 1995), but such a high density is unusual. An increase in the numbers of small mammals has also been shown to be associated with coppicing (Yalden, 1999). High small mammal densities following a seed rich autumn in areas that support any of these rare *Cryptocephalus* species could be severely damaging. Present populations are small and greatly sub-divided, rendering them acutely vulnerable to stochastic events such as a large increase in natural predator numbers.

Chapter 7. How limited is dispersal in ‘pot’ beetle species?

7.1. Introduction

Habitat management without prior knowledge of an animal’s ecology can lead to the local extinction of a species rather than its recovery (Ehrlich and Ehrlich 1981). Site management and the implementation of recovery plans for rare species, particularly rare insects, are often hampered by a lack of knowledge of the their ecology (Bedick *et al*., 1999). In particular, an understanding of their mobility and phenology is crucially important in the conservation of rare invertebrates, especially insects. Many insect species are relatively sedentary; a feature that predisposes them to local extinction even when the sub-division of their habitat is only minimal (Doak, 2000). This problem is compounded by the difficulty in finding many rare insects in any numbers in the field, which makes acquisition of information difficult (Britton *et al.,* 1994; New *et al*., 1995; Chapter 5).

Many insects rely on dynamic, early-successional habitats including woody invasive scrub. It appears counter-intuitive for these insects to be sedentary as they need to be able to disperse and populate new areas of suitable habitat as they become available, as any one habitat patch is only temporary. The opposite of this is true however, as several insect species that depend on dynamic habitats have been shown to be surprisingly sessile (Thomas, 1984; Thomas, 1991; Warren, 1987b). Two such species that depend on the dynamic scrub transition are *Cryptocephalus decemmaculatus* and *Cryptocephalus nitidulus*. These two leaf beetles are listed on the Biodiversity Action Plan with the status of Vulnerable and Endangered respectively (UKBG, 1999). Both species are known to occur in small numbers and *C. decemmaculatus* has only ever been known from a very small number of sites (Allen, 1960d; 1970a; Hyman & Parsons, 1992; Chapter 3).

In common with all species in the genus *Cryptocephalus, Cryptocephalus decemmaculatus* and *Cryptocephalus nitidulus* encase each egg in faeces as they are being laid (Erber, 1988). The eggs are then dropped from an oviposition perch onto the ground. The larvae carry this egg case with them and add to it with their faeces, forming a larval case that they eventually pupate inside. Larvae of the genus feed on leaf litter (Steinhausen, 1996).

Only anecdotal information is known about the mobility and population dynamics of *Cryptocephalus* species. This chapter describes field studies of wild populations of *C. decemmaculatus* and *C. nitidulus* and addresses the following questions: What is the size of extant populations? What is the mobility of the adult beetles? How isolated are any sub-populations? And what is the life expectancy and flight period of the adults? The answers are used to suggest steps that can be taken to safeguard the remaining populations of these species and aid the identification of sites that may be suitable for re-introductions.

7.2. Study Site

7.2.1. Cryptocephalus decemmaculatus

Data was collected at Wybunbury Moss (Cheshire, SJ6950) during the summers of 1999 and 2000. This bog is of a type represented by only two in England. Three sub-populations of *Cryptocephalus decemmaculatus* were identified at the site, occupying three discrete areas (A, B and C in Plate 25).

7.2.2. Cryptocephalus nitidulus

Data was collected from a small area on the White Downs (Surrey, TQ122492) where there is a strong sub-population of *Cryptocephalus nitidulus* (see Area A in Plate 22).

7.3. Materials and methods

7.3.1. Estimation of population sizes

Population size was estimated by marking and recapturing adult *Cryptocephalus decemmaculatus* and *C. nitidulus* along an irregular route through each site. Each captured adult was marked using typing correction fluid, which was found to adhere to the cuticle of the beetles more effectively than ink. After marking, each beetle was released immediately. The Lincoln index (Lincoln, 1930) was used to estimate the population size of the adults. The small sample sizes entailed the use of Bailey's correction (Bailey, 1952) to the simple index (the addition of one to the total individuals in the second sample and the total number of recaptures).

7.3.2. Adult movements

To assess the mobility of adult *Cryptocephalus decemmaculatus* and *Cryptocephalus nitidulus* every utilisable tree within each of the sub-population areas was marked with a numbered waterproof tape tag. These trees were then given X and Y co-ordinates by laying two 50m measuring tapes at right angles to one another to form axes. Adult beetles were exhaustively collected at dusk, when activity was minimal. The adults were marked (using typing correction fluid) and different codes were used for each of the sub-populations. The beetles were retained over-night in large storage boxes replete with food plants. In the early morning (2nd of June 2000 for *C. nitidulus* and 10th of June 2000 for *C. decemmaculatus*) these boxes were placed beneath three host trees that had been selected as the release sites at Wybunbury Moss and one tree on the White Downs. After four days the marked beetles were recaptured and then sex and location, (tree number) were recorded. The weather over both of the four day release periods was warm and dry. Recaptured beetles were retained until the whole study area had been searched and then released.

7.3.3. Life expectancy

Cryptocephalus decemmaculatus was the only species that could be found in large enough numbers over an extended period to enable their life expectancy to be studied. Successive marking events (four in total) were used to estimate the life expectancy of wild adult beetles. The Jolly-Seber method (Jolly, 1965) was used to calculate survivorship.

7.3.4. Flight Period

Cryptocephalus decemmaculatus was the only species found in large enough numbers to study its flight period in detail. The timing of the adult period and peak adult numbers were determined during transects, where adults were counted on standardised walks each time the site was visited (16 times over a period of two months).

7.4. Results

7.4.1. Estimation of population sizes.

During two years of study a total of 355 *Cryptocephalus decemmaculatus* beetles were marked at Wybunbury Moss. The recapture rate in Area A was less than the other two sub-populations in both years (Table 7.1), about half that in Areas B and C. Perhaps related to this, Area A was much larger than Areas B or C (area A ≈ 5100 m^2, Area B ≈1000 m^2 and Area C ≈ 1500 m^2). The proportion of recaptured females [47.7% (1999) and 43.3% (2000)] over the whole Cheshire site was lower than the proportion of recaptured males, although males were not significantly more catchable than females [χ^2 (d.f. 1) = 0.89, *P* =0.66 (1999); χ^2 (d.f. 1) = 0.59, *P* =0.56 (2000)].

Table 7.1. Recapture rates of marked *Cryptocephalus decemmaculatus* beetles during 1999 and 2000.

	No. marked (% recaptured)		
Year	**Area A**	**Area B**	**Area C**
1999	47 (17.0)	93 (44.1)	36 (33.3)
2000	38 (18.4)	99 (42.4)	42 (35.7)

Based on a corrected Lincoln Index, Area A had the largest estimated population size during both 1999 and 2000, although the estimate was smaller in 2000 than 1999 (Figure 7.1). The low recapture rate in this area nonetheless meant that the estimate had a high margin of error compared to the estimates in Areas B and C, and the results may not be an indication of a genuine decline. The population estimates for the smaller areas were very similar in both years at around 100 (Area B) and 75 (Area C) (Figure 7.1).

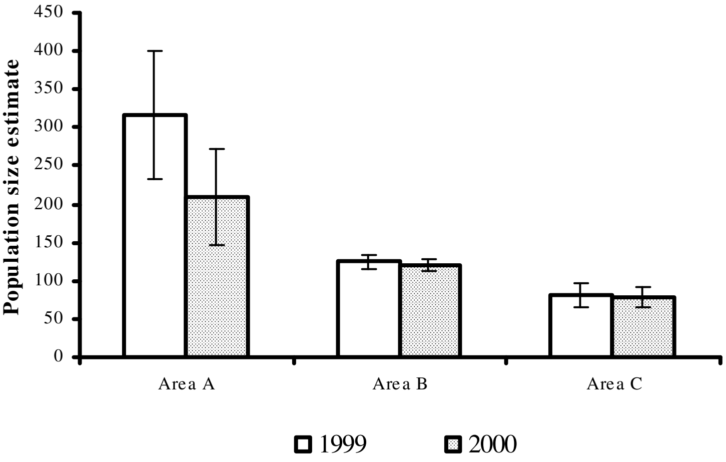

Figure 7.1. Estimates of the number of *Cryptocephalus decemmaculatus* adults in three Wybunbury Moss sub-populations during 1999 and 2000 (Mean ± S.E.)

Seventy-two *Cryptocephalus nitidulus* beetles were marked in the summer of 2000. The recapture rate in the study area was very low (4.2%), reducing the accuracy of the population estimate. Using the Lincoln index with Baileys correction it was estimated that the population size in the area studied (see Plate 22) was 666 ± S.E. 281 beetles.

7.4.2. Adult movements

The results obtained during the study show that the mean distance moved by both male and female *Cryptocephalus decemmaculatus* beetles is very small (Figure 7.2) reflecting the small patches of suitable habitats that they occupy.

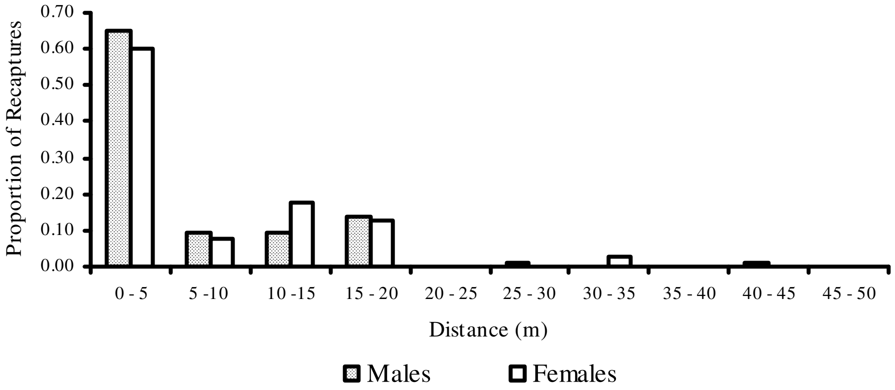

Figure 7.2. Distances moved by released *Cryptocephalus decemmaculatus* males and females as a proportion of the total captures of each sex (Areas A, B and C combined).

The greatest distance moved by an individual was 41.7m (a male in Area A). Two (6.7%); 35 (59.3%) and 15 (41.7%) adults from the Areas A, B and C were recaught on the release tree after a period of 4 days. The release *Salix cinerea* release tree in Area A was damaged during the late summer of 1999, apparently making it less attractive to adults. The sub-population in Area A resided in the habitat with the greatest utilisable area (5100m^2). Overall there was no significant difference in the median movements of males and females [males (n = 86), mean = 5.40 m ± S.D. 0.86 m, median = 1.31 m; females (n = 39), mean = 6.60 m ± S.D. 1.27 m, median = 6.24m; Mann-Whitney Z = -1.09, P = 0.27].

Adult *Cryptocephalus decemmaculatus* beetles diffuse slowly through their habitat (Area A mean = 3.1 m per day ± S.D. 2.2 m; Area B mean = 0.3 m per day ± S.D. 0.6 m; Area C mean = 1.9 m per day ± S.D. 2.1m per day). The suitable tree density in Areas A, B and C were 0.03 per m^2, 0.07 per m^2 and 0.04 per m^2 respectively. The rate of diffusion may have also been greater than in nature because of release and disturbance effects. The high tree density in Area B together with the small size of this area may explain the slow diffusion of adults. Longer flights may be very rare as the adults frequently encounter suitable plants in a very small patch that is surrounded by tall vegetation. Twenty adults (nine males and eleven females) were followed during the summer of 2000. These flights were all short (mean = 3.9 m ± S.D. 2.5 m) and erratic using suitable trees as ‘stepping-stones’. Adults observed around focal trees made short flights to different parts of the same tree. Adults take off steeply then fly rapidly towards the ground until they are intercepted by another tree. The probability of finding a marked adult on a *Salix cinerea* host tree decreased with increasing distance (Figure 7..3 and 7.4). No host-trees were located between 20 and 30 metres from the release tree in any of the three areas (Figures 7.3, 7.5, 7.6 and 7.7). The host-trees more than 30 metres away from the release tree (Area A only) were not colonised (Figure 7.5). In Area A the highest proportion of recaptures on *S. cinerea* were made on trees in the 10-15 m distance class (11.7%). In the other two areas the vast majority of the adults were recaptured on the release *S. cinerea* trees (Area B = 59.3%; Area C = 41.7%). The damaged *S. cinerea* release tree in Area A may have forced the adults to diffuse from the release tree to a greater extent than what was seen in Areas B and C. All the suitable *S. cinerea* trees in Area B were within a five metre radius of the release tree making it difficult to appreciate a diffusion effect a.

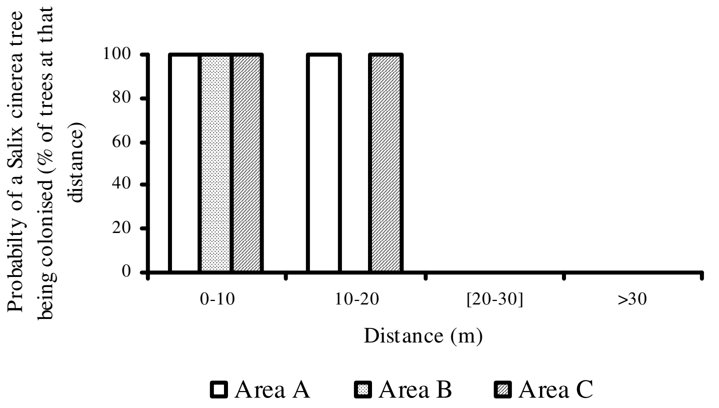

Figure 8.3. Colonisation of *Salix cinerea* trees with increasing distance from a release tree. No trees were available between 20 and 30 m.

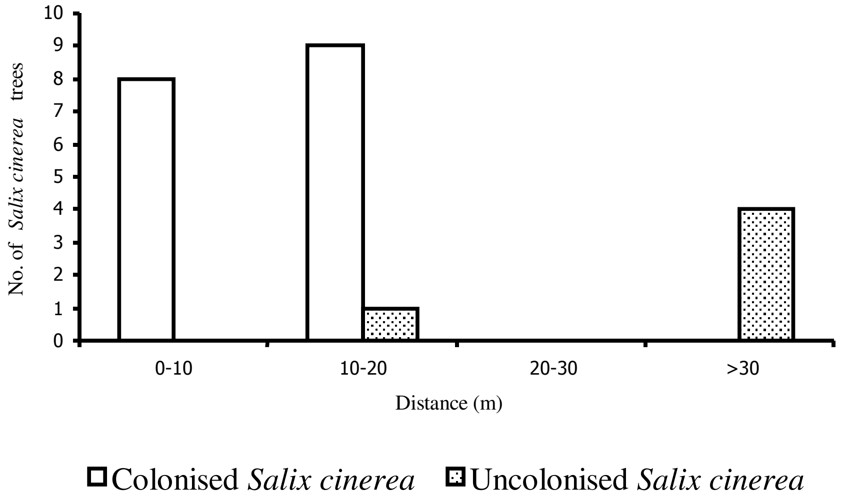

Figure 7.4. *Salix cinerea* trees colonised and not colonised by *Cryptocephalus decemmaculatus* adults in four distance classes (Areas A, B and C combined).

Adults appear to be attracted to or accumulate on suitable host trees (Figure 7.7) The relatively large distance (≈30 m) between the uncolonised *S. cinerea* trees and the release tree in area A may have impeded the attraction of the adults. In Area A no suitable *S. cinerea* trees were colonised during the four day release period if they were more than 20 m away from the release point. Taken with later figures (Figure 7.6 and 7.7) this evidence suggests that *C. decemmaculatus* adults are efficient colonisers over 10 m or so. The majority of adults in Areas B and C remained within fairly discrete pockets, on or very close to the release tree (Figure 7.6 and 7.7). All except one of the suitable *S. cinerea* trees available in Areas B and C were colonised (Figure 7.6 and 7.7). Thirteen of the adults released (36.1%) in Area C located the group of six *S. cinerea* trees 15-20 m to the north-west of the release tree (Figure 7.7). Whether the ability of adults to locate host patches is due to conspecifics being present or volatile chemicals produced by the host-plant remains to be tested. Small belts of unsuitable vegetation (tall trees or habitat lacking scrub) between the three areas appeared to act as complete barriers to mobility. This is the probable reason why three discrete sub-populations exist on the Cheshire site. Approximately 100m separate Areas A, B and C, but over two years of study no interchange was recorded between these areas.

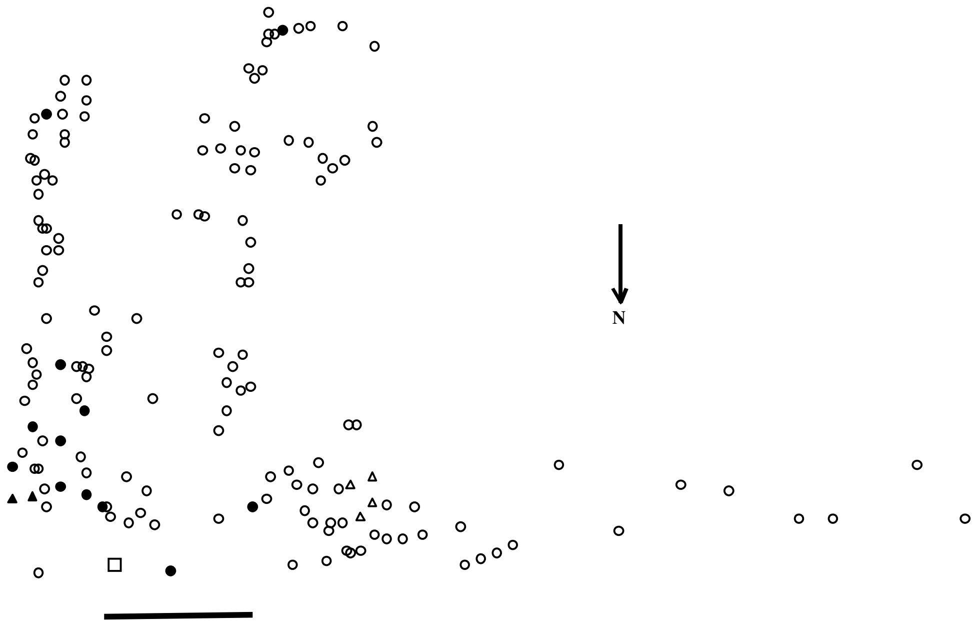

Figure 7.5. Movements of released *Cryptocephalus decemmaculatus* adults in Area A of Wybunbury Moss (Over a 4 day period in June 2000). Open square = Release tree; Filled triangle = *Salix cinerea* tree with recaptures; Open triangle = *Salix cinerea* tree with no recaptures; Filled circle = *Betula pubescens* tree with recaptures; Open circle = *Betula pubescens* tree with no recaptures; Scale bar = 20 m. *n* released = 76 (49 males, 27 females); *n* recaptured = 28 (15 males, 13 females).

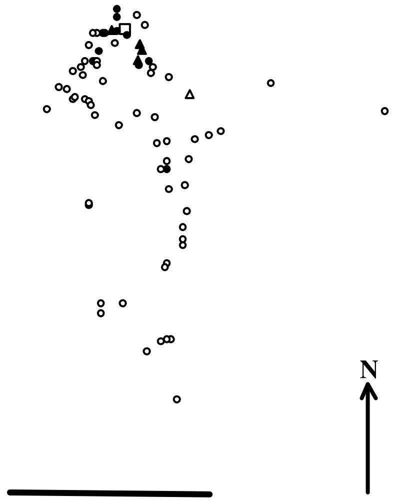

Figure 7.6. Movements of released *Cryptocephalus decemmaculatus* adults in Area B of Wybunbury Moss (Over a 4 day period in June 2000). Open square = Release tree; Filled triangle = *Salix cinerea* tree with recaptures; Open triangle = *Salix cinerea* tree with no recaptures; Filled circle = *Betula pubescens* tree with recaptures; Open circle = *Betula pubescens* tree with no recaptures; Scale bar = 20 m. *n* released = 118 (69 males, 49 females); *n* recaptured = 28 (36 males, 23 females).

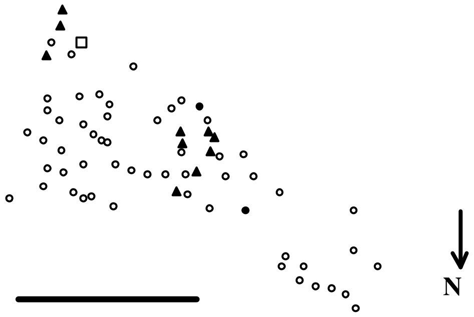

Figure 7.7. Movements of released *Cryptocephalus decemmaculatus* adults in Area C of Wybunbury Moss (Over a 4 day period in June 2000). Open square = Release tree; Filled triangle = *Salix cinerea* tree with recaptures; Filled circle = *Betula pubescens* tree with recaptures; Open circle = *Betula pubescens* tree with no recaptures; Scale bar = 20 m. *n* released = 78 (60 males, 18 females); *n* recaptured = 28 (26 males, 2 females).

Very few marked *Cryptocephalus nitidulus* adults were recaught. Dispersal among these recaught adults was not great with no marked adults being found much more than 10 m away from the release tree (Figure 7.8).

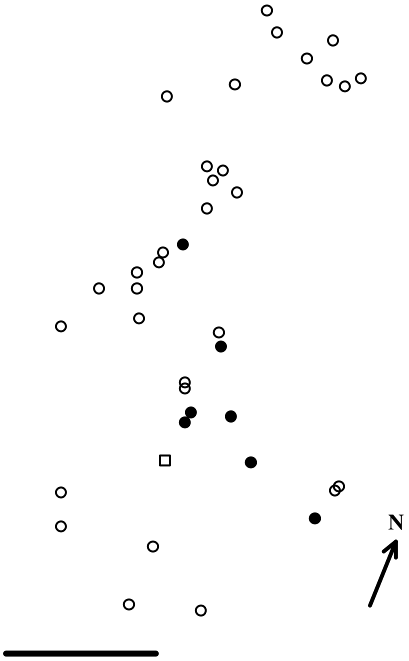

Figure 7.8. Location of *Betula pendula* trees in a *Cryptocephalus nitidulus* sub-population and movements of released individuals. (Scale bar = 10 metres). Open square = release *B. pendula* tree, filled circle = *B. pendula* tree with recaptures, open circle = *B. pendula* tree with no recaptures. *n* released = 72 (49 males; 23 females); *n* recaptured = 7 (5 males, 2 females).

7.4.3. Life expectancy

Adult *Cryptocephalus decemmaculatus* beetles were shown to be relatively long lived (Figure 7.9) using life expectancy estimates taken from mark release recapture survivorship data. The life expectancy of adult males and females appears to be approximately equal (Figure 7.9).

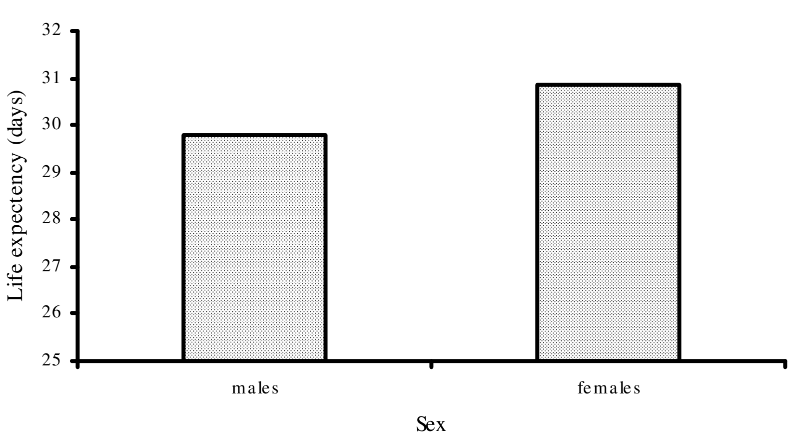

Figure 7.9. Life expectancy of male and female *Cryptocephalus decemmaculatus* estimated from mark release recapture experiments.

7.4.4. Flight Period

In Areas A and C of Wybunbury Moss *Cryptocephalus decemmaculatus* adults emerged two weeks earlier (mid-May) than the adults in Area B (early June) (Table 7.2). The peak number of adults was observed at approximately the same time in all three areas (mid-June). Adults could be found until the beginning of August.

The earliest and latest dates that *C. nitidulus* was recorded were the 15th of May 2000 and the 9th of August 2000 respectively, but numbers were too small for any more detailed patterns to be observed.

Table 7.2. The flight period of *Cryptocephalus decemmaculatus* in three areas within Wybunbury Moss.

Visit	Date	Adults Observed		
		Area A	Area B	Area C
1	08-May-00	0	0	0
2	09-May-00	0	0	0
3	10-May-00	0	0	0
4	22-May-00	28	0	5
5	24-May-00	32	0	8
6	01-Jun-00	36	48	16
7	02-Jun-00	36	52	18
8	03-Jun-00	40	60	19
9	11-Jun-00	54	83	21
10	15-Jun-00	46	99	22
11	16-Jun-00	33	58	31
12	17-Jun-00	33	54	42
13	24-Jun-00	24	43	29
14	04-Jul-00	20	37	27
15	05-Jul-00	18	11	21
16	12-Jul-00	14	4	15

7.5. Discussion

It was estimated that Wybunbury Moss supported a minimum of 460 *Cryptocephalus decemmaculatus* adults in 1999. The estimate for Area A in 2000 was smaller than 1999. This area was subject to the most intense study during 1999 and it is a possibility that trampling may have been detrimental to developing larvae or that disturbance was important. Detrimental management was also carried out in Area A during the late summer of 1999 that may have been responsible for this reduced population estimate (see Chapter 7). The relatively small area and the short host plants enabled a high proportion of adults to be recaptured in Areas B and C. The three areas that support a sub-population of *Cryptocephalus decemmaculatus* at Wybunbury Moss and the spatial arrangement of these *C. decemmaculatus* sub-populations could be best described as a non-equilibrium metapopulation, where local populations are effectively isolated from one another (Harrison, 1991). From the evidence it seems that the colonization of suitable habitat patches by *C. decemmaculatus* is very slow. Each sub-population must be regarded as an isolated unit. Many other invertebrates have been shown to fit this description (Stewart and Hutchings, 1996).

The population estimate obtained for *C. nitidulus* in one small area on the White Downs was large, although, due to the low number of recaptures the estimate has a large margin of error. The studied population is one of at least seven that are found along about 2 kms of the White Downs. Each population is separated from the next by large tracts of mature woodland or areas of scrubless habitat. The low recapture rate of *C. nitidulus* adults was probably due to the fact that utilised habitat is composed of many tall *Betula pendula* trees. Sampling the upper parts of these trees for marked adults is very difficult.

Investigation of the movement of *Cryptocephalus decemmaculatus* and *Cryptocephalus nitidulus* shows that these beetles are rather sedentary. Both species depend on a mid-successional habitat. Such habitat will have a very short life span (T. Coleshaw, pers. comm., J. Cranham, pers. comm). Good dispersal ability would appear to be a prerequisite for species inhabiting this type of habitat. However, the converse of this seems to be true (Thomas, 1984; Thomas, 1991; Warren, 1987b). The sub-populations of *C. decemmaculatus* at the Cheshire site exhibited no signs of interchange. Tall trees and areas of scrubless habitat seem to act as a barrier to the free movement of the adults. They are constrained within the pockets of suitable habitat where they are presently found, although their ability to locate the primary host-plant (*Salix cinerea*) within these small areas is efficient. If movement between the sub-populations does occur it will be dependent on one or more of the following factors: (i) the distance between the source and sink site; (ii) the vegetation structure between the source and sink site; (iii) the amount of sunny, warm weather during the flight period which could encourage a greater amount of movement. The sub-populations of *C. nitidulus* along the White Downs are probably also isolated from one another due, in some cases, to separation by relatively small areas of scrubless habitat.

Recaptures of marked *Cryptocephalus decemmaculatus* adults also showed that the females were not significantly more mobile than the males. Some female butterflies have been shown to become more mobile with age (Warren, 1987b; Murphy, *et al.*, 1983). Further investigation may reveal that *C. decemmaculatus* females also become more mobile with age. The reason for this in butterflies is that as the egg load reduces flying becomes easier. There may also be a greater impetus for the female to leave the core of the discrete sub-population due to the fact that males will attempt to mate with her during the process of oviposition. This will disturb the female and prolong oviposition, thus, reducing her reproductive capabilities. Movement away from the core of the habitat may reduce the chances of a mated female being disturbed by males. The flight period observations that were made during the two field seasons of study also suggest that newly emerged adults (teneral adults) exhibit a period of voracious feeding in common with other chrysomelids. In other chrysomelids the teneral stage is followed by a pre-ovipositional dispersal stage and a sedentary stage where the adults continue to feed, mate and oviposit. (Herzig & Root, 1996). Due to the apparently poor dispersal ability of *C. decemmaculatus* the second stage in the sequence is hard to detect. Beetles in the very small Area B exhibited a large peak in adults and a rapid decline. This observation may represent the pre-ovipositional dispersal stage away from the natal site. It has been shown in other chrysomelids that not all the adults will engage in dispersal flights (Herzig, 1995) and in the case of *C. decemmaculatus* it could be these individuals, which drop their eggs onto suitable ground where generations of larvae have developed. Individuals that disperse away from the natal site may oviposit above ground that is completely unsuitable for the larvae, even if they find anywhere with conditions that stimulate oviposition. These adults may have been effectively lost from the sub-population as no interchange was observed between the three areas was observed. Teneral *C. nitidulus* adults were also seen in large numbers in the early summer of 2000 for a very short period, after which time only very few adults were seen. This observation also suggests that *C. nitidulus* adults show a similar pattern of dispersal over time, but they may be stronger fliers than *C. decemmaculatus.* More research is needed on this species to define how far it is capable of moving during its dispersal stage.

The movement of these species may also be strongly influenced by the presence of conspecifics and volatile compounds that are given off by the primary host plants (*Salix cinerea* and *Betula pendula*). *Leptinotarsa decemlineata* adults are attracted to their host plants due to the volatile chemicals that are given off (Hare, 1990). The chrysomelid *Galerucella calamariensis* has been shown to be only able to detect host patches if they are less than 50 metres away (Grevstad & Herzig, 1997). The presence of conspecifics already present on a patch strongly induces others to colonize (Grevstad & Herzig, 1997). *G. calamariensis* has been shown to be able to fly 850 m, but high mortalities are associated with flights of this magnitude, therefore, they occur rarely (Grevstad & Herzig, 1997). It is possible that *C. decemmaculatus* also make long flights (very rarely) but the lack of suitable habitat patches in the surrounding agricultural landscape presents no focal points for the beetles and subsequent survey for migrants. The evidence here suggests that *C. decemmaculatus* adults move through their habitat, primarily, via random diffusion. Below a threshold distance and depending on prevailing winds the beetles may be attracted to conspecifics and suitable host-plants. Further study should focus on defining the mechanisms by which *C. decemmaculatus* adults move through their habitat.

Variation in the date of the peak *Cryptocephalus decemmaculat*us flight period is only very slight and this may be an artefact of the small sample sizes. The peak in the flight period is probably dependent on the weather during April and May. Immature stages of *Cryptocephalus* beetles have been shown to overwinter as larvae (Steinhausen, 1996; Chapters 3 and 6). Pupation then takes place in the spring. Low sunshine levels and air temperatures in the spring months have been shown to slow larval development and delay adult emergence in Lepidoptera (Warren, 1987a).

The very limited dispersal ability of *C. decemmaculatus* and *C. nitidulus* is compounded by the fact that ideal trees for *Cryptocephalus* adults need to have a clear south facing aspect and shelter from the wind. A complex ecotone with scrub invading wetland/grassland with many discrete ‘pockets’ where temperatures may be significantly higher than around exposed trees (Greatorex-Davis and Marrs, 1990) is required. An ovipositing female *Cryptocephalus* makes no obvious selection of where her eggs will be dropped. Apparent disappearance of mature *C. decemmaculatus* and *C. nitidulus* adults from focal trees suggests that females that disperse away from the natal site will be leaving an area that has been successfully used for many generations due to the juxta-position of suitable adult and larval habitat. It could be reasoned that teneral adults which have developed as larvae in an optimal habitat are found on the tree that their mother oviposited from. Successive generations of beetle will develop beneath the tree and lay some of their eggs from its branches. Consequently, the integrity of the population of this beetle at any one site may be dependent on an extremely limited number of bushes that provide optimal conditions for the adults and larvae.

The fragmentation of habitats is suggested to be one of the major causes for species extinction (Morris, 1995). The remaining populations of *Cryptocephalus decemmaculatus* and *C. nitidulus* have probably been isolated for a very long time. All the current sites of the two species are areas where habitat management is routinely carried out and it has often been the case where management aimed at the conservation of a species has led to its extinction (Ehrlich and Ehrlich, 1981). The information in this chapter on the population sizes of *C. decemmaculatus* and *C. nitidulus* together with the ways in which adult beetles of both species move through utilised habitat provides valuable information for the conservation of these species. The preservation and enhancement of these species at their last known sites can be assisted by: (i) altering the structure of the vegetation between the sub-populations by providing ‘stepping stones’ of bushes in suitable microclimatic conditions; (ii) maintaining the presence of a complex scrub where the sub-populations are presently found, but halting scrub maturation; (iii) planting and maintenance of host trees between sub-populations to provide artificially positioned host plants to facilitate movement between sub-populations. The above proposals take into account the needs of the adults, but any management carried out should be undertaken with equal consideration for the requirements of larvae.

Chapter 8. *Cryptocephalus* 'pot' beetle sub-populations: geographically close but genetically far.

8.1. Introduction

Determining the extent of genetic differentiation among extant populations is a fundamental facet of conserving rare species. Conservation programs are conducted at the population level (Goldstein *et al.,* 2000) and it is often the assumption that these populations must be diagnosibly distinct for protection to be justified (Goldstein *et al.,* 2000). The analysis of intraspecific genetic variation in a rare species may lead to the identification of genetically distinct extant populations (Richter *et al*., 1994; Travis *et al*., 1996). This genetic distinctiveness implies limited gene flow between populations and possible reproductive isolation (Soltis & Gitzendammer, 1999). Molecular systematics allows, in part, the identification of evolutionary significant units (Ryder 1986**;** Woodruff, 1989; Amato, 1990; Vogler & DeSalle, 1994). An evolutionary significant unit (ESU) is a population unit that merits separate management and has a high priority for conservation (Ryder, 1986). Recognition of these ESUs enables conservation efforts to be concentrated on populations that may be in need of special protection, and also allows the formulation of management strategies that are tailored for particular populations or groups of populations (Moritz, 1994; Haig, 1998; Soltis & Gitzendammer, 1999; Johnson, 2000).

An understanding of the genetic differentiation within rare species is also important if re-introductions are to be attempted. The mixing of individuals from a divergent population with another population could result in the adaptive potential and unique evolutionary trajectory of the sink population being impaired. These translocations could result in Introgression and its associated homogenising effects (Johnson & Jordan, 2000). Many of the rare insects on the Biodiversity Action Plan (BAP) will need to be introduced to sites in order to meet the plan objectives. No re-introductions should be carried out in the absence of studies to identify divergent populations.

In this study intra-specific divergence in eight species of *Cryptocephalus* Muller (Chrysomelidae) beetle were examined. The genus has some 1500 species worldwide (Erber, 1988) and 19 of these are found in the UK. Three of the species in this study are listed on the UK Biodiversity Action Plan (UKBG, 1999). *C. coryli* and *C. nitidulus* are classed as endangered and *C. decemmaculatus* is vulnerable (Hyman & Parsons, 1992). *C. coryli* and *C. nitidulus* have shown a large decline in the UK over the past 50 years (Figures 8.1and 8.3) (all distribution data from M. Cox, pers. comm.) (Hyman & Parsons, 1992). *C. decemmaculatus* has also exhibited a decline (Figure 8.2) but has never been a widespread species (Allen, 1970a; Stott, 1929). The BAP targets for the three species above all include re-introductions as a means of establishing populations in the historic range of each. Typically, five populations have to be re-introduced by 2005. The other five species used in the study (*C. bipunctatus, C. hypochaeridis, C. labiatus, C. moraei,* and *C. parvulus*) are more widespread in the UK (Figures 8.4, - 8.8).

Figure 8.1. Past and present distribution of *Cryptocephalus coryli* (filled circles = extant populations; open circles = populations presumed extinct). All maps produced using DMAP (© Alan Morton).

Figure 8.2. Past and present distribution of *C. decemmaculatus* (filled circles = extant populations; open circles = populations presumed extinct).

Figure 8.3. Past and present distribution of *C. nitidulus* (filled circles = extant populations; open circles = populations presumed extinct).

Figure 8.4. Past and present distribution of *C. bipunctatus* (filled circles = extant populations; open circles = populations presumed extinct).

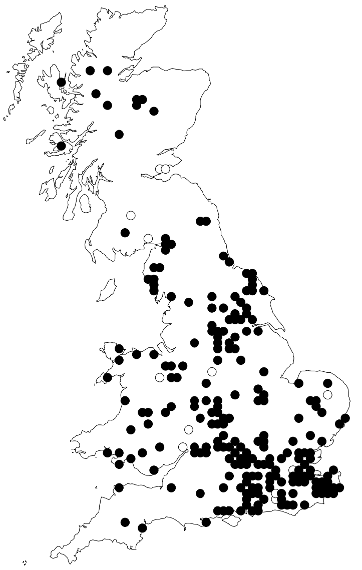

Figure 8.5. Past and present distribution of *C. labiatus* (filled circles = extant populations; open circles = populations presumed extinct).

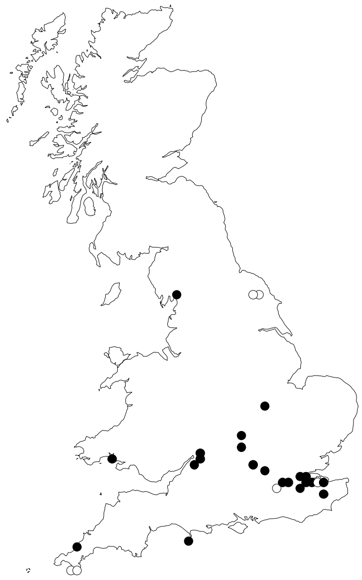

Figure 8.6. Past and present distribution of *C. hypochaeridis* (filled circles = extant populations; open circles = populations presumed extinct).

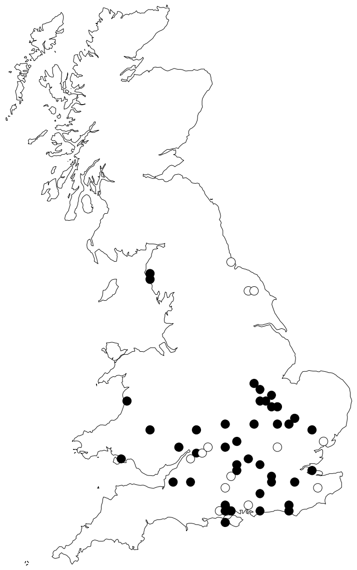

Figure 8.7. Past and present distribution of *C. moraei* (filled circles = extant populations; open circles = populations presumed extinct).

Figure 8.8. Past and present distribution of *C. parvulus* (filled circles = extant populations; open circles = populations presumed extinct).

All of the British species are widely distributed through the Western Palearctic and beyond (Warchalowski 1991). Of the above species all except *C. moraei* are essentially oligophagous. Host plants of the more catholic species include *Betula* spp*.*, *Corylus avellana* and *Crateagus monogyna*, *Hieracium* spp and *Helianthemum nummularium* while *C. moraei* only feeds on *Hypericum perforatum.*

The objective of our study was to examine the mtDNA variation between remaining disjunct populations of the three species of conservation concern (*Cryptocephalus coryli*, *C. nitidulus* and *C. decemmaculatus*). Comparisons were also made with the more widespread and common species. These exhibit a more continuous distribution, but were sampled from populations separated by, in most cases, distances similar to the rare species. Thus, we address the question is genetic distinctiveness within a species that exhibits a disjunct distribution similar to that observed within a more continuously distributed species? This comparison and sampling strategy enables inferences to be made regarding the processes that are responsible for any observed inter-population differences. Ecologically significant characters such as ecological requirements and demographic characteristics (Crandall *et al.*, 2000) are also considered as a compound means of identifying ESU's. Using this information in combination with genetic differences should allow informed recommendations to be made regarding the management and re-introduction of populations of the endangered and vulnerable *Cryptocephalus* species.

8.2. Materials and Methods

8.2.1. Field sampling

Adults, eggs or larvae of eight species of *Cryptocephalus* beetle were collected during June 2000 from several localities in England and Scotland (Figure 8.9 and Table 8.1).

Figure 8.9 Localities for collections of eight Cryptocephalus species (C. bip = Cryptocephalus bipunctatus; C. cor = C. coryli; C. dec = C. decemmaculatus; C. hyp = C. hypohaeridis; C. lab = C. labiatus; C. mor = C. moraei; C. nit = C. nitidulus and C. par = C. parvulus).

Table 8.1. Collecting sites of eight *Cryptocephalus* species.

Species	Collection sites	Grid Ref	Individuals sampled
C. coryli	Kirby Moor (Lincs.) A	TF234623	5
	Kirkby Moor (Lincs.) B	TF227636	5
	Headley Warren (Surrey) A	TQ190539	5
	Headley Warren (Surrey) B	TQ189540	5
C. decemmaculatus	Wybunbury Moss (Cheshire) A	SJ698502	5
	Wybunbury Moss (Cheshire) B	SJ696503	5
	Camghouran (Perthshire)	NN595563	5
C. nitidulus	White Downs (Surrey) A	TQ125496	5
	Headley Warren (Surrey) C	TQ193533	5
	Headley Warren (Surrey) A	TQ190539	3
C. bipunctatus	Stinchcombe Hill (Gloucs.) A	ST738981	3
	Stinchcombe Hill (Gloucs.) B	ST734986	3
	White Downs (Surrey) B	TQ116488	3
C. hypochaeridis	Ranmore Common (Surrey) A	TQ135500	3
	Ranmore Common (Surrey) B	TQ139505	3
	Rodborough Common (Gloucs.)	SO8402	3
C. labiatus	Wisley Common (Surrey)	TQ0658	3
	Wybunbury Moss (Cheshire) A	SJ698502	3
	Wybunbury Moss (Cheshire) B	SJ696503	3
C. moraei	White Downs (Surrey) C	TQ116488	3
	White Downs (Surrey) D	TQ114482	3
	Mokery Wood (Lincs.)	SK950185	3
C. parvulus	Lavington Common, (W. Sussex)	SU951192	3
	Wybunbury Moss (Cheshire) A	SJ698502	3
	Wybunbury Moss (Cheshire) B	SJ696503	3

Samples were collected in such a manner that intra-population, sub-population (i.e, specimens from discrete populations separated by only trivial distances) and inter-population differentiation could be assessed. The more common species were sampled from populations separated by distances comparable to the distances between the extant populations of the rare species. Unfortunately populations of a common *Cryptocephalus* species separated by distances similar to the distance between the sampled *C. decemmaculatus* populations were not located. Wherever possible eggs of *C. coryli*, *C. decemmaculatus* and *C. nitidulus* laid by gravid females held captive in the field were collected instead of adults to lessen the effect of sampling pressure on these sensitive populations. In these instances six-ten eggs were taken from five females from each site sampled. No siblings were used in the study. For the more common species adults were taken from each population. They were taken back to the laboratory alive and stored at –80°C before processing.

8.2.2. DNA extraction, PCR and sequencing.

DNA for subsequent amplification was extracted from an egg, adult head, thorax or legs. The DNA was extracted using standard protocols (Juan *et al.*, 1995). The mitochondrial cytochrome *b* gene was amplified using PCR. The total volume of the reaction mixtures was 25 µl. Amplification used the primers described by Simon *et al.,* (1994): CB-N-10920, 5’-TATGTTTACCTTGAGGACAAATATC- 3’ and N1-N-11841, 5’-ATCATAACGAAACCGAGGTAATGTACC- 3’. The PCR mix contained: 14.9 µl H_20, 2.5 µl *Taq* buffer, 3µl $MgCl_2$, 0.1µl (0.5 units) *Taq* polymerase, 0.25 µl dNTPs (20mM), 1.75µl (10pM/µl) of each primer, 0.25µl BSA and 2µl of template (*Taq* buffer, $MgCl_2$ and *Taq* polymerase all Promega). Temperature cycling was performed using a Biometra Trioblock. Cycling involved an initial denaturation of 92°C for 5 mins then 36 cycles of denaturation at 92°C for 1min, annealing at 50°C for 1 min 30 secs and extension at 72°C for 1 min 30 secs. A final elongation step of 72°C for 10 mins completed the DNA amplification. PCRs were checked by electrophoresis in 1% agarose gel containing ethidium bromide. The length of the amplified region was compared to the bands on a ‘100 base - pair ladder’ (Promega).

PCR products were purified using a clean up kit (Macherey – Nagel). The amplified regions were then sequenced using an automated sequencer (ABI 377 sequencer, Perkin Elmer, University of Oxford sequencing facility) with the amplification primer N1-N-11841.

8.2.3. Data analysis

93 cytochrome *b* sequences were obtained. These were edited in BioEdit (Hall, 1999) and then aligned using the Clustal W multiple alignment program (Thompson *et al.*, 1994 in BioEdit). DNA – DNA distance matrices were then produced (Felsenstein, 1993) to examine the level of genetic differentiation present. Each species was analysed separately so that inter-population, sub-population and intra-population differentiation could be examined. In order to assess the relationship of genetic differentiation with geographic distance linear distances were calculated

between the sampled sites of the eight species. Population genetic structure was analysed using an analysis of molecular variance (AMOVA in ARLEQUIN 2.0; Schneider *et al.*, 2000). The relationship between unique haplotypes was described using a minimum spanning network with the sequences as nodes of a tree instead of the terminal tips of a tree. Networks are useful when many of the sequences may be derived from the same ancestral genotype. The algorithm used was MINSPNET, a program within ARLEQUIN 2.0 (Schneider *et al.*, 2000).

8.3. Results

The mitochondrial cytochrome *b* sequences obtained (≈550 bp long) for the eight species of *Cryptocephalus* beetle yielded interesting intra-specific variation. This variation consisted of point mutations most of which were present in an intergenic spacer (27-36 bp long) between the end of the cytochrome *b* gene and the serine tRNA.

The open circles in Figures 8.10 to 8.18 represent individuals. Genetic differentiation between these individuals was high and all were separated by numerous substitutions. The branch lengths in the networks are proportional to the number of substitutions. The reason for these large differences is that the sequenced mitochondrial cytochrome *b* fragment encompassed a very variable intergenic spacer. Clear distinctions of sub-populations could be seen in most of the species, but there were exceptions. For example, the *Cryptocephalus nitidulus* population in the Flying Bomb Field of Headley Warren is more closely related to the population sampled on the White Downs than the other Headley Warren population in the Downs Field (Figure 8.11). The pattern of differentiation between the *Cryptocephalus coryli* populations suggests that the gene flow between the Kirby Moor and Ostler's plantation populations is extremely limited. Long branch lengths between geographically proximal populations suggest that the homogenizing effects of migration are non-existent or occur very rarely. For many of the species the branch lengths at the sub-population level were large, in some cases as large as the branch lengths at the inter-population level. Many of the species also exhibited abundant substitutions at the intra-population level suggesting that even at this scale gene flow is low. It is possible that the branch lengths observed in the widespread species may also be due to the small sample size. For the species with small sample sizes and long branch lengths at the intra-population level (*C. bipunctatus, C. hypochaeridis* and *C. parvulus*) it is possible that larger samples would have yielded closely linked haplotypic clusters like those seen in *C. decemmaculatus* (Figure 8.12), *C. labiatus* (Figure 8.15) and *C. moraei* (Figure 8.16).

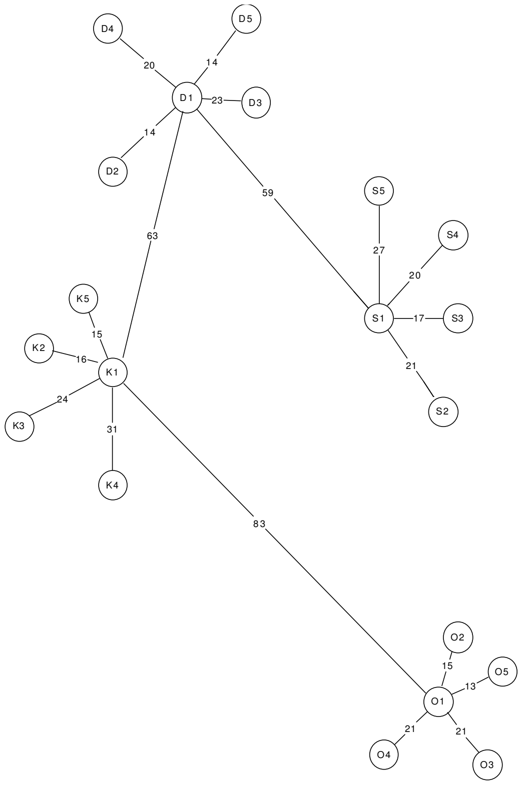

Figure 8.10. Minimum spanning haplotype network for *Cryptocephalus coryli*. D = Downs Field, S = Stainton's Field (both at Headley Warren, Surrey. K = Kirkby Moor Lake, O = Ostlers Plantation (both at Kirkby Moor, Lincs). Open circles = individuals, Branch values proportional to No. of substitutions.

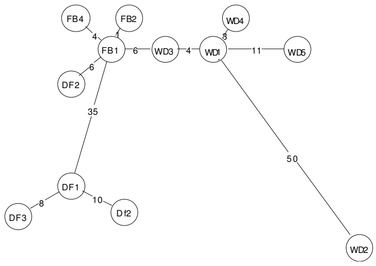

Figure 8.11. Minimum spanning haplotype network for *C. nitidulus*. FB = Flying Bomb Field, DF = Downs Field (both in Headley Warren, Surrey). WD = White Downs (Surrey).

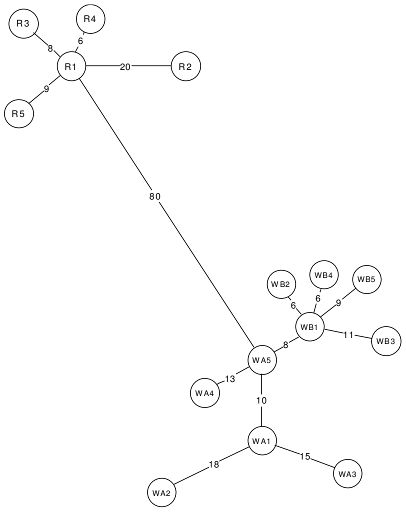

Figure. 8.12. Minimum spanning haplotype network for *C. decemmaculatus*. R = Camghouran, Perthshire. WA=Wybunbury Moss A, WB = Wybunbury Moss B (both in Cheshire)

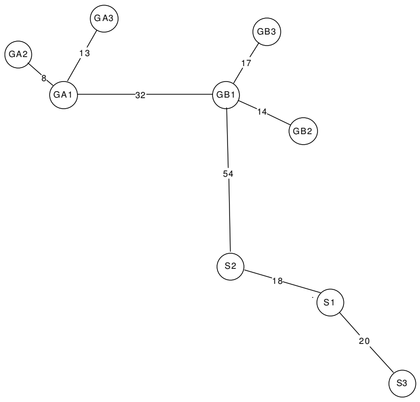

Figure 8.13. Minimum spanning haplotype network for *C. bipunctatus*. GA = Stinchcombe Hill A, GB = Stinchcombe Hill B (Both in Gloucs.). S = White Downs (Surrey).

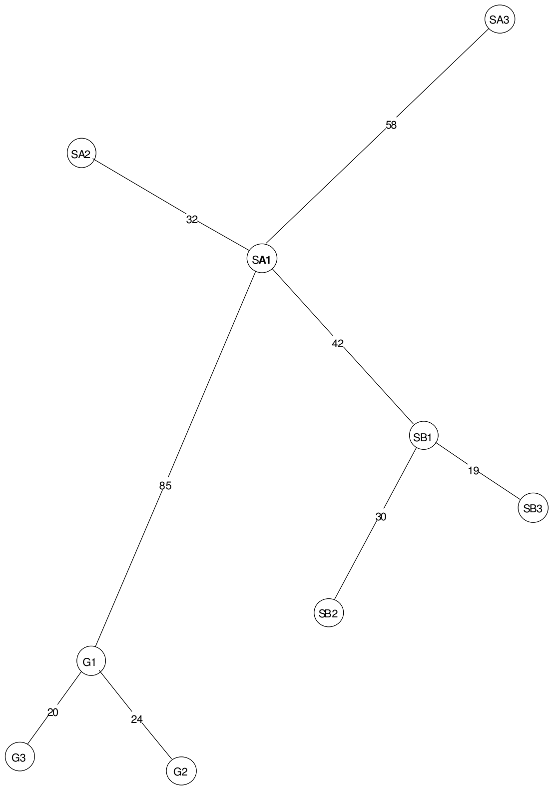

Figure 8.14. Minimum spanning haplotype network for *C. hypochaeridis*. SA = Ranmore Common A, SB = Ranmore Common B (both in Surrey). G = Rodborough Common (Gloucs.).

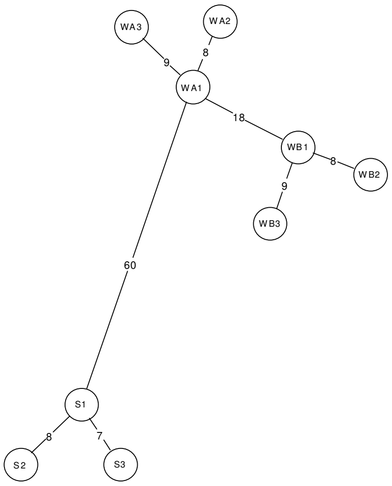

Figure 8.15. Minimum spanning haplotype network for *C. labiatus*. WA = Wybunbury Moss A, WB = Wybunbury Moss B (both in Cheshire). S = Wisley Common (Surrey).

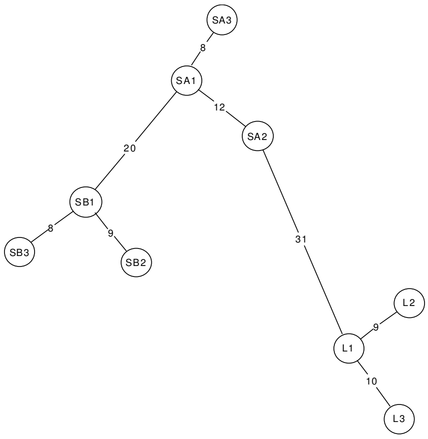

Figure 8.16. Minimum spanning haplotype network for *C. moraei*. SA= White Downs A, SB = White Downs B (both in Surrey). L = Mokery Wood (Lincs.)

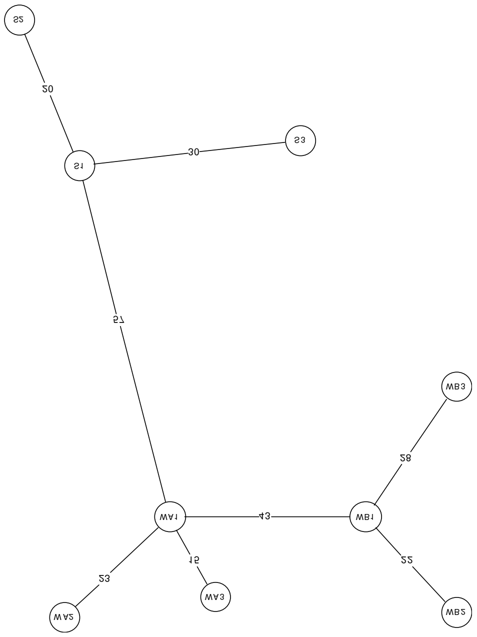

Figure 8.17. Minimum spanning haplotype network for *C. parvulus*. WA = Wybunbury Moss A, WB = Wybunbury Moss B (both in Cheshire). S = Lavington Common (W. Sussex).

Mean intra-population sequence divergence ranged from 1.1% to 3.2% (Figure 8.18). The lowest intra-population divergences were seen in *Cryptocephalus morae*i, *C. labiatus* and *C. parvulus*. The three species of conservation concern all had similar intra-population divergences. Inter-population divergence within all of the studied species, except in *C. labiatus* and *C. decemmaculatus* was almost as great as sub-population divergence. Sub-population divergence and inter-population divergence within *C. moraei* were also very similar to one another; but both were only marginally higher than intra-population divergence. The only other species with a similarly low level of sub-population divergence was *C. labiatus*. Apart from *C. moraei* and *C. decemmaculatus* the amount of inter-population divergence observed in this study was relatively consistent. The sampled populations of *C. decemmaculatus* exhibited a high level of divergence compared with that seen in the other species, but they were also separated by the greatest distance of any of the populations sampled in this study.

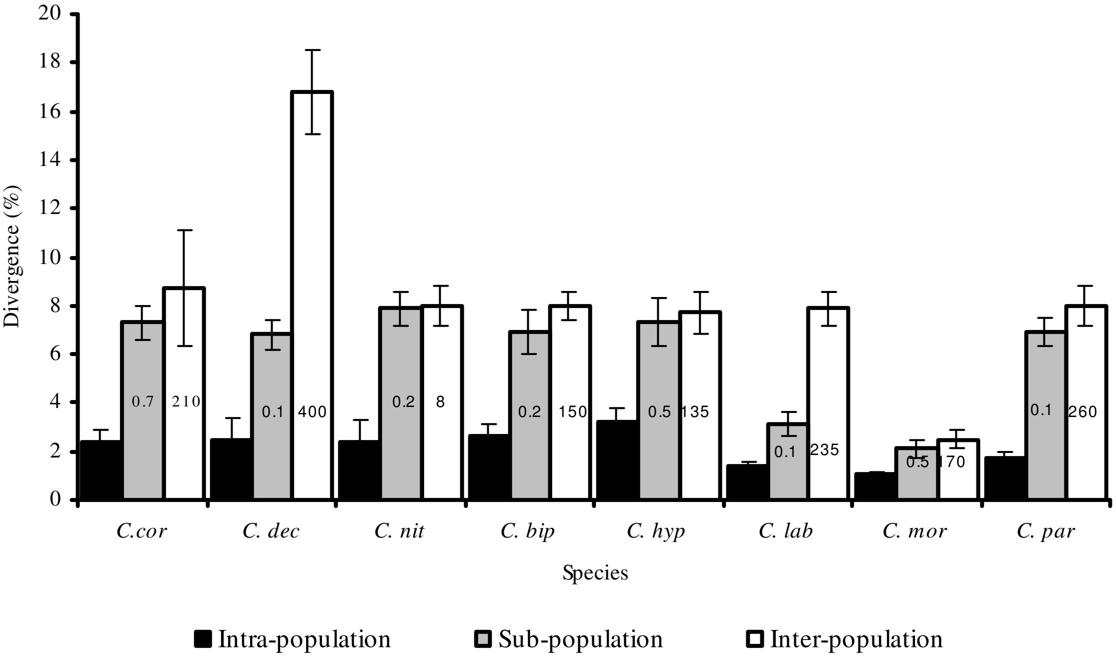

Figure 8.18. Intra population, sub-population and inter-population divergences in eight species of *Cryptocephalus* beetle (Mean ± S.D.). The first three species have few UK sites, the remaining species are more widespread. Values within columns = distances between sub-populations and inter-population geographic distances.

Of the total genetic diversity identified in *Cryptocephalus coryli* more than half (54.6 %) can be attributed to variation at the sub-population level (Table 8.2). Most variation (91.2%) observed within *C. nitidulus* was at the same level (Table 8.2). The negative value obtained for *C. nitidulus* reflects that this statistic is actually a covariance and negative values can occur when the actual values are close to zero. Most variation (71.9%) within *C. decemmaculatus* was seen at the inter-population level. With *C. bipunctatus* variation was similarly partitioned at the sub-population and intra-population levels (45.9 and 44.4% respectively). Variation within *C. hypochaeridis* was almost equally spread over the three levels. 62.8% of the variation observed within *C. labiatus* was attributable to the variation at the inter-population level, which was also the case for *C. moraei* (41.7%). Most variation within *C. parvulus* was attributable to the variation at the sub-population level.

Table 8.2. Results of the AMOVA analyses of each *Cryptocephalus* species.

Species1	Level	d.f.	Sums of Squares	Variance components	% variance
C. coryli	Inter -population	1	304.7	12.1	19.7
	Sub-population	2	366.9	33.5	54.6
	Intra-population	16	252.4	15.8	25.7
C. nitidulus	Inter -population	1	43.7	-6.7	-37.7
	Sub-population	1	69.5	16.3	91.2
	Intra-population	10	83.2	8.3	46.5
C. decemmaculatus	Inter -population	1	261.2	34.4	71.9
	Sub-population	1	31.9	4.6	9.7
	Intra-population	12	105.4	8.8	18.4
C. bipunctatus	Inter -population	1	101.4	4.4	9.7
	Sub-population	1	83.7	21.1	45.9
	Intra-population	6	122.3	20.4	44.4
C. hypochaeridis	Inter -population	1	166.4	21.2	34.5
	Sub-population	1	81.7	20.7	33.6
	Intra-population	6	118.0	19.7	32.0
C. labiatus	Inter -population	1	128.9	24.2	62.8
	Sub-population	1	32.2	8.9	23.1
	Intra-population	6	32.7	5.4	14.1
C. moraei	Inter -population	1	80.6	11.4	41.7
	Sub-population	1	35.2	9.6	35.4
	Intra-population	6	37.3	6.2	22.8
C. parvulus	Inter -population	1	97.4	5.2	9.9
	Sub-population	1	79.3	17.3	49.8
	Intra-population	6	101.3	23.6	40.3

8.4. Discussion

The levels of divergence encountered in the *Cryptocephalus* cytochrome *b* gene were of approximately the same magnitude as comparable mitochondrial genetic elements studied in other insect species (Vogler & DeSalle 1994; Vogler *et al.,* 1998; Diogo *et al.,* 1999*;* Gomez-Zurita *et al.,* 2000*;* Sperling *et al.,* 1999; Szalanski, 2000) and in very different taxa sampled from disjunct locations (Johnson & Jordan, 2000). Although many of these studies have made use of COI or COII, what comparative information does exist suggests that most of the protein coding regions of the mitochondrial genome perform equally well at resolving relationships at varying levels of acuity (Caterino *et al.* 2000).

The dispersal ability in *C. decemmaculatus* is extremely poor (see Chapter 7). Its Wybunbury Moss site contains three discrete populations that have shown no detectable interchange over two years of mark-release recapture studies. Some other insect species that exist in sub-divided habitats have also been shown to be rather sedentary (Arnold, 1983; Thomas, 1985; Warren, 1987b; Legge, 1996; Doak, 2000). It appears that species such as these are demographically isolated even when the barriers separating populations are nothing more than relatively small areas of unsuitable habitat (Doak 2000). Headley Warren, the site in Surrey that was sampled for *C. coryli* and *C. nitidulus* has four distinct Downland fields separated by bands of mature woodland, which can be up to 30 m thick and 20 m tall. *Cryptocephalus coryli* populations that are separated by apparently trivial distances exhibit considerable levels of sequence divergence. A distance of <1km between populations can be as effective at impeding gene flow as much greater distances (>200km). This implies that gene flow between geographically close populations may be very limited. Based on the genetic results and inferences made from *C. decemmaculatus* dispersal it seems as though *C. coryli*, at the Surrey site has four distinct populations. Other studies have shown that the males of a sedentary species are often far more vagile than the females. This means that populations may be demographically but not genetically separated (Doak, 2000). However, dispersal studies undertaken on *C. decemmaculatus* have shown there to be no significant difference between male and female dispersal ability (see Chapter 7). Sub-populations of *Cryptocephalus* beetles in sub-divided habitats may be demographically *and* genetically isolated.

A population should not be labelled as an ESU on the basis of molecular information alone. Populations of the saturnid moth; Cryan's *Hemileuca* were labelled as evolutionary significant units even though genetic differentiation between this and other *Hemileuca* species was not found (Legge, 1996). ESU status was applied on the basis of an ecological character, namely the host choice of Cryan's *Hemileuca*. A difference in an ecological character, such as life history traits, ecological requirements, morphologies or demographic characteristics may mean that two populations are not ecologically exchangeable (Crandall *et al.,* 2000). This exchangeablility must arise from shared fundamental properties of the populations in question (Templeton 1994). Of the *Crytocephalus* species studied here, inter-population ecological differences consist of subtle host plant and phenological differences. The former is most easily seen in *C. coryli* where adults have a choice of *Betula pendula*, *Corylus avellana* and *Crateagus monogyna* in the Surrey population, whereas adults of the Lincolnshire population only have the choice of *B. pendula* and *C. monogyna* plants (see Chapter 5). The differences between potential host availability among sites may result in underlying genetic changes initiating in divergence away from the ancestral genotype. Flight period differences can be seen between the disjunct populations of *C. decemmaculatus*. Eclosion of adults in the Scottish population takes place up to one month later than adults in the Cheshire population. This species also exhibits a melanic form (*C. decemmaculatus var. bothnicus*) that is found at frequencies of up to 50% at the Scottish site (I. Menzies, Pers. comm.) and less than 3% at the Cheshire site (Pers. obs.). This pattern of increased frequency of melanism with increasing latitude has been shown in other beetle species (de Jong *et al.*, 1998; Majerus & Zakharov, 2000). The dark surface of melanic morphs gives them a thermal advantage over non-melanics under conditions where (reproductive) activity is limited by the absorption of solar radiation (de Jong *et al.,* 1996). *C.*

bipunctatus also shows a clear ecological inter-population difference. Gloucestershire populations of this species feed on *H. nummularium* whereas the host plant of the Surrey populations is *B. pendula* or *C. avellana.*

It is hoped that with further work the reasons behind the disjunct distributions of the rare *Cryptocephalus* species will be understood. Comparative material from Scandinavia and northern France would have to be collected. Currently, two hypotheses exist to explain range contractions leading to the present distributions of rare species. The demographic hypothesis predicts that ranges should implode with final populations persisting near the centre(s) of the historical range (Brown 1995; Wolf *et al*., 1996; Mehlman, 1997). The crux of the contagion hypothesis is that populations last impacted by an extinction force persist the longest, i.e. the last populations persist at the periphery of the historical range (Towns and Daugherty 1994; Lomolino and Channell 1995; 1998; 2000). Both of these theories can explain the present disjunct populations of the rare *Cryptocephalus* species studied here. However, in order to fully address the processes responsible for producing a disjunct distribution post-glacial colonisation histories have to be considered.

Cryptocephalus moraei and *C. labiatus* exhibited levels of divergence that are difficult to explain satisfactorily. The increased level of homogeneity observed in the sequences from these species suggests a greater degree of sub-population and inter-population gene flow in *C. moraei* and greater sub-population gene flow in *C. labiatus* than that observed in the other species. Higher levels of dispersal can prevent selective differentiation among populations resulting in lower levels of total genetic variance (Whitlock 2001). *C. moraei* is the only monophagous species and its host-plant (*Hypericum perforatum*) may be more continuous in space and time than the very ephemeral scrub transition habitat or pristine calcareous grassland occupied by the other species in this study. The relative ubiquitous distribution of this species' host-plant could entail that gene flow is maintained even over large distances. *C. labiatus* is the commonest of the species but occurs in a scrub transition habitat. Low sub-population divergence in this species suggests gene flow at this scale but the divergence at the inter-population level is of the same magnitude as the other studied *Cryptocephalus* species and much higher than *C. moraei*. Interestingly, only *C. moraei* and *C. labiatus* are routinely caught in flight interception traps at Headley Warren where *C. coryli* and *C. nitidulus* also occur (G. Collins, pers. comm.). This suggests that these two species may be more vagile (either actively or passively) than the other studied *Cryptocephalus* beetles

This study has highlighted some of the genetic differences that exist between disjunct *Cryptocephalus* populations. Further, finer scale sampling of the threatened species would enable the population structure of these species to be resolved at an even smaller scale. For example, *C. nitidulus* occurs in many isolated populations along approximately 3km of the White Downs in Surrey. Each population is separated from the next by unsuitable habitat (mature tracts of woodland). Examination of the populations along the whole length of the White Downs would surely yield interesting results. Further research may also enable hypotheses to be formulated regarding the range contraction of the species in question, which is also of fundamental importance in conservation strategies (Simberloff, 1986). Understanding how and why their ranges have contracted may also enable suggestions to be made of which areas to survey for undiscovered populations of the rare *Crytocephalus* species and the planning of reintroductions (Lomolino & Channell, 1995; 1998)

The level of divergence observed in this study between geographically close populations is reflective of the findings of other studies. Other phytophagous beetle species have been shown to exhibit considerable population structure even at a microgeographic scale (McCauley *et al*., 1988; McCauley, 1991; Rank, 1992). The results of this study suggest that the populations within the disjunct sites for *C. coryli, C. decemmaculatus* and *C. nitidulus* are genetically distinct. Subtle ecological differences also exist although more study is needed in this area. On the basis of these results these disjunct populations can be tentatively termed ESUs. These populations, and their discrete nature warrant their separate management for the maintenance of genetic diversity within the relevant species. Re-introductions of these species should also take into account the presence of distinct lineages even within populations. Re-introduction programmes should aim to maintain this genetic diversity. Introgression, with its homogenising effects, could arise as a result of these translocations (Johnson & Jordan, 2000). Individuals from a divergent population translocated to another population could severely impede the adaptive potential and unique evolutionary trajectory of the sink population.

The distinctiveness of all the populations of most of the populations studied, even at an sub-population scale suggests that relatively trivial barriers to dispersal, i.e. unsuitable habitat, can limit gene flow, effectively, reproductively isolating populations. Further ecological comparisons of the *Cryptocephalus* populations in question would enable a more robust application of the ESU concept. Some authors have argued that historic levels of gene flow between populations should be maintained (Crandall *et al.,* 2000) but this is a practical impossibility when the organism in question not only depends on an acutely ephemeral habitat, but is also a very poor coloniser. In this situation the only viable means of protection is to maintain the habitats of the extant populations in a manner conducive to their survival and to conduct re-introductions in a manner that preserves genetic variability.

Discrete groups should be managed separately. Failure to recognise discrete populations within rare species as distinct groups can lead to the loss of biodiversity, especially where distinct sub-populations are allowed to go extinct (May, 1990). The findings of this study have implications for the management of the threatened species and for any attempts at translocations and re-introductions.

Chapter 9. The species status of *Cathormiocerus britannicus*, an endemic, endangered British Weevil.

9.1. Introduction

The broad-nosed weevil genus *Cathormiocerus* (Curculionidae; Entiminae) is small, but zoogeographically interesting as it is restricted to the extreme west of the Palaearctic region (Morris, 1997). Of the 70 species in total only ten are found outside the Iberian peninsula or Morocco (de la Escalera, 1918). Ten species have been reported from France (Tempère & Péricart, 1989) and five species are known from the British Isles (Morris, 1997).

The biology of the genus is very poorly known, but its species are believed to be similar in many respects to those in the related genus *Trachyphloeus*. *Trachyphloeus* species overwinter as adults (Hoffman, 1950, Hansen, 1965, Dieckmann, 1980, Borovec, 1989), and may be found around the roots of the host plants where they are believed to feed on fresh and partly decomposed plant material (Dieckmann, 1980). *Cathormiocerus* species are believed to be polyphagous and are to be found around the base of such plants as *Plantago* and *Thymus* spp. (Morris, 1997). The elytra are fused suggesting that their dispersal ability is poor, as is the case in *Trachyphloeus* species (Jermin *et al.,* 1993).

All *Cathormiocerus* species exhibit a form of parthenogenesis termed ploidy stasis (Lamb & Wiley, 1986). The causative agent of parthenogenesis in *Cathormiocerus* weevils is unclear. In the *Aramigus tessellatus* complex (Curculionidae, Naupactini) parthenogenesis is probably caused by polyploidy (Normark, 1996). The bacteria *Wolbachia* has been found in parthenogenetic insects. In these insects it has been shown to be the cause of parthenogenesis and also involved in parasite resistance (Stouthammer *et al.,* 1990a, Hsiao, 1985a,b and Hsiao, 1996).

Cathormiocerus species are normally found in marginal habitats of relatively low diversity and it has been suggested that the superior colonising ability of parthenogenetic species enables them to monopolise appropriate niches in such habitats (Lanteri & Normark, 1995).

Cathormiocerus britannicus Blair 1934 is currently listed as endemic to the UK (Morris, 1997), is described as endangered (Hyman & Parsons, 1992) and has its own Species Action Plan (UK Biodiversity Steering Group, 1999). *C. brittanicus* is very similar to *C. myrmecophilus* Seidlitz and the species are presently separated on morphological grounds, namely, differences in the elytra, striae and the rostrum. In the UK both species are confined to coastal habitats in the Southern England where they are to be found in short, stony turf (Morris, 1997). *C. myrmecophilus* also occurs in continental Europe (in Normandy, Brittany and south into the Iberian peninsula; Hoffman 1950).

Taxonomic rank is a very important criterion in assessing the conservation priority of an endangered organism. Because of the close similarity between *C. britannicus* and *C. myrmecophilus* and the complications generated by parthenogenesis and, potentially, by *Wolbachia* infection the taxonomic status of the putative UK endemic is unclear. This study is an investigation of the species status of *C. britannicus* using DNA sequencing and morphometric analysis.

9.2. Methods

9.2.1 Specimen collection and identification

Specimens of *Cathormiocerus myrmecophilus, C. britannicus* and *C. maritimus,* were collected with a suction sampler from short turf at known localities on England's south coast (Figure 9.1).

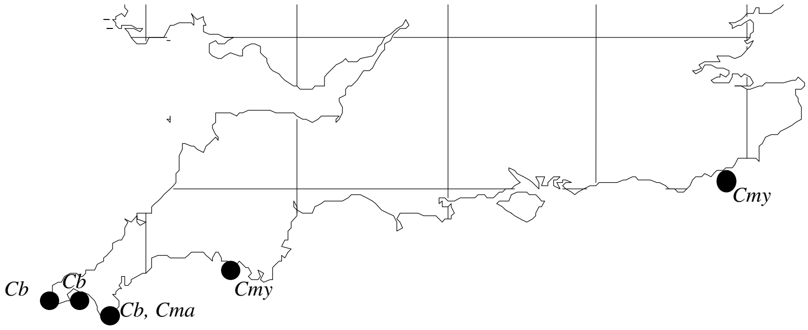

Figure 9.1. Specimen collecting localities (Cb = Cathormiocerus britannicus, Cma = C. maritimus and Cmy = C. mymecophilus)

Very few sites are known for these species and they are all in England's southern counties. Collections were made between the 21 and 28 May 1999. *C. curvipes* was collected by searching beneath stones and plants in the Oriental Pyrenees, southern France (Grid Ref: 113427) on 3 February 2000. Individuals collected were transported live to laboratories where they were transferred to absolute ethanol and refrigerated or processed immediately.

All British specimens were identified using criteria described by Morris (1997). The genitalia of the specimens were dissected to confirm that only females were present. *C. curvipes* and *C. maritimus* can easily be distinguished from *C. myrmecophilus and C. britannicus* using morphological characters. Identification of *C. curvipes* was made by using Hoffman's key (1950).

9.2.2. DNA preparation PCR and sequencing

The thorax, femurs and (to determine presence of *Wolbachia*) abdomen of specimens were ground to provide the DNA for the PCR amplification. The DNA was extracted using standard protocols (Juan *et al*., 1995). Regions within the ITS nuclear ribosomal complex were amplified using PCR. The total volume of the reaction mixture was 25µl. ITS2 amplification used the primers described by White *et al*., (1990): ITS2 (5.8s), 5'-TGTTGACTCTAAATATGACGTCGTCACCTCACCG-3' and ITS2 (28s), 5'-GACCCCGGGTAAAATGTTACGAAAATAAAC-3'. The contents of this mixture were as follows: 17.5µl H_20, 2.5µl Taq buffer, 3µl $MgCl_2$ and *Taq* polymerase (buffer, salts and polymerase all Promega), 0.25µl dNTPs (20mM), 0.175µl of each primer (20mM) 0.25µl of bovine serum albumen and 1µl of DNA extract. Cycling involved an initial denaturation of 94°C for 30 sec then 25 cycles of 92°C for 1 min, 50°C for 2 min, 72°C for 2 min and a final elongation of 72°C for 5 min. PCR products were concentrated and run through a 1% agarose gel. The stained bands containing the DNA were excised and the DNA was extracted in accordance with the QIAquick gel extraction protocol (Qiagen).

The DNA extracted from the gel was then applied to a sequence PCR reaction and sequenced following the manufacturers instructions (Perkin Elmer applied biosystems).

9.2.3. Wolbachia detection

The PCR approach used to detect *Wolbachia* used the primers desribed by O'Neill *et al*., (1992): 99f, 5'-GAATAGGTATGATTTTCATGT-3'; 994r, 5'-GAATAGGTATGATTTTCATGT-3'. Cycling involved an initial denaturation at 93°C for 5mins then 34 cycles of 93°C for 1min, 49°C for 1 min 30 sec, 72°C for 1 min and a final elongation of 72°C for 5mins.

9.2.4. Morphometric analysis

Thirteen *C. myrmecophilus* and 36 *C. britannicus* were analysed using image analysis equipment and computer software (Micro measure, version 3). Eight measurements were made on each individual (Plate 37) and these were used in a principal components analysis (PCA; SPSS).

PCA reduces data from multidimensional distributions to newly derived axes that maximally explain variation in the dataset. PCA is very useful tool for exploring the morphometric data, which can then be analysed further using discriminant function analysis (DFA). DFA generates a set of vectors that best separate *a priori* determined groups. DFA compares the variation between groups to that within groups and assesses the significance of any differences observed. Thus, both analyses were performed, with the latter using only the characters with the highest factor loadings in the former.

9.3. Results

Table 9.1 shows pair-wise Kimura two-parameter distances for all the pairs of the 13 ITS2 sequences.

Table 9.1. Pair-wise Kimura two-parameter distances for rDNA ITS2 sequences (all gaps in the aligned sequences were removed for the purposes of the pair-wise analysis) 023 = Rinsey Head (Cornwall), 050 = Cudden Point (Cornwall), 094 = Lizard Penninsula (Cornwall) 095 = Logan Rock (Cornwall), 002/004/008 = Hastings Country Park (Sussex), 009/018 = Stoke Point (Devon), 122/123 = Tour Magdeloc (S. France) and 013/052=Rinsey Head (Cornwall)].

	bri023	***bri050***	***bri094***	***bri095***	***myr002***	***myr004***	***myr008***	***myr009***	***myr018***	***cur122***	***cur123***	***mar013***	***mar052***
bri023	0.0000	0.0019	0.0059	0.0020	0.0019	0.0019	0.0019	0.0019	0.0019	0.1702	0.1684	0.2185	0.2179
bri050		0.0000	0.0039	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1683	0.1742	0.2167	0.2186
bri094			0.0000	0.0020	0.0039	0.0039	0.0019	0.0039	0.0039	0.1753	0.1746	0.2247	0.2167
bri095				0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1724	0.1682	0.2223	0.2157
myr002					0.0000	0.0000	0.0000	0.0000	0.0000	0.1676	0.1687	0.2157	0.2165
myr004						0.0000	0.0000	0.0000	0.0000	0.1647	0.1740	0.2147	0.2143
myr008							0.0000	0.0000	0.0000	0.1705	0.1735	0.2197	0.2163
myr009								0.0000	0.0000	0.1679	0.1745	0.2162	0.2176
myr018									0.0000	0.1647	0.1699	0.2147	0.2158
cur122										0.0000	0.0013	0.1290	0.1261
cur123											0.0000	0.1245	0.1279
mar013												0.0000	0.0015
mar052													0.0000

Approximately 670bp of the ITS2 region were sequenced. One specimen for each of the *C. britannicus* sites was sequenced. Three specimens for the Sussex *C. myrmecophilus* and two specimens for the Devon *C. mymecophilus* were sequenced. The two sequenced specimens of *C. maritimus* came from the same Cornwall location. The two sequenced *C. curvipes* specimens came from the same location in the oriental Pyrenees. The degree of DNA differentiation between *C. myrmecophilus* and *C. britannicus* is almost equal to the amount of differentiation that is observed within either species. However, when either of these species was compared to the two other congeners, the level of differentiation is much higher. There was no DNA differentiation observed between the *C. myrmecophilous* specimens (Table 9.1).

Results of the tests for *Wolbachia* showed that both *C. myrmecophilus* and *C. britannicus* are infected with the bacteria. The presence of the bacteria was observed in all of the populations that were sampled. No *Wolbachia* were found in *C. curvipes* or *C. maritimus*.

Generally, the morphometric characters measured were weakly correlated (Table 9.2) suggesting sufficient independence among variables for use in the subsequent multivariate analyses.

Table 9.2. **Correlation matrix of morphometric variables (*=correlation is significant at the 0.05 level. **= correlation is significant at the 0.01 level).**

	Elytra Length	Elyrtra Width	Rostrum Convergence	Scrobe Separation	Pronotum Width	Pronotum Length	Striae Convergence	Total Length
Elytra Length	1							
Elytra Width	0.60**	1						
Rostrum Convergence	0.13	0.09	1					
Scrobe Separation	0.22	0.37**	0.20	1				
Pronotum Width	-0.21	0.09	0.03	0.32*	1			
Pronotum length	-0.04	0.15	0.03	0.37**	0.72**	1		
Striae Converegnce	0.11	0.05	0.17	0.09	-0.10	-0.19	1	
Total Length	0.52**	0.37**	0.06	0.24	-0.12	0.08	0.19	1

The first two principal components of the PCA analysis explain 53.6 % of the total variance in the dataset (Figure 9.2, Table 9.3). Loadings of the first principal components are all positive.

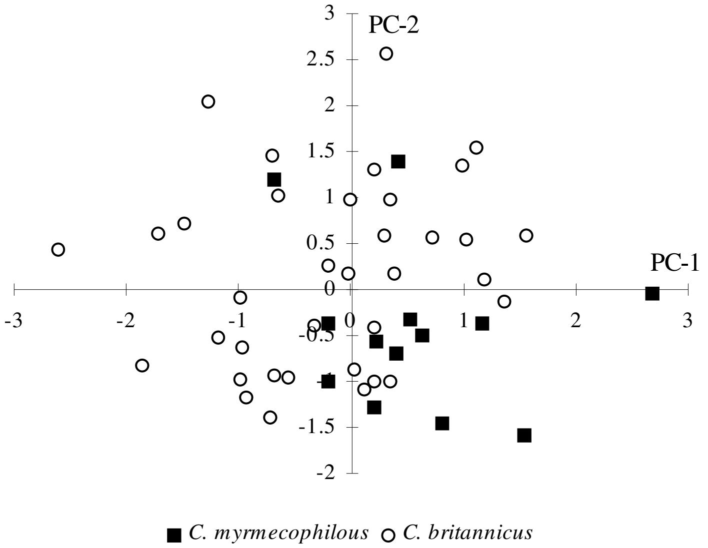

Figure 9.2. First (PC-1) and second (PC-2) principal component axes for individuals in the two putative species.

Table 9.3. Factor loadings for the first two components extracted by the principal components analysis

Morphological Characters	PC-1	PC-2
EW	0.7789	-0.1605
EL	0.7782	-0.4241
TL	0.7328	-0.2793
Sc	0.5602	0.4507
PW	0.1336	0.8940
PL	0.2982	0.8344
R	0.2490	0.1909
S	0.0423	-0.2005
% of total variance explained	27.9	25.7

Consequently this component is related to overall size (Manly, 1986). The second component as well as any other component will relate to overall shape. Discriminant analysis reveals that, on the basis of the traits measured, the two weevil species are not readily distinguishable. Discriminant classification shows that 19% of the *C. myrmecophlilus* group were misclassified as *C. britannicus* and 23% of the *C. britannicus* were misclassified as *C. myrmecophlilus.*

9.4. Discussion

Neither the molecular nor the morphometric analyses described here provide any evidence to support the species separation of *C. brittanicus* and *C. myrmecophilus*. On the basis of the multivariate analysis of the morphometrical data it is impossible to define *C. britannicus* as a species. The morphological variables that are used to separate *C. myrmecophilus* and *C. britannicus* are all of the continuous type therefore variation is expected to be apparent in these variables within, as well as between populations.

Although it may be argued that morphological features commonly used in identification, such as genitalia, were not compared in this study the use of genitalia in differentiating parthenogenetic species is best approached with caution (Jermin & Mahler, 1993). This is due to the fact that there will be disruption of the concurrent selection of male and female genitalia caused by the lack of males. Selective pressures on the genital characters will reduce or cease (Jermin & Mahler, 1993). This will result in the genital shapes varying more freely making them inappropriate for identification purposes.

The lack of genetic variation that was observed between *C. myrmecophilus* and *C. britannicus* leads to the conclusion that the two are very similar indeed. Although each species was different from *C. curvipes* and *C. maritimus*, no evidence was found for any significant degree of sequence divergence between *C. britannicus* and *C. myrmecophilus*. *C. britannicus* was originally described from 12 specimens (Blair, 1934) and in this description the author mentions that it was very difficult to define which of the specimens were *C. myrmecophilus* or *C. britannicus*.

These findings have some important implications for conservation. The continued recognition of two separate species has no phylogenetic support. *C. britannicus* is currently listed as endemic with a status of endangered and its own species action plan. If it is to be viewed as the same as *C. myrmecophilus* then will the status of *C. myrmecophilus* (RDB3 rare) be modified? If the sites that are known for *C. britannicus* are added to the sites that are all ready known for *C. myrmecophilus* then the total of inhabited 10 km squares does not reach the threshold of 15 10 km sqaures. This is the cut off point for relegation into one of the lower priority categories (Shirt, 1987).

Concern has been expressed over the application of genetic techniques to populations of conservation importance. It is believed that these techniques will lead to the exaggeration of the number of ‘species’ in the absence of any other type of distinctiveness (Avise, 1989). The results of this study show that the opposite effect can be realised by addressing the genetic differentiation among morphs previously recognised as distinct species. Work on vertebrates has shown that the definition of a species based on colour are not reflective of the underlying genetic differentiation (Avise and Nelson, 1989; Karl & Bowen, 1999).

The effect of environmental factors, such as temperature, have been shown to effect morphology. It has been shown that an array of developmental temperatures will produce variation in the morphology of the adult insects concerned (Hogue & Hawkins, 1991)

Very little is known of the biology of the *Cathormiocerus* species. Their conservation priority is based on their localised distributions. New sampling methods employed in this study have shown that in suitable habitat these beetles can be found in relatively high densities.

This study showed that *Wolbachia* is present in the species of interest. To examine if these bacteria are responsible for inducing parthenogenesis would require experiments with antibiotics. Some strains of this bacterium have been shown to induce parthenogenesis in the hymenopteran genus *Trichogramma* (Stouthammer *et al.,* 1990). Experiments with tetracycline may aid examination of the effects of infection on morphology of the adult. In the weevil *Hypera postica* it has been shown that the bacteria are responsible not only for reproductive incompatibility (Hsiao, 1985a; b) but also for conferring resistance to the hymenopteran parasite *Bathyplectes curculionis* (Hsiao, 1996). It would be most interesting to elucidate the exact relationship that *Wolbachia* has with *C. myrmecophilus*.

In conclusion it seems that the species status of *C. britannicus* is very questionable. It is therefore worth considering, on the basis of this evidence, if *C. britannicus* should be removed from the Biodiversity Action Plan and the resources better applied to another insect species of conservation concern where the systematic status is assured.

Chapter 10. Re-introductions as a tool for discovering the ecology of extremely rare insects.

Many insect species are so rare that practical conservation is very difficult (Britton *et al.,* 1994; New *et al*., 1995). Using the letter and number code classification of Rabinowitz (1981; 1986) many of the rare *Cryptocephalus* species exhibit the highest degree of rarity in the UK. Species such as *C. coryli, C. biguttatus, C. exiguus, C. frontalis C. primarius,* and *C. querceti*, have a very restricted distribution with small populations and very specific habitat requirements: H1 species (Rabinowitz 1981; 1986). *C. decemmaculatus, C. nitidulus* and *C. sexpunctatus* could be described as F2 species (Rabinowitz 1981; 1986), characterised by a small distribution, occasionally large populations and very specific habitat requirements. 17.5% (21) of the beetle species with a Biodiversity Action Plan or a priority statement have no known moderately sized population (R. Key, pers. comm.). Determining the appropriate action for conserving a species that cannot be found must inevitably be based on hearsay evidence and supposition. Sites can be conserved but if the specific habitat requirements of endangered species are not known then sites can change in ways that are detrimental to them. Many of the insect species listed on the Biodiversity Action Plan are so poorly known and are so rarely found that informed managing of their known sites is impossible.

Re-introductions are usually seen, solely as a method of enhancing the distribution or abundance of a particular species. Guidelines for re-introductions published by the IUCN in 1995 state that: “The principle aim of any re-introduction should be to establish a viable, free ranging population in the wild of a species that has become locally extinct in the wild. It should be re-introduced within the species’ former natural habitat and range and should require minimal long-term management”. Re-introductions may, however, also be the only practical method for learning the ecological requirements of invertebrate species that are only ever encountered very rarely in the wild. Re-introductions are cited on 34.5% (30) of the UK beetle biodiversity action plans (R. Key, pers. comm.). These re-introductions depend on the ability to carry out moderate scale captive rearing combined with an understanding of the insects ecology. Captive rearing is often cited as a fundamentally important part of any conservation program (Pyle, 1988; Morton, 1991; Pearce-Kelly, 1994; Pearce-Kelly *et al*., 1998), but its wider value has rarely been recognised.

Rare species within the genus *Cryptocephalus* are examples of beetles that would benefit from initial experimental re-introductions prior to, or in parallel with releases attempting to establish new populations. The proportion of *Cryptocephalus* species that are of conservation concern (Endangered, Vulnerable, Rare, Notable A and B) is extremely high (Table 10.1). It has a higher proportion of such species than comparable genera within the Chrysomelidae, other chrysomelids in total and the remainder of the UK Coleoptera as a whole (as listed in Kloet & Hincks, 1964).

Table 10.1. The status of UK *Cryptocephalus* species compared with other genera of beetles.

		Endangered, Vulnerable, Rare, Notable A and B		**Indeterminate / insufficiently known**		**No status**	
	Total	**n**	**%**	**n**	**%**	**n**	**%**
Cryptocephalus	19	14	73.7	0	0.0	4	21.1
Donacia	15	9	60.0	0	0.0	6	40.0
Chrysolina	16	8	50.0	0	0.0	8	50.0
Longitarsus	41	21	51.2	2	4.9	18	43.9
Psylliodes	14	5	35.7	1	7.1	8	57.1
Cassida	12	5	41.7	0	0.0	7	58.3
Other chrysomelids	236	107	45.3	6	2.5	21	8.9
Coleoptera total	4100	1030	25.1	372	9.1	2550	62.2

Many of the rare UK *Cryptocephalus* species are found on woody plants growing in scrub transition (Plates 15, 18 and 33). Females of the genus lay eggs that are encased in faeces that are dropped to the ground where the larvae feed on leaf litter adding to the egg case with their own faeces to produce a larval case that it pupates in. Re-introducing moderate numbers of captive-bred larvae of *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* and also adults in the case of *C. coryli* has dramatically increased the knowledge of the ecological requirements of these three species (Chapter 6).

Many of the species described in this chapter have only been seen in very small numbers in the last five years (Table 10.2). Information on their suitable larval host-plants has been obtained via captive rearing, as has information on their adult food-plants. Feeding experiments for the majority of the species shown in Table 10.2 have not been conducted; making, it impossible to define their preferred host-plants. This is especially true for the larvae as they are automatically assumed to feed on the same host-plants as the adults. Additional insights into the habitat preferences of *C. coryli, C. decemmaculatus* and *C. nitidulus* have been gained from intense field observations (Table 10.3). Experimentation using adults and larvae reared in captivity allows further information to be gained, such as the key host-plants of each species, but can only broadly mimic the field situation (Table 10.4). Critically, release of captive bred larvae also allows the ecology of this stage to be understood (Table 10.5). Furthermore, adult movement in these species is almost impossible to study as only very few wild individuals are ever seen. Releases of adults that have been marked by-passes this problem.

Table 10.2. The Present state of knowledge of the rare UK *Cryptocephalus* beetles. + = known information, - = information not yet known, A = anecdotal information.

Species	No. of adults seen 1997-2001	No. of recent location	Generation time	Larval food requirements	Adult food requirements
C. biguttatus	<20	3	+	A	+
C. coryli	>60	3	+	+	+
C. decemmaculatus	>400	2	+	+	+
C. exiguus	4	1	+	A	A
C. frontalis	>20	3	+	A	A
C. nitidulus	>150	2	+	+	+
C. primarius	2	2	-	A	+
C. querceti	<20	3	-	A	A
C. sexpunctatus	4	2	+	+	A

Table 10.3. The present state of knowledge of three rare *Cryptocephalus* beetles based on field observations. + = known information, - = information not yet known.

Species	Most utilised adult host-plant	Adult preferences	Micro-habitats of wild larvae	Parasitism
C. coryli	+	+	+	_
C. decemmaculatus	+	+	-	_
C. nitidulus	+	+	+	+

Table 10.4. The present state of knowledge of three rare *Cryptocephalus* beetles based on captive rearing. + = known information, - = information not yet known.

Species	Fecundity	Egg hatching	Larval performance	Adult feeding preferences	Sex ratios	Eclosion of adults
C. coryli	+	+	+	+	+	+
C. decemmaculatus	+	+	-	+	+	+
C. nitidulus	+	+	+	+	-	-

Table 10.5. The present state of knowledge of three rare *Cryptocephalus* beetles based on experimental larval releases. + = known information, - = information not yet known.

Species	Predation	Mortality other than predation	Micro-habitat preferences	Movement
C. coryli	+	+	+	+
C. decemmaculatus	+	+	-	-
C. nitidulus	+	+	+	+

Of the *Cryptocephalus* species described in this chapter, basic ecological information exists for *C. coryli, C. decemmaculatus* and *C. nitidulus.* The anecdotal information that exists for the species in Table 10.2 is only known because of captive rearing. Very little data can be obtained via the capture of two or three specimens using a sweep net or beating tray. It has been shown that *Cryptocephalus* species can be reared from egg through to adult relatively easy (Steinhausen, 1996, Owen, 1996; 1999; I. Menzies, pers. comm.; H. Mendel, pers. comm.; Pers obs.). Wild caught females are always gravid (Pers. obs.); therefore males do not have to be sought for captive breeding. Females in captivity have been shown to produce upwards of 200 eggs each. High fecundity coupled with the ease of rearing large numbers of larvae in very small spaces on easily obtainable leaf litter makes the rare *Cryptocephalus* species very suitable for captive rearing and subsequent experimental re-introductions.

Re-introductions of marked *Cryptocephalus* larvae using metal tags and subsequent recovery using a sensitive metal detector (see chapter 4) have given many insights into the population dynamics and habitat requirements of this very cryptic life stage. Larvae appear to present easy meals for small mammals, particularly wood mice (*Apodemus sylvaticus*). Other data shows that for a habitat to support both adults and larvae there must be juxta-position of conditions that are suitable for adults and larvae. Release of larvae and their subsequent recovery has also enabled microhabitat requirements of this life stage to be appreciated. This kind of data is of paramount importance if re-introductions to increase range and enhance populations are to be successful and can only be obtained via experimental re-introductions. Release and recovery of large numbers of marked captive bred larvae enables ecological information to be gathered on cryptic life stage of a rare species.

Re-introductions of rare species should be viewed as much more than simply a method of re-establishment within historic ranges and of enhancing populations. Releases present the only practical way of gaining knowledge of the biology of many rare invertebrate species with successful establishment as a bonus. Knowledge gained from releases is likely to greatly enhance the success rate of subsequent releases, which may or may not be carried out at the same locations. Releases with establishment as their primary goal are also likely to differ in scale and in other areas such as timing and small scale location. The numbers in experimental releases are also likely to be small compared to the numbers used in releases aimed at bio-control (Memmott *et al.,* 1998). Four introduced individuals of the butterfly *Proclossiana eunomia* produced a self-sustaining population (Neve *et al.*, 1996) suggesting that large numbers of individuals do not have to be used in re-introductions. Any release must adhere to the IUCN guidelines for re-introductions. These include molecular genetic studies, evaluation of re-introduction site and intensive pre- and post- release monitoring (IUCN, 1995). Initially the chances of re-introduction success are very low, but will improve with both the practical experience and ecological knowledge gained. The only prerequisite for the use of re-introductions as a method of understanding the ecology of rare species is the ability to rear them in captivity. In principal, all of the beetle species on the Biodiversity Action Plan could be reared in captivity (R. Key, pers. comm.), though phytophagous species are relatively easy to rear in captivity compared to those species that depend on river shingle, for example (R. Key, pers. comm.). Captive rearing is widely touted as a fundamental tool in the conservation of endangered species and its associated problems such as inbreeding depression and the loss of genetic variability have been discussed widely (Ralls and Ballou, 1986; Lande and

Barrowclough, 1987; Lande, 1988, Bryant, *et al,* 2000). With the correct strategy the detrimental effects of the captive situation can be minimised, allowing captive breeding and releases to become valuable tools in ecological research.

Chapter 11 Sites and habitat management

11.1. Introduction

Many rare insect species are very geographically limited (Bedick, *et al.,* 1999). Habitat management at sites where they occur must be carried out cautiously, based on as much knowledge as possible of the species biology and life history, otherwise human intervention aimed at recovery can lead to extinction (Ehrlich and Ehrlich, 1981). Habitat management plans aimed at rare species are often expensive to produce and execute and to be effective the needs of each species must be clearly defined (New *et al.,* 1995). They are likely to be most successful if based on knowledge gathered on the management history of sites where particular species still exist. Sites that currently support a species are likely to have done so for a very long time, unless it is highly mobile. Radical new management of a site may lead to the extirpation of a species that has persisted and possibly flourished within past land use and management regimes. This chapter provides a synthesis of information that has been gathered on the histories of various sites supporting populations of *Cryptocephalus coryli, C. nitidulus* and *C. decemmaculatus.* On the basis of this, together with what is known of the insects habitat requirements (Chapter 5) suggestions are made for sympathetic management of each site that should help ensure the survival of these very rare insects.

11.2.Cryptocephalus coryli

11.2.1. Basic requirements

Cryptocephalus coryli is a very thermophilic species that requires areas of scrub in south facing pockets that are protected from prevailing winds by windbreaks. Suitable trees and habitat for this species are shown in Plate 14 and 15. The preferred host-plant for both adults and larvae is the silver birch (*Betula pendula*). Adults most readily eat mature trees that have been coppiced perhaps once. The disjunction between adult and larval habitats results in a population at a site depending on a handful of host-plants that coincidentally offer suitable adult and larval habitat.

11.3. Detailed study sites and history

The autecological work carried out on *Cryptocephalus coryli* was concentrated at Headley Warren (Surrey) and Kirkby Moor (Lincolnshire) where strong populations of this beetle occur. A population has also been described from North Unhill Bank (Oxfordshire).

11.3.1. Headley Warren (Surrey)

Of the sites that currently support *C. coryli* Headley Warren is the only location where a detailed management history exists (Mackworth-Praed, 1996). The earliest records of *C. coryli* from this site are from 1914. The site, today, is composed of four south facing, gently sloping, downland fields separated by large hedgerows, mature woodland (planted) and coppiced tracts of *Corylus avellana* (Plate 16). The largest *C. coryli* population is found in a corner of the Downs Field (Plate 17) on one tree in particular (Plate 14)

The ground flora in the fields is very diverse, including such species as *Lotus corniculatus, Origanum vulgare, Plantago lanceolata, Prunella vulgaris,*and *Galium verum*. They are bounded to the west and east by conifer plantations. The current owners, the Mackworth-Praed family, purchased the four fields of Headley Warren in 1879. For centuries before, the site had been used as a rabbit warren, which is the reason why these downland fields had remained so open. During the 1940's and 1950's *Crataegus monogyna* and *Cornus* sp. scrub began to encroach on the open fields. This increase in scrub growth was a result of rabbit numbers being initially reduced by poaching, then, by 1954 myxomatosis had virtually eliminated rabbits from the site. The loss of rabbits led to an unprecedented increase in the amount of scrub on the site that had to be removed in subsequent years with the use of mechanised equipment. The owners, who were assisted by government subsidies and local conservation groups, carried out this scrub control in order to restore more open conditions to the four fields.

11.3.2. Kirkby Moor (Lincolnshire)

Anecdotal evidence suggests that as recently as the 1920's much of the area around what is now Kirkby Moor was *Betula pendula* and *Calluna vulgaris* heath (D. Bromwich, pers. comm.). During the 1940's Anglia Water developed the area and much of the site was bare sand that was quickly succeeded by *B. pendula* scrub. Anglia Water owned the site until 1970 when the Linclonshire Trust for Nature Conservation purchased it. By this time most of the heath had developed into woodland. The Forestry Commission has many large plantations in the area, including Ostler's plantation adjacent to Kirby Moor. Recent management of the Kirkby Moor site has focused on returning much of the area to *Calluna vulgaris* heath and today the site is a mosaic of small open areas with small *B. pendula* trees (Plate 18) surrounded by mature mixed woodland, mature coppice and conifer woodland (Plate 19).

The open areas, as well as having well developed scrub, have a range of grass and sedge species. Bracken (*Pteridium aquilinum*) is also encroaching on some of the open areas. Sections of the reserve have been rotationally grazed and others have been cleared of woodland to produce small glades that are coppiced every two to three years. This 'coppicing' is an accidental result of the failure to kill the *B. pendula* trees rather than deliberate management. In the winter of 2000/2001 an area of woodland was cleared (D in Plate 18) that effectively enlarges area C (Plate 19). The scrub in area C was also thinned to leave only small *B. pendula* trees. The woodland bordering area C from the lake was also thinned to allow more sunlight to enter this clearing.

11.3.3. North Unhill Bank (Oxfordshire)

A population of *Cryptocephalus coryli* was discovered at this site in 1991 (Hodge and Williams, 1991). North Unhill bank is on the chalk ridge of the Berkshire Downs. The site is a patchwork of calcareous grassland, scrub and trees. The site is part of a large farming and shooting estate and is managed to provide suitable conditions for pheasants (*Phasianus colchicus*). The amount of scrub cover on the site has increased considerably since 1948 (Harvey, 1998).

11.4. Responses to habitat management

11.4.1. Headley Warren

The fields that currently support *Cryptocephalus coryli* have only accidently been sympathetically managed for this species. The current overall aim at Headley Warren is to remove scrub, particularly in the southern portion of the Downs Field. Headley Warren is a rich butterfly site and scrub removal is believed to enhance the site for these insects. Wholesale removal of the scrub would nonetheless be detrimental to many insect species (Hopkins, 1996) including *C. coryli*.

11.4.2. Kirkby Moor

The main aim of management at Kirkby Moor in Lincolnshire is to encourage the predomination of *Calluna vulgaris* at the expense of woodland and scrub. A windbreak consisting of mature *Betula pendula* woodland surrounds the area that presently supports the greatest abundance of *Cryptocephalus coryli*. During the winter of 1999 and 2000 some of this woodland was cut down. This management allowed prevailing winds greater access to the small scrubby glade where *C. coryli* adults could be found. During the summer of 2000 adult beetles seemed to respond to this management by only occurring in the parts of the glade that were still shielded from the prevailing winds. The maintenance and augmentation of the windbreak at this site is very important, as the land beyond it is open and flat entailing strong winds. In the winter of 2000/2001 an area of woodland was cleared (D in Plate 19) that effectively enlarges area C (Plate 19). The scrub in area C was also thinned to leave only small *B. pendula* trees. The woodland bordering area C from the lake was also thinned to allow more sunlight to enter this clearing.

11.4.3. North Unhill Bank

There has been no relevant management of the North Unhill Bank site, but it is hoped that resources from the Species Recovery Programme may enable a scrub management plan to be initiated in the future (M. Harvey, pers. comm.).

11.5. General recommendations

The most important consideration for the management of sites that currently support this species or sites that are to be used as recipient sites for introductions is the propagation and maintenance of areas where a warm microclimate can develop. For the sites that currently support this species the windbreaks that exist should at least be maintained with attempts made to consolidate them further. Glades should be large enough and woodland rides wide enough to allow as many hours of direct sunlight as possible, especially during the late spring and early summer when the adults are active. *Betula pendula* scrub should be maintained in sheltered areas or along woodland rides. Scrub of a range of ages should be maintained. Natural regeneration of *B. pendula* should be encouraged, although, further studies of the palatability of saplings are needed. The scrub should be left to develop into a network of scattered trees and bushes as opposed to just one or two. This network of trees will facilitate the movement of adults as data in Chapter 7 suggests that short flights using “stepping stones” are the mechanism that scrub dwelling *Cryptocephalus* species use to move between host-trees in suitable habitat. Over-dense scrub is not suitable for *C. coryli*. Instead of wholesale clearing of dense scrub in areas that are chosen for introductions, pockets or “mini-glades” could be cut into the scrub. These small open areas would possess warm microclimates and the surrounding intact scrub would form a very efficient windbreak.

The ground beneath bushes utilised by adults should have a high proportion of bare ground and moss to provide a substrate for last instar larvae to burrow into (Chapter 6). Relatively open ground beneath adult-utilised trees may also lessen the effect of predation by small mammals. The ground beneath these bushes could be kept relatively open by grazing. Rabbit grazing would be preferential as trampling by large ungulates may be prove to be detrimental. Dense vegetation beneath adult utilised bushes should also be avoided as leaf litter falling from trees becomes trapped in the ground vegetation and does not reach the larvae on the ground. Dense vegetation may also result in conditions that are too wet and cool for optimal development of the larvae.

11.6. Site specific recommendations.

11.6.1. Headley Warren

This site is divided into four separate fields. The fields have different characteristics and each has been managed differently in the past. Each support *Cryptocephalus coryli*, but the strength of the populations in the different fields appears to be different. The largest numbers of individuals were observed in the Downs Field (Plate 17), whereas only one *C. coryli* was seen on the Orchid Bank (Plate 16). The windbreaks that exist around the whole of Headley Warren should be maintained.

The Downs Field is the only one of the separate fields that is currently heavily grazed by rabbits. The sward in this field is very short. At the southern border of the field scrub management has focused on the rotational cutting of *Betula pendula* and *Ligustrum vulgare*. The southern part of this field supports the greatest number of *C. coryli* adults. There are three mature *B. pendula* trees in this part of the field that have been coppiced perhaps once in their lifetime. It appears as though the conditions beneath one of these trees is currently particularly suitable for larvae as many teneral adults can be seen on this single tree in the early summer. It is likely that they eclosed from their larval cases under the same tree from which their mother was ovipositing. The aim for the management at this site should be to encourage the development of a thin, but well-managed scrub ecotone around the perimeter of each separate field providing a habitat for the species that require this transition. The scrub network of mature *B. pendula* trees in this field should be increased and the current level of rabbit activity should be maintained if possible. The mature *B. pendula* trees that are present in this field should not be removed.

Stainton's Field has similar host trees to the ones that are found in the Downs Field, but, the sward height of the ground vegetation is much taller and dense. *Brachypodium sylvaticum* is also spreading in this field. This grass forms a dense sward, preventing litter from the *B. pendula* trees collecting on the ground. This dense ground vegetation also provides excellent cover for foraging small mammals that have been shown to feed on *C. coryli* larvae (see Chapter 6). To optimise this field for *C. coryli* the dense sward of *B. sylvaticum* should be brought under control. The height of the sward deters rabbits therefore sheep grazing may initially have to be used in this field. The current network of *B. pendula* trees in the field is very scant, the majority exist in the western corner of the field. Encouraging natural regeneration of *B. pendula* could augment this scrub, although, these saplings would have to be protected from browsing. Alternatively, and more rapidly, saplings could be planted in an attempt to connect isolated trees or groups of trees.

The Flying Bomb Field was recently cleared of the dense scrub that was once dominant. *Betula pendula* trees are not abundant in this field and those that are present are surrounded by *Ligustrum vulgare* scrub. As with Stainton's Field *B. pendula* scrub should be encouraged in this field either by natural regeneration or by planting seedlings. Sheep grazing would also probably have to be used in this field to control the ground vegetation.

The fourth field (Orchid Bank) was also recently cleared and there are now many small *B. pendula* trees on the south-facing slope of this field. The majority of these trees are young re-growth although there is some natural regeneration. The ground vegetation in this field is very dense and tall. Management of this field for *Cryptocephalus coryli* should centre on grazing control of this ground vegetation. Sheep grazing would be the only way to control the ground vegetation initially, although once it is short enough then rabbits may take over the grazing looking further ahead. In three to five years the scrub in this field will be very dense and thinning the scrub now would be sensible, while the majority of the trees are small and easily removed.

11.6.2. Kirkby Moor

The majority of the adults seen on this reserve have been in area A (Plate 19). Currently the B*etula pendula* scrub in this area is relatively dense and the area could be optimised for *Cryptocephalus coryli* if this scrub was thinned out. Beneath the *B. pendula* trees there is dense ground vegetation dominated by *Calluna vulgaris*. Grazing of this ground vegetation, intermittently by sheep and then by rabbits would optimise this area for *C. coryli* larvae.

Area B (Plate 19) has also yielded adult *C. coryli*, but not as many as area A. The ground cover in this area in dominated by *Molinia caerulea*. Beneath the *Betula pendula* trees are large amounts of bare ground, which enables the accumulation of leaf litter beneath the host-trees. The *B. pendula* trees in this area are all very mature and some of them have been coppiced at least once. This area could be managed in a sympathetic way for *C. coryli* by promoting the natural regeneration of *B. pendula* trees and by planting saplings. New growth would have to be protected from browsing. Grazing of this area should be continued and even increased to maintain / increase the open conditions that presently exist under the host-trees.

Three female *Cryptocephalus coryli* were found in Area C in 2000 (Plate 19). This area was cleared very recently, but the *B. pendula* scrub has grown very rapidly and will need thinning to produce a habitat that is favourable to the *C. coryli* population. If the glade is left unmanaged then what open pockets exist in the scrub will quickly become overgrown and the area will again become unsuitable for *C. coryli*. The ground vegetation in this area is very scant and there are large patches of bare ground. This ground cover situation should be maintained by grazing.

Single specimens were found at the locations denoted by G, R and P in Plate 19. G is in a glade within the Forestry Commission-owned Ostler's Plantation. R is a ride within the same plantation. It is highly likely that both of these specimens were vagrants from area B. This site contains many other similar glades that with the appropriate management support *Cryptocephalus coryli* populations. The glades and rides would need to be open to southern aspects and suitably large so that shading is kept to a minimum, but the surrounding conifer plantation functions as an excellent windbreak. The ground cover in these glades is often tall and dense which is not suitable for *C. coryli* larvae. This situation could be improved if the glades were sheep grazed. This may be the only way to graze such sites as rabbits are considered as pests on Forestry Commision land. One male *C. coryli* was also found at P and could represent a vagrant from area A. as there is an almost continuous path from point P to area A. This path is lined with small trees with south facing aspects that could represent a means of connecting area A with area C. Some of the glades within Ostlers plantation could be made suitable for *C. coryli* (glade M and the glade around point G in Plate 19). Glade M could be planted with *B. pendula* saplings and the surrounding conifer plantation would provide an excellent windbreak. The ground vegetation could be grazed if there is a tall, dense sward. Saplings could be planted in a way to provide a scrub network for adult beetles. Management of this area could result in the propagation of another sub-population at Kirkby Moor / Ostlers plantation. Glade M (Plate 19) is rather large, therefore, thin windbreaks may have to be planted at intervals to break this larger area into smaller sections each protected from prevailing winds.

11.5.3. North Unhill Bank (Oxfordshire)

To manage this site for *C. coryli* new clearings could be cut into the scrub in areas that are adjacent to the main clearing where several *C. coryli* were found in 1991. Scallops could also be cut into the edges of the woodland around the glades to encourage natural regeneration and provide suitably warm, sheltered conditions for the adult beetles. At least one of the clearings at this site also has a dense sward of *Brachypodium sylvaticum*. Grazing could be employed in these glades to control this grass and restore a less dense sward.

11.7. Cryptocephalus nitidulus

11.7.1. Basic requirements

Cryptocephalus nitidulus, like *C. coryli,* is thermophilic but adults are found at greater heights on its host-plants. It requires host-plants growing in south facing situations at the scrub-transition between woodland and grassland or heathland, with surrounding windbreaks of taller vegetation or dense scrub on all sides. Suitable habitat and trees for this species are shown in Plate 14. The preferred host-plant of the adults and larvae is silver birch (*Betula pendula*). Females produce more cased eggs when feeding on hawthorn (*Crataegus monogyna*) but litter from this host-plant seems to be sub-optimal for the larvae (Chapter 5). As with *C. coryli* a handful of 'beetle trees' exist at the present sites, where there is a juxta-position of habitat that is suitable for adults and larvae.

11.8. Detailed study sites and history

Autecological studies were concentrated at Headley Warren (Surrey) and a large section of the White Downs (Surrey) where strong populations of this beetle occur (Plates 16 and 21). A history of the management of Headley Warren is given in 11.3.1.

11.8.1. The White Downs (Surrey)

The White Downs is a section of the North Downs (Plate 21) that is now owned by the National Trust. There are extensive areas of calcareous grasslands separated by mixed woodland. Much of the conservation value of the North Downs can be attributed to their diverse scrub cover (Hopkins, 1996) that is found in the ecotone between the woodland edges and calcareous grassland (for example see area A in Plate 22). *Cryptocephalus nitidulus* adults are found on trees like the ones shown in Plate 20. The scrub of the North Downs is dominated by *Betula pendula, Crataegus monogyna, Corylus avellana* and rare species such as *Buxus sempervirens*. Much of the woodland on this part of the North Downs was absent 150 years ago (J. Cranham, pers. comm.). Consequently, the areas of calcareous grassland would have been much more extensive in the past, maintained by the sheep grazing that was the predominant type of land use (J. Cranham, pers. comm.). Scrub may have been much less abundant apart from at field boundaries. Recent management has concentrated on scrub control. Hackhurst Down (SSSI) on the eastern edge of the White Downs had a strong *C. nitidulus* population (Plate 21) when it was surveyed in 1986 (P. Hodge, pers. comm.) Subsequent cutting and stump poisoning removed the pre-dominantly *B. pendula* scrub in this field and now *C. nitidulus* is present only in small numbers.

11.9. Responses to habitat management

There has been no specific management at Headley Warren for *Cryptocephalus nitidulus*, but as it has been known there for a very long period of time it seems that whatever management has occurred in the past has been favourable for this species. Scrub clearance over the years may have resulted in the loss of this species from Stainton's Field, although, it is equally likely that the proliferation of *Brachypodium sylvaticum* meant that ground conditions were not suitable for the larvae.

Recent management of Hackhurst Downs (west of the White Downs) has had a more direct effect on *Cryptocephalus nitidulus*. This area supported a very strong population of *C. nitidulus* until the late 1990's (P. Hodge, pers. comm.) when the *B. pendula* scrub was all removed. *C. nitidulus* is still found in this field but now seems to be restricted to its northern perimeter of the field. Natural regeneration of the scrub will probably allow *Cryptocephalus nitidulus* to recolonise the inner part of the field over the next few years.

11.10. General recommendations

Current sites for this species or sites that are to be considered as potential recipient sites for introductions should be managed in ways that encourage the development of areas which offer a warm, sheltered micro-climate. Key trees should be identified at current sites and the prevailing conditions around such trees should be replicated around other trees in adjacent areas, apart from being in warm microclimates the trees should also have a high proportion of bare ground beneath. Meagre cover could be encouraged by letting host-trees mature, developing habitat on steep escarpments and encouraging rabbit grazing. Host trees should not be allowed to become too dense. An open scrub/woodland habitat should be encouraged that offers a complex vegetation structure. Dense ground cover beneath host trees should be avoided, as leaf litter will not accumulate on the ground and small mammal activity will increase. Disturbance around the base of key trees should be avoided, i.e. trampling by livestock or humans. Over-mature scrub should be thinned out, but there should be no wholesale removal of suitable trees from any one particular area. Scrub should be developed or maintained that offers a range of species, with *Crataegus monogyna* interspersed with *B. pendula* trees, although the scrub should be predominantly *B. pendula*. Any areas that offer host trees in warm, sheltered conditions on a relatively bare substrate whether they are calcareous grassland, heathland or woodland ride sites are likely to be suitable for *C. nitidulus.*

11.11. Specific recommendations

11.11.1. Headly Warren

Cryptocephalus nitidulus is found in three of the fields of Headley Warren (Plate 16). The Downs Field supports the strongest population, which is also the field that has a strong population of *C. coryli*. The very short sward in this field is a feature that should be maintained. Rabbit grazing is unpredictable and therefore it may be necessary at some point to graze the field with sheep. The *Betula pendula* scrub that supports *C. nitidulus* in this field is found at the southern end. There should be no complete removal of the scrub in this part of the field. The scrub should be allowed to mature for a few more years and then it could be thinned out. Currently there are no *Crataegus monogyna* trees in this part of the field. Saplings of this species could be planted to allow female *C. nitidulus* beetles access to a food source that appears to increase fecundity. Although the sward in this field is very short some areas may benefit from the creation of patches of bare ground beneath host-trees. A scrub ecotone could be developed around the entire perimeter of this field. This could be initiated by planting saplings protected from rabbit browsing. Eventually, rabbit browsing could be used as a means of preventing, or slowing over-maturation of the scrub.

A second population of *Cryptocephalus nitidulus* is found in the Flying Bomb Field. This population is found along a south facing woodland edge that comprises *Corylus avellana* (coppiced)*, Crataegus monogyna, Betula pendula* and *Acer campestris*. The ground cover here is relatively dense and consists mostly of grasses. The population in this field is not strong and it could be enhanced if the ground cover was reduced by sheep grazing or other means. Patches of bare ground could also be created beneath the woodland edge. A limited amount of *B.pendula* and *C. monogyna* scrub could be encouraged in the open part of the field. The area available to the adults could also be increased in this area if the woodland edge was scalloped, providing small, sheltered pockets.

Only three *Cryptocephalus nitidulus* beetles were found on the Orchid Bank. This area was recently cleared and the ground vegetation has become very tall and dense. Heavy sheep grazing of this area may be the only way to enhance the *C. nitidulus* population. This field has many host-trees that appear to be suitable for *C. nitidulus*, but until the ground conditions are made more suitable for larvae it is unlikely that this field will support many *C. nitidulus.*.

11.11.2. The White Downs

Cryptocephalus nitidulus is found in several isolated populations along a relatively long stretch of the North Downs most of which is known as the White Downs. Several of the areas appear to be sub-optimal for *Cryptocephalus nitidulus*. The areas that support *C. nitidulus* should be managed to re-create the conditions that are found in the one small area where *C. nitidulus* is very common. In particular the generation of a low sward and bare ground beneath trees. The scrub that presently occurs between the mature woodland and calcareous grassland should be allowed to mature, but thinning of this scrub should be carried out regularly as shading and dense ground cover are not beneficial features. Most of the areas support a species rich scrub and this should be maintained, especially where *Betula pendula* and *Crataegus monogyna* are found together. To enable links to be made in between the populations of *C. nitidulus* along the White Downs large tracts of woodland could be thinned and corridors produced to connect populations. These corridors could be scalloped to provide pockets of suitable habitat. Populations separated by areas of scrubless habitat could be connected by planting *B. pendula* saplings close enough together to allow dispersal of adults. Alternatively, natural re-generation of the *B. pendula* could be encouraged but the seedlings would have to be protected from rabbit and sheep damage.

11.12. Cryptocephalus decemmaculatus

11.12.1. Basic requirements

Like the former two species, *Cryptocephalus decemmaculatus* is very thermophilic and adults require host-plants located in south-facing aspects surrounded by wind breaks of taller vegetation. A suitable tree for this species is shown in Plate 23. The preferred host-plant of the adults is the grey sallow (*Salix cinerea*), although any *Salix* species growing in the correct conditions would be suitable for the adults. Larvae have a preference for *S. cinerea* litter, but in captivity performed better on a diet of *S. alba.* A very limited number of trees identified at the one known English site possess the correct juxta-position of habitats suitable for both adults and larvae.

11.13. Detailed study site and its history

Autecological work on *C. decemmaculatus* was concentrated on Wybunbury Moss (Cheshire) the only English location where there is a strong population of this beetle (Figure 11.11 and 11.12),

11.13.1. Wybunbury Moss (Cheshire)

A detailed history exists for Wybunbury Moss (T. Coleshaw, pers. comm.), which is part of a once extensive network of mosses and bogs that existed in the north west of England. The moss was recorded in the Domesday survey of 1086 and old records suggest that it was slightly larger than today. Over the years there were many attempts to drain and reclaim the moss. Tree ring analysis implies that much drier conditions existed in the late 19th century. From 1910 onwards, however, drainage appears to have been less effective. The route of a rail track was pegged out over the moss in the 19th century, but the project was later abandoned. The moss was purchased by the Nature Conservancy Council between 1955 and 1959, but the majority of the reserve received no direct management until 1986 (the exception being a small part of the central *Sphagnum* lawn). Since 1986 rotational coppicing of small blocks of woodland dominated by birch and willow has been carried out to maintain early seral stages of woodland (Plate 25). Before this direct management of the site, scrub encroachment into the *Sphagnum* lawn would have greatly reduced the area of habitat suitable for *C. decemmaculatus.*

11.14. Responses to habitat management

Experimental habitat management was conducted here during winter of 1999. After consultation with the head warden it was decided that a planned woodland clearance would be carried out so as to effectively enlarge the area of habitat utilisable by adult *Cryptocephalus decemmaculatus* in area B (Plate 26).

It was hoped that this would allow the beetles to move freely from area B into another area of scrub to the west of area B that was previously separated by 12-15 m of unsuitable habitat. No beetles had been found in this recipient area in previous surveys. Fieldwork in the summer of 2000 confirmed that the small sallows linking the two areas were now less shaded, and that *C. decemmaculatus* adults could now be found on these now suitable host-trees and into the recipient area. This management success shows that on a small scale it is relatively simple to expand the range of this species on a particular site, so long as there are suitable host-plants that it can use as ‘stepping stones’. Unfortunately, toward the end of the summer in 1999 some other management was carried out that was not in the best interests of *C. decemmaculatus*. The lower section of one of the only *Salix cinerea* tree in area A (Plate 27) was removed during regular strimming of the walkway edge that runs around the *Sphagnum* lawn.

Many *C. decemmaculatus adults* could be found on this low growth during the early summer. The effects of this accidental removal are hard to gauge, but the population estimate for 2000 in this area was lower than 1999. Adult beetles towards the end of the summer may have been forced to feed (sub-optimally) on *Betula pubescens*. During the late summer of 2000 host-plants were cleared from the borders of the walkway. These plants had formed an almost continuous chain from areas A to B and from B to C. The goal of joining these sub-populations will now be a much more protracted process and re-planting should be undertaken.

Anecdotal evidence suggests that *Cryptocephalus decemmaculatus* was lost from Chartley Moss in Staffordshire due to unsuitable management. The species was known from this site from 1879 until 1979, but was probably always scarce there.

The small area of sallow scrub that supported *C. decemmaculatus* was not managed in a way that was conducive to the long-term survival of the species at this site, because it was allowed to mature. Furthermore, recent management undertaken by English Nature has focused on removal of all sallows from the inner part of the bog. Even if a small population of *C. decemmaculatus* remained unnoticed past 1979 its primary host-plants would have all been removed by the late 1980's. Nonetheless Chartley Moss is superficially, very similar to Wybunbury Moss and would be a suitable site for re-introduction, after preparatory management.

11.15. General recommendations

The most important consideration for the management of sites that currently support *Cryptocephalus decemmaculatus* or potential sites for introductions is the propagation and maintenance of areas with a warm microclimate. Key trees should also be identified at each site that offer suitable conditions for adults and larvae alike. Windbreaks of tall vegetation should be preserved around the sites. Pockets or glades should be created adjacent to sub-populations, into which host-plants can be planted if necessary (sub-populations should be encouraged to mix via 'corridors' of suitable habitat).

Well maintained scrub should be encouraged and removal of suitable *Salix* trees should be avoided. A network of small host-trees should be allowed to develop that act as 'stepping stones' for the adult beetles. The ground level characteristics below host-plants that are optimal for larvae still need to be fully understood, although the presence of moss may be important. Grazing does not seem to be important in the management of ground conditions, but tall dense conditions beneath host-plants should be avoided as less leaf litter is likely to accumulate on the ground. Key trees that become unsuitable for adults could be removed during the winter (and replaced by new saplings) or coppiced once or twice, although coppicing of mature trees produces foliage that is sub-optimal for adult beetles. Heavy disturbance through trampling around the base of known key trees should be avoided.

11.16. Specific recommendations

11.16.1. Wybunbury Moss

Cryptocephalus decemmaculatus is surprisingly common at this site, with several hundred individuals and is found in south facing aspects around the whole inner part of the bog. The only part of this site that naturally supports *C. decemmaculatus* is the inner *Sphagnum* lawn onto which scrub encroaches from the surrounding woodland. Three sub-populations exist as indicated in Plate 25. Recent management has focused on the control of this scrub. There are a handful of *Salix cinerea* trees that can be seen as key to the integrity of the population. Similar trees should be planted or encouraged to grow in close proximity to these trees with the eventual goal of establishing scrub links between all the sub-populations. In order to safeguard the population at this site there should be no large-scale scrub clearance anywhere near the focus of the three sub-populations. Windbreaks of taller vegetation should be maintained around all of the sub-populations. When trees are planted the species used should be *S. cinerea*. Cuttings would be the simplest method, although experience has shown these cuttings do not propagate very easily. To remedy this problem *S. alba* cuttings might be planted, as they are known to propagate relatively easily, though the preference of beetles for these plants would have to be closely monitored.

Area A (Plate 25) could be optimised if there were more *S. cinerea* trees available. Currently there is only one such tree and the individuals there are currently largely dependent on *Betula pubescens*. The nature of the scrub network in this area is very conducive to the dispersal of adults as there are many ‘stepping stones’ that adults can use to move around. Within ten years this scrub network could become too mature for *Cryptocephalus decemmaculatus*, thinning the scrub by removing some of the trees could therefore be beneficial.

Area B (Plate 25) supports the strongest sub-population on the site. There are very few *S. cinerea* trees in this area and there is one tree in particular that seems to provide optimal conditions for adults and larvae. The glade with this tree is very small and is vulnerable to scrub encroachment due to the surrounding woodland on all sides and relatively dry conditions. Careful management of the scrub in this area must be practised.

Area C (Plate 25) supports a strong sub-population. There are several small *S. cinerea* trees in this area and all are sufficiently connected to one another by scrub to enable all of them to be utilised. There are also several large *Betula pubescens* bushes and these are casting some shade onto the *S. cinerea* trees. These bushes should be cut down to limit shading, but not removed as they provide useful shelter from the prevailing wind. The utilised trees are also very close to mature woodland that may cast some shade that is not beneficial to the adults. If confirmed the lower edge of the canopy of these trees could be raised to remove this shading effect.

11.16.2. Camghouran (Perthshire)

This site has not been studied in depth and further work is therefore required before formal recommendations can be made. The area in question is a south-facing bank that supports a wet heath community. The area that supports *Cryptocephalus decemmaculatus* is approximately only 100 m^2 (Plate 28) and is acutely vulnerable to scrub maturation.

The site is alongside a track that along its whole length supports *S. cinerea* and *S. caprea.* This sallow border could be scalloped and *Salix* saplings or cuttings could be planted to allow the beetles a way of accessing scallops that exist along the whole length of the track. To safeguard the current population the scrub that occurs should be maintained and augmented via natural regeneration or cutting/sapling planting.

All three *Cryptocephalus* species in this chapter are essentially oligophagous, although, it seems as though both larvae and adults perform optimally on one particular host plant. Host-plant selection may also affect cased egg production as in *C. nitidulus* an observation that has obvious implications for site management. When ovipositing from the main host-plant eggs would fall onto the ground, scattered predominantly, with the host-plant litter. Wind blown litter may result in debris from other tree species representing a small fraction of the total under any host-plant. The dispersal abilities of *Cryptocephalus* larvae are limited this may entail that larvae are at a selective advantage if they are able to develop optimally on the type of leaf litter that is most ubiquitous under their place of oviposition. Like many other endangered insects *C. coryli, C. nitidulus* and *C. decemmaculatus* are (i) restricted to relatively small areas within reserves, (ii) relatively sessile and (iii) sensitive to subtle changes in vegetation structure.

The scrub type habitat that these species depend on is a relatively management intensive type of habitat. Scrub that is of high conservation value is typically composed of a diverse range of shrubs with a complex canopy structure together with the presence of large gaps that permits the survival of a species rich ground fauna (Kirby, 1991; Hopkins, 1996; Crofts & Jefferson, 1999).

The recommendations in this chapter only concern the requirements of the *Cryptocephalus* species. The scrub transition habitat on which the rare *Cryptocephalus* species depend is a important habitat for many invertebrates, particularly thermophilic species. The conservation value of areas like the North Downs is due, in large part, to the presence of scrub and the flora and fauna that it supports. The whole assemablage of scrub species should be considered in any management plan. Species should be identified that could benefit or suffer from the type of management carried out to enhance sites for the rare *Cryptocephalus* species.

Small open pockets that naturally occur in scrub can become unsuitable in as little as nine years for thermophilic insects (Warren, 1987c) such as a *Cryptocephalus* beetle, although for areas of *Betula pendula* scrub glades can be become too scrubbed over for *C. coryli* after 3 years (Pers. obs). Misguided habitat management has been implicated in the demise of many endangered species (Ehrlich and Ehrlich, 1981). Without direct sympathetic management based, in part, on the information in this chapter and Chapter 5 the remaining populations of these species could be lost very quickly.

Chapter 12. General Discussion

There is a lack of the basic information on many of the insect species that are of conservation concern in the UK and this can only be addressed with intensive field and laboratory studies. The research in this thesis is of an applied nature and will hopefully help lead to the successful conservation of the species that were studied. The data obtained will also hopefully suggest ways forward for the conservation of other rare insect species that are of conservation concern. The ecological knowledge gained during this PhD also allows comparisons with what is known about other species of conservation concern. For example the duke of burgundy fritillary (*Hamearis lucina*), heath fritillary (*Mellicta athalia*) grizzled skipper (*Pyrgus malvae*) and the dark green fritillary (*Argynnis aglaja*) amongst several other butterflies have been shown to have broadly similar requirements to most of the *Cryptocephalus* beetles in this study. These species require early to mid successional stages in woodland and are the ones that have shown the greatest decline in the last 150 years (Heath *et al.,* 1984). Many butterflies associated with mid-successional stages have been shown to be very sedentary (Thomas, 1991). Most species form closed colonies within discrete areas (Thomas, 1984), and few individuals leave the habitat patch in which they emerged. The autecological information on *Cryptocephalus* species now parallels with what is known about orthopteran species such as the wart-biter (*Decticus verrucivorus*) (Cherill & Brown, 1990a, 1990b). This species, like the *Cryptocephalus* beetles, has very narrow habitat requirements, that differ between stadia, all of which have to be present for the species to persist (Cherill & Brown, 1990a, 1990b).

Review of results

The data in chapter 2 shows that the way in which conservation is prioritised needs to be addressed. A more rigorous selection process would help to ensure that the correct species are being targeted for conservation. Present distributions were used as the only criteria to define the conservation status of many of the species on the BAP list. As a result of this process some species that are of genuinely high conservation concern have been overlooked, which means that resources may have been inappropriately targeted.

The work in Chapter 3 was coupled with the gathering of old information on the biology and distribution of species that have proven to be very elusive. This work yielded a lot of information on areas that were not widely known to have supported the relevant species. This chapter also presented miscellaneous ecological information findings on some of the species together with information on the captive rearing of *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus*.

The studies of released larvae recovered by visual searching alone can only yield scant ecological information (Nicholls & Pullin, 2000). The development of a technique to relocate larvae, described in this Chapter 4, bypassed this problem. Recovery rates of released *Cryptocephalus* larvae were high and a small monitoring experiment showed that larvae could be recovered on numerous occasions over many months.

Cryptocephalus coryli, C. nitidulus and *C. decemmaculatus* were the only rare *Cryptocephalus* that could be found in reliable, moderately sized populations. Field and laboratory study of these species enabled useful biological information to be gathered (Chapter 5). Larval rearing enabled the feeding preferences and performance of this life stage to be determined. Food-plant preferences were defined for all three species and they seem to be affected by coppicing. Coppiced foliage has been shown to be sub-optimal for lepidopteran larvae (Montgomery & Meyer, 1987) and was generally preferred less by adult *Cryptocephalus*. Observations suggest that *Cryptocephalus* adults, like many rare UK insects (Thomas & Morris, 1995), are very thermophilic. The preferred conditions in which the host-plants were to be found were also elucidated. A complex relationship was found to exist between the needs of the adults and the needs of the larvae. The integrity of a population of any one site depends on a very limited number of trees that offer the juxta-position of suitable adult and larval habitats. Larvae were found to be relatively catholic in their taste for leaf litter, although their performance was optimised on one particular type of leaf litter, which corresponded with adult food preferences. Females seem to feed optimally in favour of ovipositing in conditions that will optimise larval performance.

The autecological requirements that were defined for *Cryptocephalus coryli, C. decemmaculatus* and *C. nitidulus* were used to help provide sympathetic habitat recommendations for each current site (Chapter 11). This was integrated with information concerning the past use and management of each site (Chapter 11). Ill advised management from a *Cryptocephalus* perspective has been carried out at many of these sites. This may have been detrimental to a range of species, not just *Cryptocephalus* beetles and it is often the case that the conservation of flag ship taxa such as butterflies and lizards takes priority over the needs of many obscure invertebrate species that do not share the same habitat needs as some Lepidoptera or reptiles. The importance of good quality scrub at these sites needs to be recognised.

Before the work described in this thesis *Cryptocephalus* larvae were very poorly known and what information existed originated from captive larvae. Wild larvae are exceptionally difficult to find due to their extreme crypsis. This problem was countered by the use of the technique described in Chapter 4. Large numbers of *Cryptocephalus coryli C. decemmaculatus* and *C. nitidulus* larvae reared in captivity were released and then monitored over the winter and into the spring (Chapter 6). This strategy enabled insights to be gained into the ecology of wild larvae. Small mammal predation was found to be important factor in the mortality of *C.coryli* larvae and this type of predation has been identified as important mortality factor in post diapause larvae generally (Duffey, 1968; Webb & Pullin, 1996) There seems to be a paradoxical relationship between the female oviposition preference and the survival of larvae in that oviposition occurs in habitat where larval mortality is likely to be high. This observation has important implications for the identification and preparation of sites for re-introductions, and for management of nascent populations.

The population of *Cryptocephalus decemmaculatus* at its one remaining site was relatively large, as was the strongest *C. nitidulus* population (Chapter 7). Their estimated population sizes compare favourably to some estimates of other insect species of conservation concern (Warren, 1987b; Curtis-Creighton & Schnell, 1998; Bedick *et al.,* 1999). Recapture rates of *C. decemmaculatus* adults were higher than in other published studies of rare beetle MRR studies (Curtis-Creighton & Schnell, 1998; Bedick *et al.,* 1999) although it was more difficult to recapture marked *C. nitidulus* adults. Many insect species living in early successional habitats have been shown to be surprisingly sessile (Warren, 1987b; Thomas, 1991) and *C. decemmaculatus* and *C. nitidulus* were both shown to have very limited powers of dispersal. Movement around their habitat may depend on the presence of a network of host-plants that can be used as ‘stepping stones’. Exchange between sub-populations, separated by only small distances, appears to be very rare if barriers to dispersal exist, i.e. scrubless habitat or tracts of woodland. This is similar to other studies on the dispersal of lepidopteran species that depend on similarly dynamic habitats (Warren, 1987b; Thomas, 1991). Creation and management of ‘stepping stone’ trees between the cores of sub-populations should be a fundamental part of habitat manipulation for these species.

This poor dispersal ability of the *Crytpocephalus* species in Chapter 7 is reflected in the genetic variation that exists between sub-populations at a particular site (Chapter 8). Many phytophagous beetle species have similarly been shown to possess high levels of genetic diversity even over small distances (McCauley, 1991; Rank, 1992). The observed variation at this scale was large and in most cases was of a similar magnitude to the variation that exists between populations that are separated by very large distances. Re-introductions should take this into account in order to preserve the genetic diversity that exists within each species (Johnson and Jordan, 2000).

A conservation status must only be applied with taxonomic assurance (Avise, 1989) otherwise conservation resources will be wasted on species that are not truly species or even distinct races. Investigation of the species status of *Cathormiocerus britannicus* (Chapter 9) showed that extreme caution must be exercised when assigning a conservation status to poorly known insect species, especially when there is the complication of parthenogenetic reproduction. This species was shown to be genetically and morphologically indistinct from *C. myrmecophilus*. Other studies of this nature will undoubtedly reveal many other obscure rarities to be wrongly identified commoner species, only separated on the basis of continuous morphological characters. This is particularly important for putative UK endemic species, which automatically gain a high conservation status in the UK as the glacial history of this country is strongly against the presence of any unique insect species.

Little information can be gained from species for which no moderately sized populations are known (Britton *et al.,* 1994; New *et al*., 1995). Captive rearing and the release of moderately large numbers of marked recoverable insects gives the invertebrate ecologist a useful tool for understanding the biology and requirements of species that are naturally very rare (Chapter 10). Although releases are primarily used as a means of enhancing or re-introducing a population of a species. Any successful establishment can in some circumstances be regarded as a bonus when experimental releases are first being deployed as a way of gaining fundamental autecological information.

Using the results

There are five major objectives within the Biodiversity Action Plans for *Cryptocephalus coryli, C. decemmaculatus,* and *C. nitidulus* (UKBG 1999). Most of these have been completely or partially met for each species as a result of the research in this thesis. The causes of decline for each of the species have been elucidated, although in the case of *C. decemmaculatus* there has not been a marked decline in recent years at least. Surveys of extant colonies and historic sites were undertaken for the three species although a lot of work still needs to be undertaken here. The landowners of the sites have also been advised as to the requirements of the species and this will be fundamental in maintaining their extant populations. The first re-introductions of populations using the information gained has been initiated with *C. coryli* in Lincolnshire. *C. decemmaculatus* should follow in 2002. Suitable recipient sites still need to be identified for *C. nitidulus* re-introductions.

The BAP’s for each of the three species draws links with the relevant Habitat Action Plans, however, the HAP’s for lowland calcareous grassland and heathland do not really take into account the needs of species that depend on a scrub transitional habitat. Scrub is rarely welcomed at sites when it is spreading onto grassland, heathland or wetland (Hopkins, 1996), despite being rich in rare invertebrates and plants (Hopkins, 1996). Consequently, scrub habitats are at risk from conservation workers and the conservation importance of good quality scrub needs to be considered in the production of revised HAP's.

Employing consultant entomologists during the course of this PhD enabled the survey of many areas that would otherwise have been impossible due to the relatively short period of adult beetle activity each year. They could only provide minimal ecological data however. Further studies may benefit from recruiting a team of assistants who can be collectively taught a range of techniques for the collection of comparable data from a number of sites in combination with their general survey work. This approach would be relatively cheaper and more efficient that employing consultant entomologists.

The narrow habitat requirements of the rare *Cryptocephalus* beetles coupled with their unusual life cycles developmental strategy and their tendency to become split into geographically and genetically isolated sub-populations are among the reasons for their rarity. These traits predispose them to having limited distributions and in some cases low abundances. Habitat fragmentation and unsympathetic management of their remaining sites have compounded these traits. Many of the findings of this thesis were species specific and applied in nature, but, the '*mother knows best*' argument was a running theme and the results of many of the chapters were discussed in this context. The *naïve adaptionist* hypothesis (Courtney & Kibota, 1990) argues that: "female phytophagous insects should oviposit where their offspring have the greatest probability of survival". This hypothesis has been supported in some studies (Price, 1991; Ohgushi, 1995), but many other studies have shown that females seem to oviposit in conditions that are optimal for themselves, not their larvae (Courtney & Kibota, 1990, Craig *et al.,* 2000; Scheirs *et al.,* 2000). The observations of adult habitat preferences and larval performance suggest that *Cryptocephalus* beetles do not fit the *naïve adaptationist* hypothesis.

What next?

There is a great deal of further work to be done on members of the genus *Cryptocephalus*. The effect of coppicing on the leaf chemistry of the host-plants and its knock-on effects on adult feeding preferences should be further examined. Larval performance on leaf litter originating from coppiced host-plants should also be examined. Releasing relatively large numbers of *C. coryli* should enable the dispersal ability of this species to be more fully understood, as wild individuals are only found in small numbers. Further molecular studies also need to be carried out to elucidate the relatedness of the disjunct populations of the rare species, as many have been recorded from the south of England as well as Scotland. These populations may represent very different genetic races and if so should be conserved separately. Comparative material from Scandinavia and France could be used to determine the origins of these disjunct populations. Many miscellaneous observations among the studied species could, with further research, yield interesting findings, such as leaf cutting by adult *C. coryli* and extended larval development

Surveys of areas that could still support populations of the rare *Cryptocephalus* species also need to be undertaken, in particular, reliable populations of *C. exiguus, C. primarius* and *C. sexpunctatus* still need to be located, if they exist. This can only be achieved by intensive surveying of new areas with suitable habitat, areas where individuals have been recorded recently or re-surveying historic locations. Surveys to confirm absences should also form the initial stages of identifying sites for re-introductions. The use of introductions as an ecological tool should be expanded as this is the only way that autecological information will be gained on the most elusive species. This will also allow an investigation into the minimum propagule sizes that are needed for of re-introductions.

References

Allen, A.A. (1960d) A new capture of *Cryptocephalus 10-maculatus* (Col., Chrysomelidae) in Scotland. *Entomologist's Monthly Magazine*, **96**, 271.

Allen, A.A. (1970a) An overlooked Sussex record of *Cryptocephalus 10-maculatus* L. (col., Chrysomelidae). *C. biguttatus* Scop. In Surrey. *Entomologist's Monthly Magazine*, **106**, 120.

Alyokhin, A. V. & Ferro, D. N. (1999) Reproduction and dispersal of the summer-generation Colorado potato beetle (Coleoptera: Chrysomelidae). *Environmental Entomology,* **28**, 425-430.

Amato, G.D. (1991) Species hybridisation and protection of endangered animals. *Science,* **253**, 250.

Arnold, R.A. (1983) Ecological studies of six endangered butterflies (Lepidoptera, Lycaenidae): island biogeography, patch dynamics and the design of the habitat preserves. *University of California Publishing. Entomology*. **99**, 1-161

Ashe, G.H. (1922) Coleoptera in Worcestershire in 1921. *Entomologists Monthly Magazine*. **58**, 108.

Atty, D.B. (1983) *Coleoptera of Gloucestershire*. Cheltenham.

Avise, J.C. (1989) A role for molecular genetics in the recognition and conservation of endangered species. *Trends in Ecology and Evolution*, **4**, 279-281.

Avise, J.C. & Nelson, W.S. (1989) Molecular genetic relationships of the extinct dusky seaside sparrow. *Science*, **243**, 646-648.

Backus, V.L., Bryant, E.H., Hughes, C.R. & Meffert, L.M. (1995) Effects of migration or inbreeding followed by selection on low-founder-number populations: implications for captive breeding programs. *Conservation Biology*, **9**, 1216-1224.

Bailey, N.T.J. (1951) On estimating the size of mobile populations from recapture data. *Biometrika*, **38**, 293-306.

Bailey, N.T.J. (1952) Improvements in the interpretation of recapture data. *Journal of Animal Ecology*, **21**, 120-127.

Barrs, M.A. (1979) Patterns of movement of radioactive carabid beetles. *Oecologia*, **44**, 125-140.

Bedick, J.C., Ratcliffe, B.C., Hoback, W.W. & Higley, L.G. (1999). Distribution, ecology and population dynamics of the American burying beetle *Nicrophorus americanus* Olivier (Coleoptera, Silphidae) in south central Nebraska, USA. *Journal of Insect Conservation*, **3**, 171-181.

Bedwell, E.C. (1899) *Cryptocephalus exiguus,* Schneid *(=Wasastjernae,* Gyll): an addition to the Suffolk fauna. *Enmologist's Monthly Magazine*, **35**, 45-46.

Bedwell, E.C. (1926) *Cryptocephalus querceti* at Windsor, Berks. *Entomologists Monthly Magazine,* **62,** 240-241.

Berdegué, M., Reitz, S.R. & Trumble, J.T. (1998) Host plant selection and development in *Spodoptera exigu*a: do mother and offspring know best? *Entomologia Experi-mentalis et Applicata,* **89**, 57–64.

Bernays, E.A. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology,* **69**, 886–892.

Best, R.L., Beegle, C.C., Ownes, J.C. & Ortiz, M. (1981) Population density, dispersion and dispersal estimates for *Scarites substriates, Pterostichus chalcites* and *Harpalus pennsylvanicus* (Carabidae) in an Iowa cornfield. *Environmental Entomology*, **10**, 847-856.

Blair, K.G. (1934) A new species of *Cathormiocerus* from Britain. *Entomologists Monthly Magazine*, **70**, 26-28.

Borovec, R. (1989) Les espèces Françaises du genre *Trachyphloeus* Germar, 1824, (ed J. Tempère), **81**, 157, Paris.

Bratton, J. H. (1991) British Red Data Books, 3. Invertebrates other than insects. Joint Nature Conservation Committee. Peterborough.

Britton, D.R., New, T.R. & Jelinek, A. (1994) Rare Lepidoptera at Mount Piper, Victoria – the role of a threatened butterfly community in advancing understanding of insect conservation. *Journal of the Lepidoptera Society*.

Brown, K.S. Jr. (1991) Conservation of neotropical environments: insects as indicators. *The Conservation of Insects and Their Habitats* (eds N.M. Collins & J.A. Thomas), pp. 349-404. Academic Press, London.

Brown, JH, (1995) *Macroecology*, 269pp. University of Chicago Press, Chicago, USA.

Bryant, E.H., Backus, V.L., Clark, M.E. & Reed, D.H. (2000) Experimental tests of captive breeding for endangered species. *Conservation Biology,***13** (6), 1487-1496.

Buckner, C.H. (1969) The common shrew (*Sorex araneus*) as a predator of the winter moth (*Operophtera brumata*) near Oxford, England. *Canadian Journal of Entomology,* **101**, 370-375.

Burlini, M. (1955) Revisione dei *Cryptocephalus* Italiani e della maggior parte delle specie di Europa. *Memorie Societa Entomologica Italiana,* **35**, 1-287.

Carcamo, H.A.,Prescott, C.E., Chanway, C.P. & Abe, T.A. (2001) Do soil fauna increase rates of litter breakdown and nitrogen release in forests of British Columbia, Canada? *Canadian Journal of Forest Research*, **31** (7), 1195-1204.

Caterino, M.S., Cho, S. & Sperling, F.A.H. (2000) The current state of insect molecular systematics: A thriving tower of Babel? *Annual Review of Entomology*, **45**, 1-54

Champion, G.C. (1908) Coleoptera in the Woking district. *Entomologist's Monthly Magazine*, **44**, 254.

Channell, R, & Lomolino, M.V. (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography*, **27**, 169-179.

Charnov, E.L. (1982) *The theory of sex allocation theory*. Princeton University Press, 355 pp.

Cherill, A.J. & Brown, V.K. (1990a) The life cycle and distribution of the wart biter *Decticus verrucivorus* (L.) (Orthoptera: Tettigonidae) in southern England. *Biological Conservation,* **53,** 125-143.

Cherill, A.J. & Brown, V.K. (1990b) The habitat requirements of the wart biter *Decticus verrucivorus* (L.) (Orthoptera: Tettigonidae) in southern England. *Biological Conservation,* **53,** 145-157.

Clayson, P (1994) *The Coleoptera of Whixhall Moss*. BSc Hons. Dissertation. University of Nottingham Trent.

Collins, N. M. & Thomas, J. A., eds (1991) *The conservation of insects and their habitats*. Academic Press, London.

Collins, G.A. (1999) *Cryptocephalus coryli and Cryptocephalus nitidulus* in Surrey. A survey into the distribution and habits of two Red Data Book leaf-beetles on the Surrey North Downs in 1999. English Nature Research Report. English Nature, Peterborough.

Corbet, G.B. & Harris, S., eds (1991) *The Handbook of British Mammals.* 588pp. Blackwell, London, UK.

Courtney, S.P. & Kibota, T.T. (1990) Mother doesn't know best: selection of hosts by ovipositing insects. *Insect-plant Interactions* (ed E. A. Bernays) pp. 161-188. CRC Press, Boca Raton, Florida.

Cox, D. (1948) Food-plants of *Cryptocephalus sexpunctatus* L. (Col., Chrysomelidae) *Entomologists Monthly Magazine,* **84**, 185.

Cox, M.L. (1994) The hymenoptera and diptera parasitoids of Chrysomlidae. *Novel Aspects of the Biology of the Chrysomelidae* (eds P.H. Jolivet, M.L. Cox & E. Petitpierre) pp 419-467. Kluwer Academic Publishers, Netherlands.

Craig, T.P., Itami, J.K., Shantz, C., Abrahamson, W.G., Horner, J.D. & Craig, J.V. (2000) The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis. Ecological Entomology*, **25**, 7-18.

Crandall, K.A., Bininda-Edmonds, O.R.P., Mace, G.M. and Wayne, R.K. (2000) Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution*, **15**, (7), 290-295.

Crofts, A. & Jefferson, R.G. (1999) The lowland grassland management handbook. 2nd edition. Peterborough, English Nature/The Wildlife Trusts.

Curtis-Creighton, J. & Schnell, G.D. (1998) Short-term movement patterns of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation*, **86**, 281-287.

de Jong, P.W., Gussekloo, S.W. & Brakefield, P.M. (1998) Differences in thermal balance, body temperature and activity between non-melanic and melanic two-spot ladybird beetles (*Adalia bipunctata)* under controlled conditions. *Journal of Experimental Biology*, **199**, 2655-2666.

Department of the Environment (1994) *Biodiversity. The UK Action Plan.* Her Majesty's Stationery Office, London.

Dieckmann, L. 1964. Die mitteleuropaischen Arten aus der Gattung *Bagous* Germ. *Entomologische Blatter fur Biologie und Systematik,* **60** (2), 88-111.

Dieckmann, L. (1980) "Beitrage zur insekten fauna der DDR: Coleoptera Curculionidae (Brachycerinae, Otiorryhnchinae, Brachyderinae)." *Beitrage Entomologische*, **30**, 145- 310.

Diogo, A.C., Vogler, A.P., Gimenez, A., Gallego, D & Galian, J. (1999) Conservation genetics of *Cicendela deserticoloides*, an endangered tiger beetle endemic to southeastern Spain. *Journal of Insect Conservation*, **3**, 117-123.

DMAP for Windows (version 7.0c 32bit). Alan Morton, Copyright © 1993-1999.

Doak, P (2000) Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. *Ecology,* **81,** 1828-1841.

Donisthorpe, H.St J.K. (1938) A few notes on *Cryptocephali. Entomologist's Record and Journal of Variation*, **50**, 208-209.

Drane, A.B. (1990) Annual Exhibition. Imperial College, London, 28th October 1989. Coleoptera . *British Journal of Entomology and Natural History*, **3**, 84-85.

Duffey, E. (1968) Ecological studies on the large copper butterfly *Lycaena dispar* Haw. *batavus* Obth. At Woodwalton Fen National Nature Reserve, Huntingdonshire. *Journal of Applied Ecology,* **5**, 69-96.

Duffey, E. & Watt, A.S. eds (1971) *The Scientific Management of Animal and Plant Communities for Conservation*. Blackwell, Oxford.

Dysart, R.J., Maltby, H.L. & Brunson, M.H. (1973) Larval parasites of Oulema melanopus in Europe and their colonization in the United States. *Entomophaga*, **18**, 133-167.

Ehnstrom, B., Gardenfors, U. & Lindelow, A. (1993) Rodliustade Evertebrater I Sverige. The Swedish Threatened Species Unit. Stockholm, Sweden.

Ehrlich, P.R. and Ehrlich, A.H. (1981) *Extinction: the causes and consequences of the disappearance of species*. 305pp. Random House, New York.

Erber, D. (1988) The Camptosomata. *Biology of the Chrysomelidae* (eds E. Petitepierre, P. Jolviet & T.H. Hsiao). Kluwer Academic Publishers. Netherlands.

Escalera, M.M. de la, (1918) Revision de las especies del gen. *Cathormiocerus* Sch. de la Peninsula y Marruecos. *Trabajos del Museo nacional de Ciencias naturales Madrid (Serie Zoologia),* **38**, 1-64.

Felsenstein, J. (1993) DNADIST version 3.5c -Program to compute distance matrix from nucleotide sequences. University of Washington.

Fitzgibbon, C.D. (1997) Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology,* **34**, 530-539.

Forestry Commission. (1984). Census of woodland trees, 1979-1982, Great Britain, Forestry Commission, Edinburgh, UK.

Foster, G.N. (1991). Conserving insects of aquatic and wetland habitats, with special reference to beetles. *The Conservation of Insects and their Habitats* (eds N. M Collins & J. A. Thomas), pp 237-262. Academic Press, London.

Fowler, W.W. (1890) *The Coleoptera of the British islands.* Volume 4. Reeve Press, London,

Fowler, W.W. and Donisthorpe, H.St. J.K. (1913) *The Coleoptera of the British islands.* Volume 6. Reeve Press, London,.

Frankham, R. (1995a) Effective population size/adult population ratios in wildlife: a review. *Genetical Research*, Cambridge, **66**, 95-107.

Geiser, R. (1998) Rote liste Gefahrdeter Tiere Deutschlands.Schriftenreihe fur landschaftespflege und naturschutz. Heft 55. Bundesant fur naturschutz. Bonn Badd Godesburg.

Goldstein, P.Z., DeSalle, R., Amato, G. & Vogler A.P. (2000) Conservation genetics at the species boundary. *Conservation Biology,* **14** (1), 120-131.

Gomez-Zurita, J., Juan, C. & Petitpierre, E. (2000) The evolutionary history of the genus *Timarcha* (Coleoptera, Chrysomelidae) inferred from Mitochondrial COII gene and partial 16S rDNA sequences. *Molecular Phylogenetics and Evolution*, **14** (2), 304-317.

Greatorex-Davis. J.N. & Marrs, R.H. (1990). The quality of coppice woods as habitats for invertebrates in Coppiced Woodlands, their management for wildlife. Nature Conservancy Council. Peterborough, England.

Green, R. (1979) The ecology of wood mice (*Apodemus sylvaticus*) on arable farmland. *Journal of Zoology*, **188**, 357-377

Grevstad, F.S. & Herzig, A.L. (1997) Quantifying the effects of distance and conspecifics on colonization: experiments and models using the loosestrife beetle, *Galerucella calamariensis*. *Oecologia*, **110**, 60-68.

Groombridge, B. ed. (1992) *Global Biodiversity. Status of the Earth's Living Resources.* Chapman and Hall, London.

Hadley, N.F. (1994) *Water Relations Of Terrestrial Arthropods.* Springer, New York.

Haig, S.M. (1998) Molecular contributions to conservation. *Ecology,* **79**, 413-425.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series, **41**, 95-98.

Hambler, C. & Speight, M.R. (1995) Biodiversity conservation in Britain: science replacing tradition. *British Wildlife*, **6**, 137-147.

Hambler, C. & Speight, M.R. (1996) Extinction rates in British non marine invertebrates since 1900. *Conservation Biology,* **10** (3), 892-896.

Hansen, V. (1965) Danmarks fauna. *Snudebiller,* **69**, 524pp.

Hansen, M. (1996) Catalogue of the Coleoptera of Denmark. *Entomologiske meddelelser,* 191-192.

Hanski, I. (1992) Insectivorous mammals. *Natural Enemies. The Population Biology of Predators, Parasites and Diseases* (ed. M.J. Crawley), pp. 163-187. Blackwell Scientific Publications, Oxford.

Hansson, L. (1985) The food of bank voles, wood mice and yellow necked mice. *Symposia of the Zoological Society of London,* **55**, 141-168.

Harding, P.T. & Rose, F. (1986) Pasture-Woodlands in Lowland Britain. Monks Wood, Institute of Terrestrial Ecology.

Hare, J.D. (1990) Ecology and management of the Colorado potato beetle. *Annual Review of Entomology*, **35**, 81-100

Harold, E. (1917). Coleoptera captured in North Middlesex and Hertfordshire in 1917. *Entomologist's Monthly Magazine*, **53**, 110-111.

Hawksworth D.L. ed (2001) *The changing wildlife of Great Britain and Ireland*. 454 pp. Taylor and Francis London.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) A review of British Mammals: population estimates and conservation status of British mammals other than cetaceans. Joint Nature Conservancy Council, Peterborough, England.

Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnaen society*, **42**, 73-88

Harvey, M. (1998) *Cryptocephalus coryli* (Coleoptera: Chrysomelidae) and other invertebrates at North Unhill Bank, Oxfordshire, in 1998. English Nature Research Report. English Nature, Peterborough.

Harwood, P. (1947) *Cryptocephalus coryli* in Inverness-shire. *Entomologists Monthly Magazine,* **83**, 88.

Heath, J., Pollard, E. & Thomas, J.A. (1984) *Atlas of Butterflies in Britain and Ireland.* Viking, Middlesex.

Henderson, C.W. (1944) *Bagous lutosus* Gy. (Col., Curculionidae) and *Cryptocephalus frontalis* Marsh. (Col., Chrysomelidae) in Leicestershire. *Entomologists Monthly Magazine*, **80**, 24.

Herzig, A.L. (1995) Effects of population density on long distance dispersal in the goldenrod beetle, *Trirhabda virgata*. *Ecology*, **76**, 2044-2054

Herzig, A.L. & Root, R.B. (1996) Colonization of host patches following long-distance dispersal by a goldenrod beetle, *Trirhabda virgata*. *Ecological Entomology*, **21**, 344-351.

Hobby, B.M. (1955) *Cryptocephalus primarius* Harold (Col., Chrysomelidae) in Berkshire. *Entomologist's Monthly Magazine*, **91**, 173.

Hodge, P. & Williams, S. A. (1997) *Cryptocephalus coryli* (L.) (Col., Chrysomelidae) - Survey and monitoring for proposed species recovery programme. English Nature Research Report. English Nature, Peterborough, England.

Hoffman, A. (1950) *Fauna de France. Coléoptères Curculionides Première Partie,* **52**. Paris.

Hogue, J.N. and Hawkins, C.P. (1991) Morphological variation in adult aquatic insects, associations with developmental temperature and seasonal growth patterns. *Journal of the North American Benthological Society*, **10** (3), 309-321.

Holland, W. (1903) *Gynandrophthalma affinis*, Hellw. in Wychwood Forest. *Entomologist's Monthly Magazine*, **39**, 202.

Hopkins, J.J. (1996) Scrub ecology and conservation. *British Wildlife*, **8**, 28-36

Hsiao, C. & Hsiao, T.H. (1985a) Rickettsia as the cause of cytoplasmic incompatibility in the alfalfa weevil *Hypera postica* (Gyllenhall). *Journal of Invertebrate Pathology,* **45**, 244-246.

Hsiao, T.H. & Hsiao, C. (1985b) Hybridisation and cytoplasmic incompatibility among alfalfa weevil strains. *Entomologia Experimentalis et Applicata,* **37**, 155-159.

Hsaio, T.H. (1996) Studies of interactions between alfalfa weevil strains, *Wolbachia* endosymbionts and parasitoids. *The Ecology of Agricultural Pests* (eds W.O.C. Symondson & J.E. Liddell). Chapman and Hall, London.

Hyman, P.S. and Parsons, M.S. (1992) A review of the scarce and threatened Coleoptera of Great Britain. Joint Nature Conservancy Council, Peterborough, England.

IUCN. (1986) Why conserve invertebrates? IUCN Report. Gland, Switzerland.

IUCN (1995) Guidelines for re-introductions. Prepared by the SSC Reintroduction specialist group. Gland, Switzerland.

Jermin, L.S. & Mahler, V. (1993) Revised descriptions of the morphology of *Trachyphloeus bifoveolatus, T. angustisetulus, T. spinimanus* and *T. digitalis* (Coleoptera: Curculionidae). *Entomologist's Gazette*, **44**, 139-153.

Johnson, C. (1965) Coleoptera report 1959-64. Thirty-fifth report and report of recorders. *Lancashire and Cheshire Fauna Committee*, **47**, 46-55.

Johnson, J.B. & Jordan, S. (2000) Phylogenetic divergence in leatherside chub (*Gila copei*) inferred from mitochondrial cytochrome *b* sequences. *Molecular Ecology*, **9**, 1029-1035.

Jolivet, P. (1952) Quelques donness sur la myrmecophilie des Clytrides (Col. Chrysomelidae). *Bulletin de la Institute National Belgique*, **28**, (8) 1-12.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, **52**, 225-247.

Jones, R.A. (1988) Annual Exhibition. Imperial College, London SW7 – 24th October 1987. Coleoptera. *Britsih Journal of Entomology and Natural History*, **1**, 40-41.

Joy, J. & Pullin, A.S. (1999) Field studies on flooding and survival of ocerwintering large heath butterfly *Coenonympha tullia* larvae on Fenn's and Whixall Mosses in Shropshire and Wrexham, U.K. *Ecological Entomology*, **24**, 426-431.

Juan, C., Oromi, P. & Hewitt, G.M. (1995). Mitochondrial DNA phylogeny and sequential colonization of canary islands by darkling beetles of the genus *Pimelia* (Tenebrionidae). *Proceedings of the Royal Society of London B,* **261**, 173-180.

Jung, W. (1940) Ernahrungsversuche an *Carabus*-Arten. *Entomologists Bulletin,* **36**, 117-124.

Karl, S.A. & Bowen, B.W. (1999) Evolutionary significant units versus geopolitical taxonomy: Molecular systematics of an endangered sea turtle (genus *Chelonia*). *Conservation Biology,* **13** (5), 990-999.

Kevan, P. G. (1975). Sun Tracking solar furnaces in high arctic flowers: significance for pollination and insects. *Science,* **189**, 723-726.

Key, R. S., M. Drake, & D. A. Sheppard (2000) Conservation of invertebrates in England: a review and framework. English Nature Science, No. 35. English Nature, Peterborough, England.

Kidson-Taylor, J. (1904) Occurrence of *Cryptocephalus coryli* in Sherwood Forest. *Entomologist's Monthly Magazine*, **40**, 32.

Kidson-Taylor, J. (1906) Coleoptera captured in Sherwood Forest, June, 1906. *Entomologist's Monthly Magazine*, **42**, 272.

Kidson-Taylor, J. (1909) Coleoptera captured in various localities in 1908 *Entomologist's Monthly Magazine*, **45**, 163.

Kirby, P. (1992) Habitat management for invertebrates: a practical handbook. RSPB. Sandy. UK.

Kloet, G. (1964) A check list of british insects; by George Sidney Kloet and the late Walter Douglas Hincks. *Royal Entomological Society of London.*

Koch, K.C. (1992) *Die Kafer Mitteleuropas. Ecologie 3*. Goecke & Evans, Krefeld.

Lachance, S. & Mangan, P. (1990) Performance of domestic, hybrid and wild strains of the brook trout, *Salvelinus fontinalis*, after stocking: the impact of intra and inter-specific competition. *Canadian Journal of Fish and Aquatic Science*, **47**, 2278-2284.

Lamb, R.Y. & Wiley, R.B. (1986) Cytological mechanisms of thelytokous parthenogenesis in insects. *Genome,* **29**, 367-369.

Lane, S.A. & Forsythe, T.G. (2000) Noteworthy beetles found in Warwickshire (VC38) in 1999. *The Coleopterist,* **9** (2), 102-104.

Langenheim, J.H., Foster, C.E. & McGinley, R.B. (1980) Inhibitory effects of different quantitative compositions of *Hymnea* leaf resins on a generalist herbivore *Spodoptera exigua*. *Biochemical Systematics and Ecology*, **8,** 385-396.

Lande, R. (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455-1460

Lande, R. & Barrowclough, G.F. (1987) Effective population size, genetic variation, and their use in population management. *Viable populations for conservation* (ed M.E. Soule) pp 87-123 Cambridge University Press. Cambridge.

Lanteri, A.A. & Normark, B.B.(1995) Parthenogenesis in the tribe Naupactini (Coleoptera: Curculionidae). *Annals of the Entomological Society of America,* **88**, (6) 722-731.

Latter, B.D.H. & Mulley, J.C. (1995) Genetic adaptation to captivity and inbreeding depression in small laboratory populations of *Drosophila melanogaster*. *Genetics*, **139**, 255-266.

Legge J.T., Roush, R., Desalle, R., Vogler, A.P. and May, B. (1996) Genetic criteria for establishing evolutionary significant units in Cryan's Buckmoth. *Conservation Biology,* **10** (1), 85-98.

LeJeune, R. R., Fell, W. H. & Burbridge, D. P. (1955) The effect of flooding on the development and survival of the larch sawfly *Pristiphora erichsonii* (Tenthredinidae). *Ecology*, **36**, 63-70.

Lesage, L. (1985) The larvae of *Cryptocephalus fulguratus*. *Canadian Entomology,* **118**, 97-112.

Lesage, L. & Stiefel, V.L. (1996) Biology and immature stages of the North American Clytrines *Anomoea laticlavia* (Forster) and *A. flavokansiensis* Moldenke (Coleoptera: Chrysomelidae: Clytrinae). *Chrysomelidae biology, vol.3: General Studies* (eds. P.H.A. Jolivet and M.L. Cox) *pp 93-105.* SPB Academic Publishing, Amsterdam, The Netherlands.

Lincoln, F.C. (1930) Calculating waterfowl abundance on the basis of banded returns. U.S.D.A Circ., **118**, 1-4.

Lomolino, M.V. & Channell, R. (1995) Splendid isolation: patterns of geographic range collapse in endangered mammals. *Journal of Mammology*, **76**, 335-347.

Lomolino, M.V. & Channell, R. (1998) Range collapse, reintroductions and biogeographic guidelines for conservation: a cautionary note. *Conservation Biology*, **12** (3), 481-484.

Lovei, G., Stringer, I.A.N., Devine, C. & Cartellieri, M. (1997) Harmonic radar – a method using inexpensive tags to study invertebrate movement on land. *New Zealand Journal of Ecology*, 21 (2), 187-193.

Lucht, W.H. (1987) Die kafer Mitteleuropas, Katalog 254-257

Luff, M.L. (1975) Some features influencing the efficiency of pitfall traps. *Oecologia*, **19**, 345-357.

McCauley, D.E., Wade, M.J., Breden, F.J. & Wohltman, M. (1988) Spatial and temporal variation in group relatedness: evidence from the imported willow leaf beetle. *Evolution*, **42**, 184-192.

McCauley, D.E. (1991) The effect of host plant patch size variation on the population structure of a specialist herbivore insect *Tetraopes tetraophtalamus*. *Evolution*, **45**, 1675-1684.

Macfayden, A. (1968) Notes on methods for the extraction of small soil arthropods by the high gradient apparatus. *Pedobiologia*, **8**, 401-406.

Mackworth-Praed, H. (1996) *More Conservation Pieces*. pp 195. Jacka publishing. UK.

Majerus, M.E.N. & Zakharov, I.A. (2000) Does thermal melanism maintain melanic polymorphism in the two-spot ladybird *Adalia bipunctata* (Coleoptera: Coccinellidae)? *Zhurnal Obshchei Biologii,* **61** (4), 381-392

Mascanzoni, D. & Wallin, H. (1986) The harmonic radar: a new method of tracking insects in the field. *Ecological Entomology*, **11**, 387-390

Mason, C.F. (1970) Snail populations, beech litter production and the role of snails in litter decomposition. *Oecologia*, **5**, 215-239.

Massee (1947) Abundance of *Cryptocephalus sexpunctatus* L. (Col., Chrysomelidae) in Kent in 1947. *Entomologist's Monthly Magazine*, **83**, 211.

Masutti, L. (1960) Ecologia ed etologicadel *Cryptocephalus pini* L. *Bolletino Zoologica agrica Bachic*, **3**, 143-178.

May, M.L. (1985) Thermoregulation. *Comprehensive Insect Physiology*, *Biochemistry and Pharmacology*, (ed G.A. Kerjut & L.I. Gilbert) pp 145-192, Vol 4. Oxford: Pergamon Press.

May, R.M. (1990) Taxonomy as destiny. *Nature*, **347**, 129-130.

Mayhew, P.J. (1997) Adaptive patterns of host-plant selection by phytophagous insects. *Oikos,* **79** (3), 417-428

Mayhew, P.J. (2001) Herbivore host choice and optimal bad motherhood. *Trends in Ecology and Evolution*, **16** (4), 165-167.

Mehlman, D.W. (1996) Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614-624.

Memmott, J. Fowler, S.V. and Hill, R.L. (1998) The effect of release size on the probability of establishment of biological control agents: Gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand). *Biocontrol science and technology*, **8**, 103-115.

Mendel, H. (1987) Notable coleoptera at Pashford Poors Fen, Suffolk. *Entomologist's Record and Journal of Variation*, **99**, 95-96.

Mendel, M. Collier, M. (1997) Pashford beetle *Cryptocephalus exiguus* species recovery programme survey project. English Nature Research Reports. English Nature, Peterborough, England.

Mendel, H. (1998) History of *Cryptocephalus exiguus* in Britain. *The Coleopterist,* **7**, 7-10.

Merritt, A. (1994) Wetlands, industry and wildlife. The Wildfowl and Wetlands Trust, Slimbridge, UK.

Meyer, G.A. & Montgomery, M.E. (1987) Relationships between leaf age and food quality of cottonwood foliage for the gypsy moth, *Lymantria dispar*. *Oecologia*, **72**, 527-532.

Mitchell, P.L. & Woodward, F.I. (1987) Instrument for measuring temperature, photosynthetically active radiation and daylength, and its use in the measurement of daylength and temperature in coppice. *Journal of Applied Ecology*, **24**, 239-249.

Mohr, K.H. (1966) Familie: Chrysomelidae. *Die Kafer Mitteleuropas* (eds H. Freude, K.W. Harde & G.A. Lohse) Band 9. Krefeld: Goecke & Evers. Munich.

Momoi, S. (1973) On ichneumonid parasites of the rice leaf-beetle, *Oulema oryzae*, in Japan and Korea (Hymenoptera: Ichneumonidae). *Kontyu*, **41**, 444-445.

Montgomery, W.I. (1989) Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. *Journal of Animal Ecology*, **58**, 465-475.

Moore, N.W. (1976) The conservation of Odonata in Great Britain. *Odonatologica,* **5**, 37-44.

Moritz, C. (1994) Defining 'evolutionary significant units' for conservation. *Trends in Ecology and Evolution*, **9**, 373-375.

Morley, C. (1895) Coleoptera at Ipswich in 1895. *The Entomologists Record and Journal of Variation*, **7**, 182-184

Morley, C. (1899) The Coleoptera of Suffolk. Plymouth: J.H. Keys.

Morris, D.W. (1995) Earth's peeling veneer of life. Nature, **373**, 25.

Morris, M.G. (1987) Changing attitudes to nature conservation; the entomological perspective. *Biological Journal of the Linnean Society*. **32**, 213-223.

Morris, M.G., Collins, N.M., Vane-Wright, R.I. & Waage, J. (1991) The utilisation and value of non-domesticated insects. *The Conservation of Insects and Their Habitats.* (eds N.M. Collins, & J.A. Thomas) pp 319-349. Academic Press, London.

Morris, M.G. (1997) *Broad-Nosed Weevils. Coleoptera: Curculionidae (Entiminae).* Handbooks for the Identification of British Insects.

Morton, A.C. (1991) Captive breeding of butterflies and moths. II. Conserving variation and managing bio-diversity. *International Zoo Yearbook,* **30**, 89-97.

Murphy, D.D., Launer, A.E. & Ehrlich, P.R. (1983). The role of adult feeding in egg production and population dynamics of the checkerspot butterfly*, Euphydras editha. Oecologia,* **56**, 257-263.

Nahrung, H.F. & Merritt, O. J. (1999) Moisture is required for the termination of egg diapause in the Chrysomelid beetle *Homichloda barkeri*. *Entomologia Experimentalis et Applicata,* **93**, 201-207.

Neve, G., Barascud, B., Hughes, R., Aubert, J., Descimon, H., Lebrun, P. & Baguette, M. (1996) Dispersal, colonisation power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). *Journal of Applied Ecology,* **33**, 14-22.

New, T.R., Pyle. R.M., Thomas. J.A., Thomas, C.D. and Hammond, P.C. (1995) Butterfly conservation management. *Annual Review of Entomology*, **40**, 57-83.

Nicholls, C.N. & Pullin, A.S. (2000) A comparison of larval survivorship in wild and introduced populations of the large copper butterfly (*Lycaena dispar batavus*). *Biological Conservation*, **93**, 349-358.

Nicholson, G.W. (1921) *Cryptocephalus biguttatus* Scop. on *Erica tetralix Entomologist's Monthly Magazine*, **57**, 36-37.

Normark, B.B. (1996) Phylogeny and evolution of parthenogenetic weevils of the *Aramigus tessellatus* species complex (Coleoptera: Curculionidae: Naupactini): evidence from mitochondrial DNA sequences. *Evolution,* **50** (2), 734-745.

Obermaier, E. & Zwolfer, H (1999) Plant quality or quantity? Host exploitation in three chrysomelid species associated with Arteraceae host plants. *Entomologica Experimentalis et Applicata,* **92**, 165-177.

Ohgushi, T. (1995) Adaptive behaviour produces stability in herbivorous lady beetle populations. *Population Dynamics: New Approaches and Synthesis* (ed. N. Cappuccino & P.W. Price) pp. 303-319. Academic Press, San Diego, California.

Okajima, S. and Urushihara, H. (1992) Leaf-litter thrips (Thysanoptera) found in Jinmuji Forest, the Miura Peninsula, Kanagawa Prefecture, Japan. *Japanese Journal of Entomology*, **60** (1), 157-173.

O'Neill, S.L., Giordano, R., Colbert, A.M.E., Karr, T.L. & Robertson, H.M. (1992) 16s rRNA phylogenetic analysis of the bacterial endosybionts associated with cytoplasmic incompatibility in insects. *Proceedings of the National Academy of Sciences USA*, **89**, 2699-2702.

Orians, C.M., Huang, C.H., Wild, A., Dorfman, K.A., Zee, P., Dao, M. T. T. & Fritz, R.S. (1997) Willow hybridisation differentially affects preference and performance of herbivorous beetles. *Entomologia Experimentalis et Applicata,* **83,** 285-294.

Owen, J.A. (1997) Some notes on the life history of *Cryptocephalus sexpunctatus. Entomologist's Record and Journal of Variation,* **25**, 43-48.

Owen, J.A. (1999) Notes on the biology of *Cryptocephalus coryli* (Linnaeus) (Coleoptera: Chrysomelidae). *Entomologist’s Gazette*, **50**, 199-204.

Palo, R.T. (1984) Distribution of birch (*Betula spp.*) willow (*Salix spp*) and poplar (*Populus spp*) secondary metabolite and their potential role as chemical defence against herbivores. *Journal of Chemical Ecology*, **10** (3) 499-520

Pasteels, J.M., Rowell-Rahier, M., Braekman, J.C. and Daloze, D. (1984) Chemical defence in leaf beetles and their larvae. The ecological, evolutionary and taxonomic significance. *Biochemical Systematic Ecology*, **12**, 395-406.

Pearce-Kelly, P. (1994) Invertebrate propagation and re-establishment programmes : the conservation and educational potential of zoos and related institutions. *Creative Conservation: Interactive Management of Wild and Captive Animals* (eds P.J.S. Olney, G.M. Mace & A.T.C. Feistner) Chapman and Hall, London.

Pearce-Kelly, P., Jones, R., Clarke, D., Walter, C., Atkin, P. & Cunningham, A.A. (1998) The captive rearing of threatened orthoptera : a comparison of the conservation potential and practical considerations of two species’ breeding programmes at the Zoological Society of London. *Journal of Insect Conservation*, **2**, 201-210

Peterken, G. F. 1981. *Woodland conservation and management*. Chapman and Hall, London.

Powers, T (1859) A capture of *Cryptocephalus primarius* in Cambridgeshire. *Entomologists Annual*, **143**.

Pray. L.A. & Goodnight, C.J. (1995) Genetic variation in inbreeding depression in the red flour beetle *Tribolium castaneum*. *Evolution*, **49**, 176-188.

Price, P.W., Cobb. N., Craig, T.P., Fernandes, G.W., Itami, J.K. & Mopper, S. *et al.* (1990) Insect herbivores dynamics on trees and shrubs: new approaches relevant to latent and eruptive species and life table development. *Insect –Plant Interactions*, **2** (ed E.A. Bernays) pp. 1-38. CRC Press, Boca Raton, Florida.

Price, P.W. (1991) The plant vigour hypothesis and herbivore attack. *Oikos*, **62**, 244-251.

Pride, I.G. & Swift, S.M. eds (1992). *Wildlife telemetry. Remote monitoring and tracking of animals*. Horwood, New York, USA. 542pp.

Pyle, R.M., Bentzien, M. & Opler, P.A. (1981) Insect Conservation. *Annual Review of Entomology*, **26**, 233-258.

Pyle, R.M. (1988) Captive breeding of butterflies for conservation. *Proceedings of the Fifth World Conference of Breeding endangered species in captivity. Cincinnati Zoo and Botanical Garden Centre for the Reproduction of Endangered Wildlife* (eds B.L. Dresser, R.W. Reece & Marustae, E.J.) pp 423-430, Cincinnati.

Rabinowitz, D. (1981) Seven forms of rarity. The biological aspects of rare plant conservation (ed H. Synge) pp 205-217. John Wiley and Sons, Chichester.

Rabinowitz, D., Cairns, S. and Dillon, T. (1986) Seven forms of rarity and their frequency in the flora of the British Isles. *Conservation Biology, the Science of scarcity and diversity* (ed. M.E. Soule), pp 182-204, Sinauer, Mass., USA.

Rackham, O. (1995) The history of the countryside. Weidenfield and Nicolson, London.

Ralls, K., & Ballou, J.D. eds (1986) Proceedings of the workshop on genetic management of captive populations. *Zoo Biology,* **5**.

Ralls. K & Ballou, J.D. (1986) Captive breeding programs for populations with a small number of founders. *Trends in Ecology and Evolution*, **1**, 19-22.

Rank, N.E. (1992) A hierarchical analysis of genetic differentiation in a montane leaf beetle *Chrysomela aeneicollis*. *Evolution*, **46**, 1097-1111.

Rank, N.E. (1994) Host-plant effects on larval survival of a salicin-using leaf beetle *Crysomela aenicollis* Schaeffer (Coleoptera: Chrysomelidae). *Oecologia,* **97**, 342–353.

Reddy, M.V., Kumar, V.P.K. & Reddy, B.K. (1992) Occurrence of *Gonocephalum* sp. (Tenebrionidae: Coleoptera) as a pest of groundnut in India. Tropical Pest Management, **38**, 1, 108.

Reyment, R., Blackhith, R.E. & Campbell, N.A. (1984) Multivariate Morphometrics.
2nd. ed. Vii + 233pp. London.

Rice, R.L., Lincoln, D.E. & Langenhein, J.H. (1978) Palatability of monoterpenoids compositional types of *Satureja douglasii* to a generalist molluscan herbivore *Ariolimax dolichophallus. Biochemical and Sytematical Ecology,* **6**, 45-53

Richards, O.W. (1927) *Cryptocephalus primarius* in Berkshire. *Entomologist's Monthly Magazine,* **63**, 161.

Richter, T.S., Soltis, P.S. & Soltis, D.E. (1994) Genetic variation within and among populations of the narrow endemic *Delphinium viridescens. American Journal of Botany,* **81**, 1070-1076.

Rieske, L.K. & Buss, L.J. (2001) Influence of site on diversity and abundance of ground- and litter-dwelling coleoptera in appalachian oak-hickory forests. *Environmental Entomology*, **30** (3), 484-494.

Riley, J.R. (1989). Remote sensing in entomology. *Annual Review of Entomology*, **34**, 247-271.

Rjinsdorp, A.D. (1980) Pattern of movement in and dispersal from a Dutch forest of *Carabus problematicus* Hbst (Coleoptera, Carabidae). *Oecologia*, **45**, 274-281.

Roland, J., McKinnon, G., Backhouse, C. & Taylor, P.D. (1996) Even smaller radar tags on insects. *Nature*, **381**, 120.

Rose, R.J., Webb. N.R., Clarke, T. & Traynor, C.H. (2000) Changes on the heathlands of Dorset, England, between 1987 and 1996. *Biological Conservation*, **93**, 117-125

Ryder, O.A. (1986) Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution,* **1**, 9-10.

Rye, E.C. (1871) Coleoptera. New British Species, corrections of nomenclature, etc. noticed since the publication of the Entomologist's Annual, 1870. *Entomologist's Annual.* 18-54.

Samways, M.J. (1994). *Insect Conservation Biology*. Chapman & Hall, London.

Scheirs, J. De Bruyn, L. & Verhagen, R. (2000) Optimization of adult performance determines host choice in a grass miner. *Proceedings of the Royal Society of London B. Biological Sciences*, **267**, 2065-2069.

Scherney, F. (1959a) Unsere Laufkafer. Wittenberg: Ziemsen.

Schneider, S., Roessli, D. & Excoffier, L. (2000) Arlequin ver. 2.000. A software for population genetics data analysis. University of Geneva, Switzerland.

Scriber, J.M. & Slansky, F. (1981) The nutritional ecology of immature insects. *Annual Review of Entomology*, **26**, 183-211

Sharon, R., Degani, G. & Warburg, M. (2001) Comparing the soil macro-fauna in two oak-wood forests: does community structure differ under similar ambient conditions? *Pedobiologia*, **45** (4), 355-366.

Sharp, W.E. (1867) Some coleoptera from Scotland during 1866. *Entomologist's Monthly Magazine,* **4,** 109.

Sharp, W.E. (1871) *Cryptocephalus bipunctatus and Cryptocephalus biguttatus. Entomologist's Monthly Magazine,* **53**, 76-79.

Shirt, D.B. ed. (1987) British Red Data Books: 2. Insects. Nature Conservancy Council, Peterborough, England.

Simberloff, D. (1986) The proximate causes of extinction. In *Patterns and Processes in the History of Life* (eds D.M. Raup & D. Jablonski), pp 259-276 Springer-Verlag, Berlin.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87 (6), 651-701.

Skidmore, P (1966) Noteworthy coleoptera in the Doncaster museum collection. *Entomologists Monthly Magazine,* **99**, 228-229.

Snyder, N.F.R., Derrickson, S.R., Bessinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D. & Mitter, B. (1996) Limitations of captive breeding in endangered species recovery. *Conservation Biology*, **10** (4) 338-348.

Soetens, M., Rowell-Rahier, M. & Pasteels, J.M. (1991) Influence of phenoglucosides and trichome density on the distribution of insects herbivores on willows. *Entomologia Experimentalis et Applicata*, **59**, 175-187.

Soltis, P.S. & Gitzendanner, M.A. (1999) Molecular systematics and the conservation of rare species. *Conservation Biology*, **13**, 471-483.

Southwood, T.R.E. (1978) *Ecological Methods*. Chapman and Hall. London.

Speight, M.C.D. (1973) A greased belt technique for the extraction of arthropods from organic debris. *Pedobiologia*, **13**, 99-106.

Sperling, F.A.H., Raske, A.G. & Otvos, I.S. (1999) Mitochondrial DNA sequence variation among populations and host races of *Lambdina fiscellaria* (Gn.) (Lepidoptera: Geometridae). *Insect Molecular Biology,* **8** (1), 97-106.

Spring, A. & Kok, L. T. (1999) Winter survival of *Cassida rubiginosa* (Coleoptera: Chrysomelidae), a biological control agent of canada thistle. *Journal of Entomological Science.* **34** (4) 489-492.

Steinhausen, W.R. (1996) Biological remarks on rearing and collecting of middle European leaf beetle larvae. *Chrysomelidae biology, vol.3: General Studies,* (eds P.H.A. Jolivet & M.L. Cox) pp 93-105. SPB Academic Publishing, Amsterdam.

Stewart, A.J.A. and Hutchings, M.J. (1996) Conservation of populations, 122-141. In *Conservation biology* (ed. I.F. Spellerberg). pp 239. Longman. UK.

Stewart, C.A., Chapman, R.B., Barrington, A.M. & Frampton, C.M.A. (1999) Influence of temperature on adult longevity, oviposition and fertility of *Agasicles hygrophila* Seman and Vogt (Coleoptera: Chrysomelidae). *New Zealand Journal of Zoology,* **26**, 191-197.

Stott, C E (1929) Re-occurrence of *Cryptocephalus decemmaculatus* in Staffordshire. *Entomologist's Monthly Magazine* **65,** 268-269.

Stouthammer, R., Luck, R.F. & Hamilton, W.D. (1990a) Antibiotics cause parthenogenetic *Trichogramma* (Hymenoptera: Trichogrammatidae) to revert to sex. *Proceedings of the National Academy of Sciences USA*, **87**, 2424-2427.

Szalanski A.L., Sikes D.S., Bischof, R. & Fritz, M. (2000) Population genetics of the endangered American burying beetle, *Nicrophorous americanus* (*Coleoptera: Silphidae*) *Annals of the Entomological Society of America*. **93** (3) 589-594.

Tahvanainen, J., Julkunen-Titto, R. & Kettunen, J. (1985) Phenolic glycosides govern the food selection pattern of willow feeding leaf beetles. *Oecologia*, **67**, 52-56.

Takizawa, H. (1976) A review of the *approximatus* group of *Cryptocephalus* in Japan. *Kontyu,* **43**, 422-436.

Tanhuanpaa. M., Rouhomaki, K., Kaitaniemi, P. & Klemola. T. (1999) Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *Journal of Animal Ecology*, **68**, 562-570.

Tear, T.H., Scott, J.M., Hayward, P.H. & Griffith, B. (1993) Status and prospects for success of the endangered species act: a look at recovery plans. *Science*, **262**, 976-977.

Tear, T.H., Scott, J.M., Hayward, P.H. & Griffith, B. (1995) Recovery plans and the endangered species act: are criticisms supported by data? *Conservation Biology*, **9**, 182-195.

Tempère, T. & Pericart, J. (1989) *Coléoptères Curculionidae (4me partie).* Vol. 74. Fauna de France. *Paris: Fédération Française des Societie Science Naturelles.*

Templeton, A.R. & Read, B. (1983) The elimination of inbreeding depression in a captive herd of Speke's gazelle. *Genetics and Conservation* (eds C.M. Schoenwald-Cox, S.M. Chambers, B. Macbryde & L. Thomas) pp. 241-161. Benjamin/Cummings, Menlo Park, California.

Templeton, A.R. & Read, B. (1984) Factors eliminating inbreeding depression in a captive herd of Speke's gazelle. *Zoo Biology*, **3**, 177-199.

Templeton A.R. (1994) The role of molecular genetics in speciation studies. *Molecular Ecology and Evolution: Approaches and Applications* (eds B. Schierwater), pp455-477, Birkhauser.

Thomas, J. A. (1983b) The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. *Journal of Applied Ecology*, **20**, 59-83.

Thomas, C.D. (1985) Specializations and polyphagy of *Plebejus argus* (Lepidoptera: Lycaenidae) in North Wales. *Ecological Entomology*, **10**, 325-340.

Thomas, J.A. (1984) The conservation of the butterflies in temperate countries: past efforts and lessons for the future. *Symposium of the Royal Entomological Society of London*, **11**, 333-353. Academic Press, London.

Thomas, J.A. (1991) Rare species conservation: Case studies of European butterflies in the scientific management of temperate communities for conservation (eds I.F. Spellerberg, F.B. Goldsmith & M.G. Morris). *31st Symposium of the British Ecological Society*, Southampton, 1989. Blackwell, Oxford, 149-197.

Thomas, J. A. (1993) Holocene climate changes and warm man-made refugia may explain why a sixth of British Butterflies inhabit unnatural early-successional habitats. *Ecography*, **16**, 278-284.

Thomas, J. A., D. Moss, & E. Pollard 1994. Increased fluctuations of butterfly populations towards the northern edges of species' ranges. *Ecography,* **17**, 145-157.

Thomas, J.A. & Morris, M.G. (1995) Rates and patterns of extinctions among British invertebrates. *Extinction Rates.* (ed J.H. Lawton & R.M. May) pp 111-130.

Thomas, J. A., Rose, R.J., Clarke, R.T., Thomas, C.D. & N. R. Webb. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology,* **13**, 55-64.

Thomas, C.D. (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 139-145.

Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia experimentalis et applicata*, **47**, 3-14.

Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalities and weight matrix choice. *Nucleic Acids Research.*

Thornley, A. (1899) *Cryptocephalus exiguus,* Schneider, in Lincolnshire. *Entomologist's Monthly Magazine*, **35**, 93-94.

Tilden, J.W. (1949) Oviposition of *Cryptocephalus confluens* Say (Coleoptera, Chrysomelidae). *Entomological News,* **60** (6), 151-154.

Towns, D.R. & Daugherty, C.H. (1994) Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonistaion. *New Zealand Journal of Zoology*, **21**, 325-339.

Tozer, D. (1944) Notes on Midland Coleoptera for 1943. *Entomologist's Monthly Magazine*, **89**, 135.

Travis, S.E.J, Maschinski, J. & Keim, P. (1996) Analysis of genetic variation in *Astragalus cremnophylax var. cremonphylax.* a critically endangered plant, using AFLP markers. *Molecular Ecology,* **5**, 735-745.

Turchin, P. (1991) Translating foraging movements in heterogenous environments into the spatial distribution of foragers. *Ecology*, **72**, 1253-1266.

UK Biodiversity Steering Group (1995) Biodiversity Action Plans: English Nature, Peterborough, England.

UK Biodiversity Steering Group (1999a) Action Plans: Volume IV—Invertebrates. English Nature, Peterborough, England.

UK Biodiversity Steering Group (1999b) Tranche 2 Action Plans: Volume VI—Terrestrial and freshwater species and habitats. English Nature, Peterborough, England.

Valladares G. & Lawton J.H. (1991) Host-plant selection in the holly leaf-miner - does mother know best? *Journal of Animal Ecology*, **60** (1), 227-240.

Vogler, A.P. & DeSalle, R. (1994) Diagnosing units of conservation management. *Conservation Biology,* **8** (2) 354-363.

Vogler, A.P., Welsh, A. & Barraclough, T.G. (1998) Molecular phylogeny of the *Cicendela maratima* (Coleoptera: Cicindelidae) group indicates fast radiation in Western North America. *Annals of the Entomological Society of America.* **91**, 185-194

Warchalowski, A (1991) Chrysomelidae-stonkowate. (Insecta: Coleoptera). cz.II. Clytrinae, Cryptocephalinae. Fauna Polski, XIII. PAN-PWN, 346 pp.

Warren, M.S. (1987a) The Ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. I. Host selection and phenology. *Journal of Applied Ecology,* **24**, 467-482.

Warren, M.S. (1987b) The Ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. *Journal of Applied Ecology,* **24**, 483-492.

Warren, M.S. (1987c) The Ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. III. Population dynamics and the effect of habitat management. *Journal of Applied Ecology,* **24**, 499-513.

Warren, M.S and Key, R.S. (1989) Woodlands: past, present and potential for insects. *Conservation of insects and their habitats. 15th Symposium of the Royal Entomological Soceity of London.* 155-203.

Warren, M. S. 1994. Managing local microclimates for the high brown fritillary. *Ecology and Conservation of Butterflies* (ed A.S. Pullin) pp 198-215 Chapman and Hall, London.

Watts, C.H. (1968) The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *Journal of Animal Ecology*, **37**, 25-41.

Webb, J. (1999) *Cryptocephalus decemmaculatus*: A survey of three possible sites in Cheshire, Shropshire and Staffordshire. English Nature Research Reports. English Nature, Peterborough, England.

Webb, M.R. & Pullin, A.S. (1996) Larval survival in populations of the large copper butterfly *Lycaena dispar batavus*. *Ecography*, **19**, 279-286.

Webb, M.R. & Pullin. A.S. (1998) Effects of submergence by winter floods on diapausing caterpillars of a wetland butterfly, *Lycaena dispar batavus*, *Ecological Entomology,* **23**, 96-99.

White, T.J., Bruns, T., Lee. S. & Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics, *PCR Protocols: a Guide to Methods and Applications* (ed. M.A. Innis, D.H. Gelfand, J.J. Sninsky, T.J. White) pp 315-322. Academic Press, San Diego,

Whitlock, M.C. (2001) Dispersal and the genetic properties of metapopulations. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp 273-282. Oxford University Press, NewYork.

Willmer, P.G., Hughes, J.P., Woodford, J.A.T. & Gordon, S.C. (1996) The effects of crop microclimate and associated physiological constraints on the seasonal and diurnal distribution patterns of raspberry beetle (*Byturus tomentosus*) on the host plant *Rubus idaeus*. *Ecological Entomology,* **21**, 87-97.

Wilson, W.L. (1992) Behavioural Ecology and Population Regulation of the Wood Mouse (*Apodemus sylvaticus*). PhD. Thesis. Queens University, Belfast.

Withers, P.C. (1992) *Comparative Animal Physiology*. Saunders College Publishing, Philadelphia.

Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. (1996) Avian and mammalian translocations : update and reanalysis of 1987 survey data. *Conservation Biology,* **10** (4), 1142-1153.

Woodruff, D.S. (1989) The problem of conserving genes and species. *Conservation for the Twenty-First Century* (eds D. Western & M.C. Pearl), pp 95-113. Oxford University Press, New York.

Yalden, D. (1999) *The History of British Mammals*. 305pp. Poyser, London.

Yates, F. 1934 Contingency tables involving small numbers and the χ^2 test. *Journal of the Royal Statistical Society Supplement*, **1**, 217-235.

Appendix 1. Surveys of sites where *Cryptocephalus* species have been recorded. Data provided by Peter Hodge.

Species	**Site**	**Grid Ref.**	**Original Record**	**Surveyed/ present**	**Surveyed/ absent**	**Site appears suitable**
C. aureolus						
	Kelsey Head SSSI	SW775600	1983	X		
	Braunton Burrows	SS4735	1967-87	X		
	Great Breach Wood	ST504323	1987		X	Y
	Old Winchester Hill NNR	SU645208	1981-1985	X		
	Butser Hill SSSI	SU7119	1979	X		
	Lewes Railway Land	TQ4109	1987-1989	Not resurveyed		
	Farningham Wood SSSI	TQ5468	1954-1960		X	Y
	Totternhoe Knolls	SP980220	1968		X	N
	Pingle	TL314815	1988	X		
	Harbury Spoilbank	SP3858	1988		X	Y
	Newborough Warren	SH4461	1979	X		
	Rhosneigr	SH3173	1979	X		
	Traeth Cwmyran	SH3074	1979	X		
	Castle Eden Dene	NZ4238	1833		X	N
C. biguttatus						
	Chartley Moss NNR	SK0028	1896		X	Y
	Bournemouth	SZ09	1904		X	Y
	Parley Common SSSI	SZ090990	1932		X	Y
	Parley Heath	SZ0999	1964		X	Y
	Lyndhurst	SU20	1912		X	Y
	The New Forest	SU30	1897		X	Y
	Eversley	SU7762	1905		X	N
	Pamber Forest and Silchester	SU6161	1910		X	Y
	Lavington Common	SU9519	1980-89	X		
	Walmer	TR379500	1942		X	N
	Chobham Common SSSI	SU9765	?		X	Y
	Esher Common	TQ1362	1875		X	N
	Esher Surrey	TQ1464	?		X	N
	Wellington College Bog SSSI	SU832628	1923		X	Y
	Chat Moss	SJ7096	1908		X	N
	Fen Bogs	SE854975	1983		X	Y
C. bilineatus						
	Compton Down SSSI	SZ3685	1982-84		X	Y
	Old Winchester Hill NNR	SU645208	1981-1985		X	Y
	Butser Hill SSSI	SU7119	1973		X	Y
	Arundel Park south SSSI	TQ0108	1949		X	Y
	Cradle Hill	TQ5001	1993		X	Y
	Deep Dean	TQ5402	1971-1991		X	Y

	Lewes Downs	TQ455110	1988-91	X		
	Malling Down Lewes	TQ4210	1970-90	X		
	Willingdon Downs	TQ5802	1988-91		X	Y
	Ham Marshes	TR0263	1977-86		X	Y
	Denbies Hillside	TQ145502	1983		X	Y
	White Downs	TQ1149	1983	X		
	Barnack Hills and Holes	TF076047	1989		X	Y
	Sheepscombe Common	SO890105	1958		X	Y
	Rodborough Common SSSI	SO8503	1890-2000	X		
	Gait Barrows	SD480771	1995		X	Y
C. bipunctatus						
	Morroch Bay	NX0152	1972		X	Y
	Castle Drogo	SX7290	1990		X	Y
	Sandford Hill	ST4259	1986		X	Y
	Balmer Lawn SSSI	SU3103	1974		X	Y
	Bramshaw Commons SSSI	SU2717	1991		X	Y
	Whitley Wood SSSI	SU2905	1966		X	Y
	Beedingto Newtimber Hill SSSI	TQ232112	1973-1980		X	Y
	Trottiscliffe Downs	TQ6360	1955		X	Y
	Esher & Oxshott Heaths	TQ1362	1951		X	Y
	Esher Common	TQ1362	1887		X	Y
	Brassey Reserve and Windrush	SP1322	1965-1969		X	Y
	Colesbourne (vague)	SP01	1946		X	Y
	Cranham Common SSSI	SO888123	1977		X	Y
	Rodborough Common SSSI	SO8503	1890-2000	X		
	Ellerside Moss	SD350801	1954		X	Y
C. coryli						
	Blean Woods Complex	TR16	1967		X	Y
	Cobham Park	TQ6868	1942		X	N
	Cobham Woods	TQ6968	1932		X	N
	Darenth Wood	TQ5873	1910		X	N
	Westerham	TQ4454	?		X	Y
	BoxHill	TQ1852	22-Jun-08	X		
	Cobham (vague)	TQ15	20-May-43		X	Y
	Dorking	TQ1649	15-Jul-86		X	Y
	Headley Warren	TQ188539	1912-2001	X		
	Mickleham Surrey	TQ1753	21-May-23		X	N
	North Unhill Bank	SU561833	01-Jun-91	X		
	Stockgrove	SP9129	?		X	N
	Bedford Purlieus	TL042995	1935-70		X	N
	Cannock Chase	SK0017	1910		X	Y
	Kirkby Moor	TF225625	01-Aug-87	X		
	Linwood Warren	TF132875	1955		X	N
	Middle Rasen	TF1091	10-Jun-65		X	N
	North Wood	TF130870	1946		X	N
	Langford Moor	SK8555	1899		X	N

	Sherwood Forest	SK66	1904-1909		X	Y
	Witchampton	?	1939		X	Y
	Inverness area	NH64	1946		X	Y
C. decemmaculatus						
	Chartley Moss NNR	SK0028	1876-1979		X	N
	Abbots Wood	TQ5607	1890		X	N
	Wybunbury Moss NNR	SJ695503	1981-2001	X		
	Chat Moss	SJ7096	1983		X	N
	Rannoch	NN595563	1983-2000	X		
	Braemararea	NO1491	1959	Not resurveyed		
	Muir of Dinnet	NO4399	1986	Not resurveyed		
C. exiguus						
	Oulton Broad	TM5192	JUN1898		X	Y
	Barton Mills	TL7274	14JUN1899		X	Y
	Pashford Poors Fen	TL7383	1980-2000	X		
	Bure Marshes	TG3316	1870		X	Y
	Freshney Bog	TA2308	1898-1954		X	N
C. frontalis						
	Harvey's Lane	TQ4714	1978-2001	X		
	Thorndon Park	TQ617913	1984-1985		X	Y
	Kilby-Foxton Canal	SP699899	?		X	Y
	Lighthorne	SP3357	1999	X		
	SP41	1900-70		Not resurveyed		
	TL34	1900-70		Not resurveyed		
	TL45	1900-70		Not resurveyed		
	TL88	1900-70		Not resurveyed		
	TQ23	1900-70		Not resurveyed		
	SU49	1900-70		Not resurveyed		
	SW72	1900-70		Not resurveyed		
	Kemerton	SO93	1993		X	Y
	SP69	1900-70		Not resurveyed		
	TL10	1900-70		Not resurveyed		
C. fulvus						
	Braunton Burrows	SS4735	1967		X	Y
	Upright Cliff Hartland	SS230268	1992		X	Y
	Sullington Warren	TQ0914	1990-1993		X	Y
	Weavers Down Longmoor	SU8130	1990-1993		X	Y
	Deep Dean	TQ5402	1991		X	Y
	Deer Park	TR0640	1991	X		
	Bookham Common SSSI	TQ1356	1947	X		
	Esher & Oxshott Heaths	TQ1362	1926	X		
	Stibbington Pits	TL086993	1993	X		
	Bedford Purlieus	TL042995	1936	X		
	Barnsley Warren SSSI	SP0506	1966	X		
	Longford Tip	SP3483	1986		X	Y
	Kenfig Burrows & Pool	SS7980	1983		X	Y
	Eskmeals Dunes	SD0794	1979-1985		X	Y
C. hypochaeridis						
	Mitcham Common	TQ2868	1990		X	Y
	Culand Pits	TQ7361	1966		X	Y
	Hoads Wood	TQ9542	1972		X	Y

	Queendown Warren	TQ8262	1979		X	Y
	Darenth Wood	TQ5873	1974		X	Y
	Kemsington Wrotham Downs	TQ5459	1979		X	Y
	Box Hill	TQ1852	1987	X		
	Riddlesdown	TQ323604	1987		X	Y
	Grays Chalk Pit	TQ6078	1975		X	Y
	Aston Rowant NNR	SU72296	1965	Not resurveyed		
	Wakerley Railway Cutting	SP960996	1986	Not resurveyed		
	Swifts Hill SSSI	SO8706	1972	Not resurveyed		
	Rodborough Common SSSI	SO8503	1903-2001	X		
	Laugharne Burrows	SN300070	1985-1989	Not resurveyed		
	Newtondale	SE88	1992	Not resurveyed		
C. labiatus						
	Cobham Park	TQ6868	1970-1997		X	Y
	North Unhill Bank	SU561833	19-Jun-83-1996	X		
	Wisley Common	TQ0658	?-2000	X		
	Buckingham Thick Copse	SP706433	1988-1994	Not resurveyed		
	Combes Valley	SK0053	Unknown	Not resurveyed		
	Bretton Park & Lake	SE2812	1973	Not resurveyed		
	Affric Forest	NH3029	1981	Not resurveyed		
	Doire Darach SSSI	NN2841	1981	Not resurveyed		
	Wybunbury Moss	SJ6950	1981-2001	X		
	Fenns and Whixall Moss	SJ4835	1999	X		
	Lavington Common	SU951191	?-2000	X		
	White Downs	Many	?-2001	X		
C.moraei						
	Ashurst	SU344115	1969			
	Keeping and Spearbed Copse	SU4001	1984	Not resurveyed		
	Kingspark Wood and Shortlands	SU9932	1972-1981		X	Y
	Rewell Wood	SU9808	1979		X	Y
	Malling Down Lewes	TQ4210	1970-1985	X		
	Kemsing to Wrotham Downs	TQ5459	1979		X	Y
	Kingsnorth	TQ8071	1987		X	Y
	Stoke Saltings	TQ8474	1987-1988		X	Y
	Denbies Hillside	TQ145502	1983	Not resurveyed		
	Castor Hanglands	TF119015	1954	Not resurveyed		
	Old Sulehay Quarry	TL054984	1984	Not resurveyed		
	The Frome Valley (whole site)	SO90	1985	Not resurveyed		
	Llandeilo Graban Verge	SO04	1984	X		
	Morkery Wood	SK950185	1985	X		
	Clints Quarry	NY0012	1982	Not resurveyed		
C. nitidulus						
	Ashdown Forest		1916		X	N
	Bournemouth	SZ09	1912		X	N
	The New Forest	SU30	1925		X	Y
	Cobham Woods	TQ6968	1922		X	N

	Darenth Wood	TQ5873	1922		X	N
	BoxHill	TQ1852	1900	X		
	Coulsdon Surrey	TQ3058	22-Jun-19		X	N
	Hackhurst Downs SSSI	TQ0948	29-Jun-86		X	N
	WhiteDowns	Many	1986-2001	X		
	Headley Warren	TQ25	Jun-05	X		
	Mickleham Surrey	TQ1753	1893		X	N
	Wychwood Forest (whole site)	SP3315	1905-54		X	N
	Colesbourne (vague)	SP01	1922-46		X	N
	Gulf Scrubs, Colesbourne	SP0214	1945		X	N
	Sherwood Forest	SK66	1906		X	Y
C. parvulus						
	Denny Wood SSSI	SU3305	1968	Not resurveyed		
	Pig Bush and Shepton Water SSSI	SU3604	1971	Not resurveyed		
	Lavington Common	SU9519	1990-2000	X		
	Eridge Park	TQ5735	1993		X	Y
	Tellis Coppice	TQ7115	1990	Not resurveyed		
	Darenth Wood	TQ5873	1906	Not resurveyed		
	Esher & Oxshott Heaths	TQ1362	1953		X	Y
	Thursley Common SSSI	SU902406	1988		X	Y
	Grays Chalk Pit	TQ6078	1975		X	Y
	Cannock Chase, whole area	SK0017	1976		X	Y
	Wybunbury Moss NNR	SJ695503	1990-2001	X		
	Chat Moss	SJ7096	1971		X	N
	Hatfield Moor	SE7000	1992		X	N
	Thorne Moors	SE71	1976		X	N
	Meathop Moss	SD4481	1971		X	Y
C. primarius						
	Cholsey	SU5886	1927-1955		X	Y
	Gog Magog Hills	TL4953	1859-1938		X	N
	Colesbourne (vague)	SP01	1942-44		X	N
	Breakheart Hill	ST7596	1992	X		
	Rodborough Common	SO8503	1890-1985		X	Y
	Stinchcombe Hill SSSI	ST7498	1992-2000	X		
	Nr Loch Rannoch	NN3352	1900		X	Y
C.punctiger						
	Aviemore Area	NH64	1946	Not resurveyed		
	Lavington Common	SU9519	1990-2000	X		
	Darenth Wood	TQ5873	1906		X	N
	Cannock Chase	SK0017	1976		X	Y
	Combes Valley	SK0053	1973		X	Y
	Haw Park	SE3615	1960-1970		X	Y
	Sherwood Forest	SK66	1904		X	Y
		ST91	Post 1970	Not resurveyed		
		TQ06	Post 1970	Not resurveyed		
		TQ57	Pre1900-70	Not resurveyed		
		TQ66	1900-1970	Not resurveyed		
	Ambersham Common	SU9019	1997	X		
	Wisley Common	TQ0658	2000	X		
C. pusillus						
	Chartley Moss NNR	SK0028	1975-1979	X		
	Pondhead Inclosure	SU3007	1969	Not resurveyed		

	SSSI					
	Red Rise	SU2403	1962	Not resurveyed		
	Midhurst Common	SU8721	1980-1989		X	Y
	Lewes Railway Land	TQ4109	1996	X		
	Dungeness	TR0817	1981	Not resurveyed		
	Richmond Park	TQ2073	1980-1983		X	Y
	Sheepleas SSSI	TQ0951	1960-1969		X	Y
	Dagnam Park	TQ5593	1987	X		
	Colne Point	TM100123	1990	X		
	Barnack Hills and Holes	TF076047	1990	X		
	Bedford Purlieus	TL042995	1937		X	
	Barnsley Warren SSSI	SP0506	1966	Not resurveyed		
	Colesbourne Park	SP005135	1963	X		
	Brandon Marsh	SP3875	1988	Not resurveyed		
C. querceti						
	Windsor Great Park	SU97	1930-2000	X		
	Donington Park SSSI	SK414269	1988-1991	X		
	Birklands & Bilhaugh	SK620683	1906-1993		X	Y
	Chat Moss	SJ7096	?		X	N
	Colchester (District)		`May-48		X	?
	Lord's Wood Southampton	SU3916	1887		X	N
C. sexpunctatus						
	Stockbridge Down SSSI	SU3834	1990-1996	X		
	Orlestone Forest	TQ9835	1958		X	N
	Cobham Park	TQ6868	?		X	N
	Cobham Woods	TQ6968	?		X	N
	Darenth Wood	TQ5873	1905-47		X	N
	Grays Chalk Pit	TQ6078	1978-86		X	N
	Ham street woods		1957		X	Y
	Colchester	TM0024	May 1944-47		X	N
	Colesbourne (vague)	SP01	1946		X	N
	Gulf Scrubs, Colesbourne	SP0214	1945		X	N
	Lime Woods	TF094750	1956		X	Y
	Scotgrove Wood	TF130704	1956		X	N
	Glen Affric Area	NH22	1963	Not resurveyed		
		SU41	?		X	N
	SU91	1900-1970			X	N
	TQ35	Pre	1900		X	N
	Nr Ipswich	TL92	1895	Not resurveyed		
		ST5534		Not resurveyed		
	TM11	1900-70		Not resurveyed		
	SY88	1900-1970		Not resurveyed		
	Nr Dalry	NS2949	1867	Not resurveyed		
		NX76			X	?
	Nr Worcester	SO87	1921	Not resurveyed		
	Kirkconnell Flow	NX967698	1995	X		
		NT27		Not resurveyed		