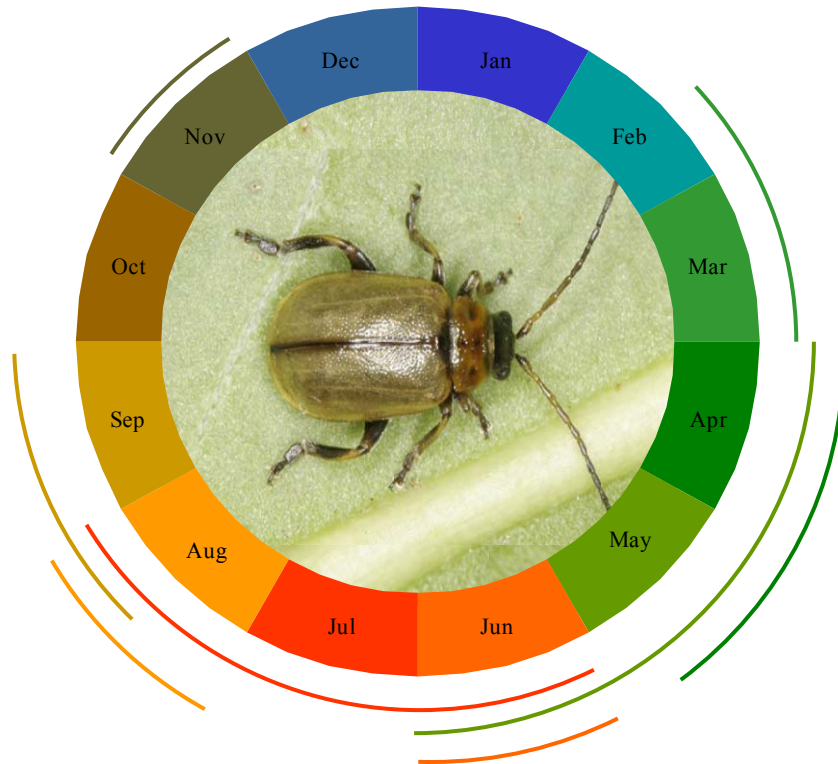


The Heather Beetle: a review

Report to the Heather Trust



Angus Rosenburgh & Rob Marris

Applied Vegetation Laboratory
School of Environmental Sciences
University of Liverpool
Liverpool
L69 7ZB

Tel: +44 151795 5173
Fax: +44 151 795 5171

<http://www.appliedvegetationdynamics.co.uk>
calluna@liv.ac.uk

April 2010

Executive summary

- The heather beetle is present at low numbers on most heathlands and moorlands in the UK. An outbreak of the beetle occurs when numbers rise and the population is no longer controlled by its predators and other regulatory factors.
- During these outbreaks, there is the opportunity for considerable damage to occur to the *Calluna* with complete death in the worst cases. This leads to reduced productivity in the short-term, and large-scale vegetation change in the longer-term.
- Inevitably this damage will impact on livestock grazing and grouse production and will affect the income of land owners and tenants.
- The occurrence and severity of heather beetle outbreaks appears to be exacerbated by increased levels of nitrogen in the soils and plant tissues, which has been blamed on high nitrogen pollutant inputs from the atmosphere in recent years. The high nitrogen in the leaves provides the beetles with more high quality food to consume.
- The current management advice is conflicting and based on piecemeal approaches to the problem. Current suggested advice ranges from doing nothing, ignoring the problem and the moor will recover, through to burning the affected areas. Some preventative measures have also been attempted; for example burning areas which may contain larvae and hibernating adults.
- Research is needed to produce an evidence base for providing good practice management. The following five general questions need to be addressed:
 - What shifts a natural population of heather beetles by predators and parasites to increase in numbers to cause an outbreak;
 - What is the extent of the current problem, can it be mapped by remote sensing and can this information be used predictively?
 - Why some heathlands/moorlands are affected to a greater extent than others? There is some evidence that older plants are killed rather than younger ones, and older plants are less likely to recover following an attack.
 - How can management help as a preventative measure, a cure and a means to rapid recovery?
 - Are there any other insect herbivores living in moorlands that might cause similar problems in the future.
- Only through intensive multi-site experimental work can good practice management approach be developed.

Contents	Page
Executive summary	
1. Aims of this report	1
2. Introduction	1
3. The heather beetle's life-history	1
4. The effects of a heather beetle outbreak	5
4.1. Damage to the plants	6
4.2. Impacts on soils	7
4.2. Damage to the ecosystem	8
4.3. The potential economic importance of heather beetle attacks	9
5. Contributing factors	11
6. Factors that might limit heather beetle populations	12
6.1. Climatic controls	12
6.2. Biotic controls	12
6.3. Management controls	13
7. Vegetation recovery from heather beetle attack	13
8. Future research	16
8.1. Natural control processes	16
8.2. The extent of the current problem	16
8.3. Why are some moors affected to a greater extent than others	17
8.4. The role of management as a prevention and cure	17
8.5. Any other potential pests?	18
9. References	19

The Heather Trust

The Heather Trust is a charity that promotes moorland management across the UK. The Trust encourages sound management practices and seeks to apply science to develop and promote appropriate management techniques. The Trust deals with practical issues and often finds itself working between groups with different objectives, but with a common interest in moorland. The Trust commissions research projects and publishes documents, including an Annual Report, to further its aims.

Tel: +44 1387 723201 www.heathertrust.co.uk

1. Aims of this Report

This report has been commissioned by The Heather Trust with the aims of:

- a. reviewing the literature on heather beetle and the existing knowledge about the impact this beetle has on heather and moorland management, and
- b. identifying knowledge gaps and recommending areas for further research.

2. Introduction

The heather beetle can be a major problem species on heaths and upland moors in the UK and elsewhere and there is anecdotal evidence that damage to moorland through large increases in the numbers of these beetles are increasing in frequency. When these large scale outbreaks of the beetles occur, vegetation dominated by common heather *Calluna vulgaris* is often severely defoliated and in some cases there is a complete kill. This can have substantive economic impacts for sheep and grouse production on moorland managers.

However, at the moment there is almost no recent information on the scale of the problem or if there are certain parts of the UK that are more at risk than others. There are several aspects to the assessment of risk and these might include: (a) the chance of an outbreak occurring, (b) the impact that the outbreak would have on the vegetation in terms of the percentage of the vegetation that is damaged, and (c) the vegetation recovery. The vegetation recovery clearly has two main parts, how quickly does the vegetation recover, and what is the composition of the vegetation. Clearly, all of these factors will impinge on the economics of managing moorland in the UK.

Unfortunately, there is almost no recent research on heather beetle in the UK, and most of what is available has been derived either from lowland areas or from continental Europe. Past research (Cameron *et al.*, 1944) provided an excellent overview. However, the climate and nitrogen pollution, both of which might increase heather beetle populations, have changed since the 1940s, so new research is sorely needed. Part of the aim of this review was to identify where research is needed.

3. The heather beetle's life history

The heather beetle (*Lochmaea suturalis* Thomson (Coleoptera: Chrysomelidae); Brunsting, 1982) is a small beetle, about 6mm long, (Fig. 1.) which occurs on almost all heathlands, although its local abundance varies (Webb, 1989). It is frequently cited as an herbivorous insect that feeds exclusively on common heather (or ling) *Calluna vulgaris* (Brunsting, 1982; Brunsting & Heil, 1985; Cameron *et al.*, 1944; Scandrett & Gimingham, 1991; Schaick Zillesen & Brunsting, 1983), but it has also been reported to feed on other on other closely-related plant species within the Heather family (*Ericaceae*).

Feeding has been reported on bell heather (*Erica cinerea*) and cross-leaved heath (*Erica tetralix*) (Pakeman *et al.*, 2002; Waloff, 1987), although to a much lesser extent than on *Calluna*.



Fig. 1. The adult heather beetle (www.kerbtier.de).

The distribution of the heather beetle is, therefore, closely correlated with the distribution of common heather *Calluna* (Brunsting, 1982), with an adult requirement for *Calluna* appearing to be absolute (Scandrett & Gimingham, 1991). The beetle is present in low numbers in most upland heathlands in the UK, although outbreaks also occur, when the beetle becomes a pest, causing a great deal of damage to heathland vegetation. In the past beetle outbreaks appeared to be more frequent in the lowland heaths of southern England, and in the Netherlands, where they create a serious problem for the conservation of heathlands (Scandrett & Gimingham, 1991). However, recently the outbreaks have been increasing in upland areas.

The life-cycle is shown diagrammatically in Figure 2. The adult beetles hibernate over winter in plant litter, and become active in the spring, when the mean daily temperature rises above 9°C. The beetles then leave the litter and climb up into the *Calluna* foliage. At this time, the beetle density may be very high (locally up to 2000/m²), especially at the edges of areas where there had been high infestations in the previous year (Brunsting, 1982). The beetles are carried away by a gentle breeze, and they appear to be unable to choose their direction of flight, despite adults showing well-developed flight muscles during a large part of their lifetime (Schaick Zillesen & Brunsting, 1983). Temperature appears critical; swarms of many millions have been reported in April and May (Morison, 1963), and according to Schaick Zillesen & Brunsting (1983) this occurred on the first calm, sunny days in spring, and when the mean daily temperature rose above 16°C (Brunsting, 1982). Sunny and calm weather (high temperature, low wind speed, high incident radiation) appears critical, because as soon as cloud obscured the sun, or the wind rose, the beetles landed (Brunsting, 1982; Schaick Zillesen & Brunsting, 1983). During these migrations, the beetles can travel several kilometres (Morison, 1963),

although mortality can be very high. The period during which dispersal by flight occurs may last several weeks, but later in spring similar weather conditions no longer cause the beetles to take flight (Brunsting, 1982). Copulation takes place during this dispersal period (Webb, 1989). There is only one generation of beetles per year (Waloff, 1987), and after copulation the adult beetles die, although some may survive until the end of June.

The eggs are laid between April and June, and larvae emerge from June until the end of August. The beetles require damp conditions during these stages (Pakeman *et al.* 2002), and accordingly the beetle is more abundant on wet, boggy ground, or in areas with an underlying moss carpet (Waloff, 1987). The eggs are laid at the base of *Calluna* stems and often in *Sphagnum* (Scandrett & Gimingham, 1991) or litter (Webb, 1989). The larvae climb onto the plants, making their way to the young shoots where they feed by chewing the leaves and cortex, leaving the debris (Scandrett & Gimingham, 1991). There is little lateral migration through the canopy and distribution appears to be at random, representing the distribution of eggs (Scandrett & Gimingham, 1991). Once they reach their maximum size, they develop through three larval life-history stages [these are technically called instars] (Scandrett & Gimingham, 1991; Webb, 1989), and then descend to the ground to pupate, where they remain for four weeks beneath the surface of the soil or moss (Scandrett & Gimingham, 1991). The new adult beetle generation emerge from mid-August onwards, and during late summer and autumn they increase in weight and develop flight muscles (Brunsting, 1982; Cameron *et al.*, 1944; Waloff, 1987). Growth of the beetle occurs almost exclusively during the larval stage and variations in food quality are found to have the clearest effect in this phase (Brunsting & Heil, 1985). It is estimated that from egg hatch to reproducing adult of 4.5 mg dry weight, requires 151mg of food (dry weight), of which 64 mg is assimilated and 87 mg excreted (Brunsting, 1982). The total food intake of the beetles usually appears to be less than the amount available, but the intake was calculated to exceed that of sheep at a stocking density of 0.8 per ha (Brunsting, 1982).

In November, when temperatures drop below 9°C, the adult beetles retreat into the litter and hibernate (Brunsting, 1982). Prior to this, the new generation of beetles walk to the edges of the damaged area in search of food, resulting in a high density of beetles around the edges of foci, up to 2000/m². This high density 'front' remains in the litter layer during winter the life-cycle starts again with the spring emergence and migration in the following spring (Brunsting, 1982).

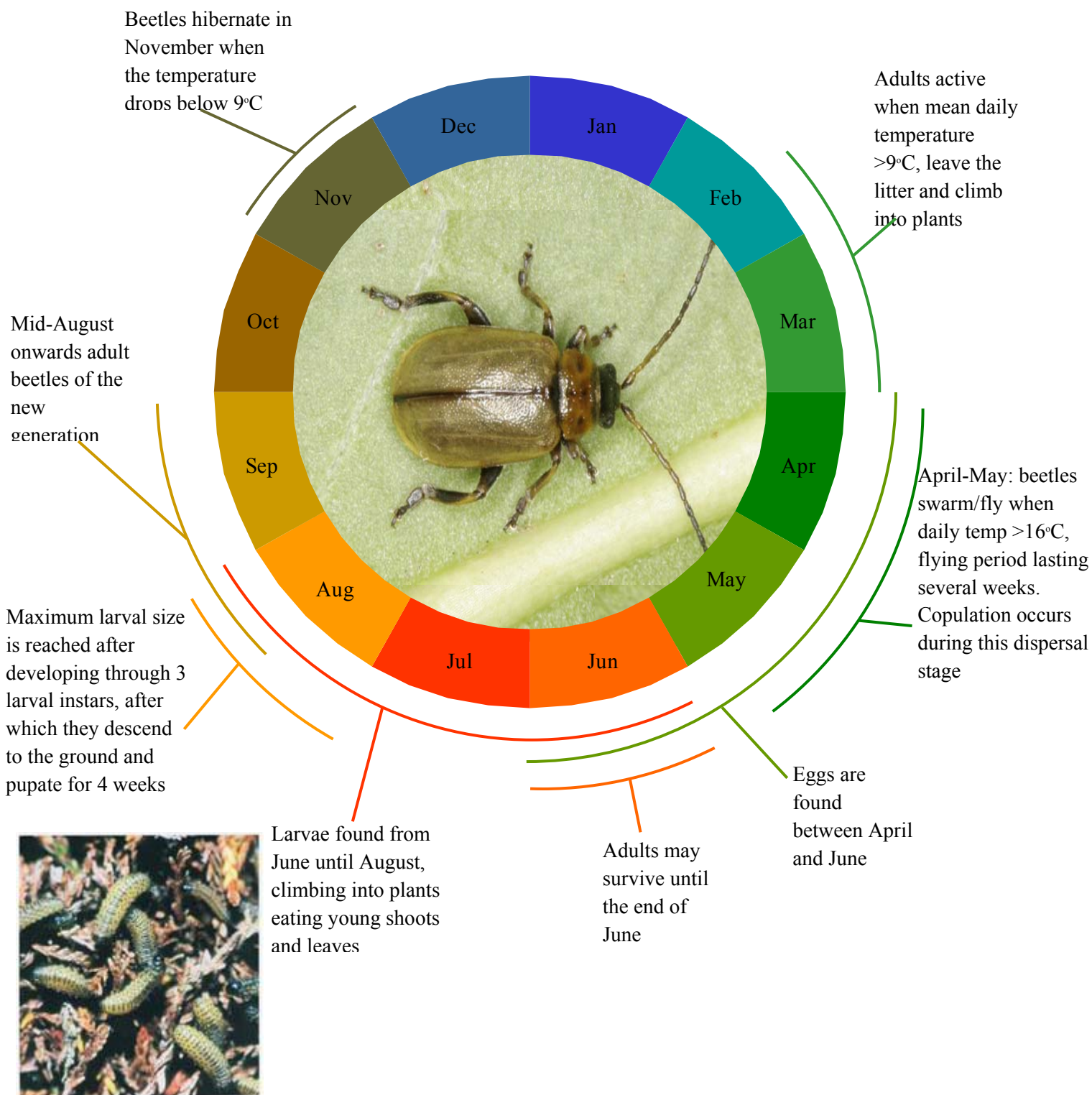


Fig. 2. Diagrammatic outline of the life-cycle of the heather beetle.

Like other pest species, the heather beetle can be regularly affected by shortages of its preferred food supply, the new green shoots of *Calluna*, even though there may be other food available. The heather beetle is able to survive depletion of its food source through its capacity for dispersal by flight and migration by walking (Brunsting, 1982), however mortality during dispersal is high as many beetles do not succeed in finding suitable habitats and die (Blankwaardt, 1968). In other literature on the dispersal of beetles, this feature has been emphasised as of significance in the survival of species (den Boer, 1977, 1981). Females show this capacity during early spring only, prior to laying eggs (Brunsting, 1982). A shortage of food, or a lack of moisture, enhances the animal's disposition to flight and delays laying eggs and the associated gradual breakdown of the wing muscles (Cameron *et al.*, 1944; Brunsting, 1982). From dissection, it has been concluded that wing muscles break down in females at the same time as laying eggs (Brunsting, 1982; Schaick Zillesen & Brunsting, 1983). Males maintain their flight muscles throughout their life, irrespective of feeding conditions (Schaick Zillesen & Brunsting, 1983). This mechanism allows the beetle to leave places where there is a shortage of food.

4. The effects of a heather beetle outbreak

Outbreaks occur when the density of the beetles increase to much greater levels than normal; they have been reported from Great Britain, Belgium, Denmark, Germany, Sweden, France, Switzerland, and especially the Netherlands (Blankwaardt, 1977) where they occur approximately every 10 years in lowland areas (Blankwaardt, 1977). Whilst there have always been outbreaks on northern grouse moors in the UK (Webb, 1989), there is some evidence to suggest they are becoming more frequent (MacDonald, 2000; Pakeman *et al.*, 2002).

On lowland heaths with a more continental climate (Dutch and East Anglian heaths) heather beetle attacks are common and can have a devastating effect on large areas of vegetation (de Smidt, 1977; Brunsting, 1982). They have been reported as locally-serious in Scotland and in south-west England, but our knowledge of beetle outbreaks is quite poor and lacks co-ordination. An attempt by the Heather Trust to gather information on the scale and severity of the heather beetle problem took place in 2009, and the limited amount of data collected, identified the difficulty of collecting information about outbreaks. However, the data show that in 2009 significant outbreaks occurred in many parts of the UK. (http://www.heathertrust.co.uk/output/heather_beetle.asp).

This lack of knowledge in the British uplands is surprising given the reliance of many land-based industries on the heather resource (35,600km²) (Pakeman *et al.*, 2002). The feeding of heather beetle on *Calluna* plants can result in severe damage or even death of the plants over variable patch sizes within 6 months of an attack (Schrier, 1981; Brunsting, 1982; Berdowski & Zeilinga, 1983, 1987); in the Breckland heaths of East Anglia large patches (>1 ha) of *Calluna* are often killed (Marrs, 1986);

with patches from <2 ha to >5 ha reported in Scotland (Pakeman *et al.*, 2002). Past outbreaks and large scale die-off can be observed in the growth rings of *Calluna* stems (Diemont & Heil, 1984). Damage can also be detected on bell heather and cross-leaved heath although it is usually of a minor nature. In *Calluna* the affected heather is usually in the building phase (6-10 years old; Watt, 1955), the mature phase (10-20 years) or older (Pakeman *et al.*, 2002). The outbreaks appear to spread by both increasing the size of already damaged patches, and, more commonly, by producing new patches (Pakeman *et al.*, 2002).

4.1. Damage to the plants

The damage to heather comes about in two ways, first by direct consumption of leaf material, and second indirectly through the physiological consequences of this leaf damage. It appears to be the latter that can kill plants, with drought and severe frost proving fatal to severely-damaged plants (Pakeman *et al.*, 2002). Damaged plants show a characteristic reddening of the foliage to a foxy-red colour (Fig. 3.) and on close inspection the damage caused by the beetle (defoliation and loss of fine twigs) is clear (Webb, 1989; Grimshaw, 1911). The onset of an outbreak is marked by the appearance of damaged areas of *Calluna*, of variable size ranging from tens of square meters to many hectares. These damaged areas contain high densities of heather beetle larvae, sometimes as many as 1000/m². In Scotland, outbreaks usually start in degenerate *Calluna*, especially in wet and shaded conditions which may then spread to adjacent, younger heather (Cameron *et al.*, 1944). In the degenerate stands, the older stands are often killed, and any younger, more-vigorously growing plants may survive (Cameron *et al.*, 1944; Gimingham, 1972; Marrs, 1986). There is no current protocol that provides predictive information relating heather damage or recovery to the amount of beetle defoliation (MacDonald, 2000). The death of plants can take several months following an outbreak, but new shoots may develop the following spring from plants that “appear dead” but have suffered a low infestation (Ladekarl *et al.*, 2001). At Cavenham Heath in lowland England, the oldest stands were most affected, and moreover recovery was slower than either younger stands, or uneven-aged plants. (Marrs, 1986). These old plants have very limited, if any, ability to resprout (Miller & Miles 1970; Berdowski & Zeilinga, 1987).

In Dutch heathlands, *Calluna* rarely dies from old age (de Smidt, 1977a; 1979), rather the plants are killed in three ways, through: (1) management factors (e.g. mowing and burning); (2) abiotic factors (e.g. summer drought) or winter cold; and, (3) biotic factors (e.g. pests, e.g. the heather beetle). From data collected over 25 years de Smidt (1977a) concluded that in most cases the changes in pattern in heathland vegetation could be related to both the cover of *Calluna* and the density of the heather beetle (Berdowski & Zeilinga, 1987).



Fig. 3. Characteristic ‘frosted’ damage of *Calluna* by heather beetle (Heather Trust, 2005).

4.2. Impacts on soils

The death of the *Calluna* has important implications for the functioning of the heathland ecosystem, because these systems occur only on very infertile soils. However, during and following heather beetle outbreaks, relatively large amount of nutrients become deposited on the soil surface and become available for plant growth. This is due to a combination of faeces produced by the larvae and, thereafter by an increased decomposition of the *Calluna* debris and a reduced uptake from plants (Brunsting, 1982). It has been estimated the amounts of nutrients released in heathland as a result of infestation by heather beetle is similar to the quantities of nutrients applied in fertiliser experiments in which Sheep fescue *Festuca ovina* was found to replace *Calluna* as the dominant species (Heil & Diemont, 1983).

Increases in soil nitrogen availability were due to a combined effect of (1) increased inputs from dead plants, litter, faeces and dead beetles, and (2) reduced uptake by vegetation (Kristensen & McCarty, 1999). The level of nitrogen returned to the soil through faeces and corpses alone has been estimated to be similar to the annual input from the atmosphere (Brunsting, 1982). Since atmospheric sources can be enough to initiate vegetation shift itself, this surge of nutrients will undoubtedly cause some changes in the vegetation. The addition of nutrients can trigger these outbreaks (Heil & Brunsting, 1985) leading to altered N cycling processes and increased nutrient availability. This can become a positive feedback, with faster nitrogen mineralization, high soil nitrogen availability and promotion of grass rather than *Calluna*.

However, other interacting factors contribute to the initiation of heather beetle outbreaks, and these include the nutritional status of plants, climate, vegetation composition, local factors, growth factors and random factors (Berdowski, 1987).

4.3. Damage to the ecosystem

One of the major impacts that can occur after an outbreak of heather beetle damage is that gaps in vegetation cover of varying size are created where there is very little competition, and as the vegetation is consumed there is an increase in nutrients deposited on the soil surface. Two types of change in species composition have been reported in a lowland setting:

1. An acceleration of succession to woodland, colonization by birch (*Betula* spp.) was much greater in the patches of *Calluna* that suffered the most severe heather beetle damage (Marrs, 1986).
2. A change to an alternative semi-natural vegetation type; on lowland heaths this is usually a colonization and subsequent dominance of grasses. In the Netherlands, and to a lesser extent in S. England, Wavy hair grass *Deschampsia flexuosa* and Purple moor-grass *Molinia caerulea* are the most common invasive species, the former on the drier sites and the latter on the wetter ones (Aerts & Heil, 1993; Marrs, 1993; Waloff, 1987; Brunsting, 1982; Diemont & Heil, 1984; Van Heusden, 1983; de Smidt, 1983)

Because the impacts of heather beetle outbreaks were first judged to be causing a problem on lowland heaths, most research has been focussed on these types of heath. Indeed most of the detailed research was carried out in the Netherlands where heather beetle caused significant damage, and indeed vegetation change, on areas that were protected for nature conservation (de Smidt, 1983). There has been very little research carried out on upland moors in the UK; if the experience of the lowland situation was to be repeated in the uplands then a replacement of *Calluna* with grasslands would be predicted, and in the wetter places this would likely be by Purple moor-grass *Molinia caerulea*, a very problematic species to control (Milligan *et al.*, 2004).

During these large outbreaks the heather beetle can, initiate a massive change in ecosystem structure and function by creating gaps (Berdowski & Zeilinga, 1987; de Smidt, 1977; Brunsting, 1982; Diemont & Heil, 1984). These changes have been well documented in the Netherlands (Berdowski, 1987; Berdowski & Zeilinga, 1987; Bokdam, 2001) and Denmark (Ladekarl *et al.*, 2001). Brunsting (1982) showed on one site that a change in vegetation structure from heather to a heather/grass mosaic was entirely due to the dynamics of the heather beetle outbreak.

Gap creation involves the defoliation and death of *Calluna*, which in turn increases light penetration and hence a warmer micro-climate, space for new seedlings to colonize becomes available (Berdowski & Zeilinga, 1987), which together with the increased nutrients stimulates grass invasion. Once established the increased nutrient availability favours grasses over *Calluna* (Aerts, 1993; Alonso & Hartley, 1998). In the UK, at that time, the problem did not appear to be as severe as on the continent. Scandrett & Gimingham (1991) noted no increase in grasses in the 1980s, with possible explanations including lower nutrient status, especially in atmospheric deposition, lower pH and poor drainage of the soils. However, more recently in south west Scotland Purple moor-grass *Molinia caerulea* has replaced heather in wet heathland vegetation after heather beetle attack (Milne *et al.*, 2002), and Pakeman *et al.* (2002) also noted that even where *Calluna* regeneration occurred, there was evidence of replacement by moorland grasses.

In the Netherlands it has been argued that the increase in soil available nutrients is the main cause of the increase in grass invasion (Berendse, 1985) and in determining the competitive balance between *Calluna* and grasses (Brunsting, 1982, 1985; Berdowski, 1985; Waloff, 1987). Diemont & Heil (1984) showed application of an equivalent of about 28kg N/ha/year over four years' turned a *Calluna*-dominated heathland into a grass heath of Sheep fescue *Festuca ovina*. It has also been calculated that the amount of nitrogen from dead plant material in a *Calluna* stand after a heather beetle outbreak was of the same magnitude, and it has been inferred that mineralisation of nitrogen after *Calluna* death may be the reason why grasses take over as the dominants. Even in Holland, transition from *Calluna* to grass does not always occur; however, at one site this was ascribed to a lack of grass seed (Diemont & Heil, 1984).

There is a clear difference in the way that damage to ecosystem processes occurs, which is dependent on the initiator of change. Where the initiator of change brought about through management (e.g., mowing, burning, turbarry, sod cutting) all of the species present are damaged, and nutrients are usually removed from the system. However, when the initiator is either abiotic (climate) or biotic (heather beetle), often only the *Calluna* is damaged, hardly any nutrients are removed from the system, and indeed there is an increased nutrient supply through recycling.

4.4. Potential economic importance of heather beetle outbreaks

During outbreaks, the heather beetle becomes a pest of economic importance on upland moors in the UK, where sheep and increasingly cattle graze. Moreover, on many moors grouse shooting is a very important economic activity, and *Calluna* is the principal food of Red Grouse (*Lagopus lagopus scoticus* (Lath.)). In worst-case scenarios grouse will desert a badly attacked moor (Morison, 1963). Grazing by deer will also be affected, although deer are sufficiently mobile to move to other grazing area.

Clearly, if heather is severely damaged or killed by beetle outbreaks, then it must affect the economic returns seen by the graziers and sporting enterprises. In 2000, upland moors in Scotland produced annual revenue for grouse shooting in the region of £10.2m (Pakeman *et al.*, 2002 from data in a report by the University of Strathclyde, 2001) and £12m for deer shooting (Association of Deer Management Groups, 2002). Pakeman *et al.* (2002) estimated the worth and damage caused to the heathland by the heather beetle. Depending on the assumptions made, estimates of total damage in the last five years within the Deer Management Groups varied between 1311 and 2514 km², 5.4 to 10.4% of the heather present. Extrapolated to all the heather in Scotland this range could be from 1917 to 3676 km². A survey of Deer Management Groups estimated costs to members in the region of £120k to £520k per annum, representing between 0.7 and 3.1% of grouse related revenue lost and 0.2 to 0.7% of deer related revenue. A reduction in *Calluna* in flower will also reduce heather honey production.

In addition, heather moorland is one of the UK ecosystems that contribute to European and global diversity, and delivery of ecosystem services such as water harvesting and carbon accounting (Pakeman *et al.*, 2002; Marrs *et al.*, 2007). Damage from heather beetle will reduce the ability to deliver these services and there is an increasing awareness that these services have an economic value.

Pakeman *et al.* (2002) showed that the greatest losses were for income derived from grouse (61% of reported losses), with lesser amounts from deer (17.3%), and small losses related to tourism (including shooting lets) and livestock. Total losses for the five year period 1997 to 2001 were in the range of £0.6m to £2.6m, this is divided into ranges of £0.36 m - £1.6 m for losses to grouse and £0.1m - £0.44m to deer related income. Assuming these revenue figures, the effects of heather beetle in the total revenue of grouse moors in Scotland ranges is equivalent to 0.7 to 3.1% reduction of income per annum. Similar calculations for deer based incomes suggest heather beetle reduces revenue by 0.2 to 0.7% p.a. depending upon the method of calculation (all data from Pakeman *et al.*, 2002).

5. Contributing factors

Observations and field studies have suggested that a change in dominance from ericaceous vegetation to grasses is often related to soil nutrient conditions (Berdowski & Zeilinga, 1987). *Calluna*-dominated heathlands are maintained in nutrient-poor ecosystems, and as such are vulnerable to the addition of nutrients, such as atmospheric deposition (Gordon *et al.*, 1999), leading to succession to forest (Gimingham *et al.*, 1979; Aerts & Heil, 1993). Several grass species have been demonstrated to be stronger competitors than *Calluna* plants at a high nutrient supply (Loach, 1968; Heil & Diemont, 1983), and that when nitrogen increases, *Calluna* is replaced by grasses (Brunsting, 1982). Other drivers implicated in this change from *Calluna* to grass were the heather beetle, soil type, levels of atmospheric deposition, the interaction between the beetle presence and grasses already present (Berdowski, 1987), and climatic extremes (Marrs & Britton, 2000).

The nutritional value of *Calluna* plants influences insect grazing (McNeill & Southwood, 1978; Ladekarl *et al.*, 2001), and it should be no surprise that where leaf nitrogen concentration was elevated there was an increased intensity and frequency of heather beetle outbreaks (Brunsting & Heil, 1985; Berdowski, 1993; Bobbink & Heil, 1993; Ladekarl *et al.*, 2001). This is especially important in the larval stage; larvae grow faster and reach a higher adult weight when feeding on plants with a higher nutritional status. The shorter larval period may also make them less vulnerable to predators and other enemies (Brunsting & Heil, 1985). It is also a widespread phenomenon that large female insects lay more eggs and so an increase in nutrient levels of plants may enhance beetle population densities (Brunsting & Heil, 1985).

Assuming the generalised relationship between insect herbivory (heather beetle attack) and foliar nitrogen concentration is valid, then we would expect greatest impacts in areas where foliar concentrations were high. Whilst there is no direct evidence to confirm this; it is interesting that foliar nitrogen concentrations in *Calluna* within Great Britain showed a linear relationship with levels of atmospheric nitrogen depositions (Pitcairn *et al.*, 1995). The lowest concentrations were found in the north-west of Scotland and the highest in Breckland heaths. Whilst not proven, it is interesting to note that the Breckland site was adjacent to the large heather beetle outbreak in the late 1970s, reported by Marrs (1986). The atmospheric inputs of nitrogen have increased over the last 50 years and are just starting to decline. Assuming that this decline continues this may reduce the risk of future heather beetle outbreaks.

6. Factors that might limit heather beetle populations

There are several important environmental factors and natural enemies, which limit the population of heather beetle. Environmental conditions can help to reduce the population by providing unsuitable conditions for the various life stages and instars. Natural enemies of the beetle generally keep population numbers low. However, occasionally the beetle population escapes regulation by these predators and parasitoids, and an outbreak can occur. Outbreaks normally build up and die out over 2 to 3 years, as the natural enemies slowly build up their populations (Pakeman *et al.*, 2002).

Direct control of the heather beetle using pesticides has been seen as difficult and probably undesirable (MacDonald, 2000) since there are no specific pesticides developed, and application would be devastating to all other heathland invertebrates along with those species which rely on them. Thus, we are reliant on climatic, biotic and management controls. However, it might be possible to target insecticide applications to control the larvae population in late July/early August. However, the impact of this approach would need to be evaluated through careful research as other invertebrate species might be affected by the treatment.

6.1 Climatic controls

Weather conditions can exert similar influence upon heather beetle populations. Few pupae survive below 70% relative humidity, with mortality occurring during hot, dry summers which dries out the litter (Cameron *et al.*, 1944). Conversely, high temperatures in April favour early maturation and egg laying of the beetle, whereas high rainfall in June favours the growth of *Calluna*, which tends to remain green and healthy throughout the summer. As a contrast, *Calluna* can appear desiccated by June, especially the older bushes. The contrasting weather conditions in spring and summer 1982 with those of 1983 indicated that the effects of climate on the survival of heather beetle populations is largely determined by the conditions of their host plant (Waloff, 1987). Following an attack, dry conditions can also inhibit the grass invasion by (Riis-Nielsen, 1997).

The increase in mild, wet winter, warm spring and wet summer weather in the last ten years or so may be one reason for the perceived increased number of recent outbreaks. There are also potential feedback effects if there are climatic extremes; it is likely that if there are very severe winters or very hot, dry summers then the *Calluna* plants are debilitated and this makes them more susceptible to insect attack. A large outbreak in Breckland followed this course in the late 1970s (Marrs, 1986).

6.2. Biotic controls

There are several documented predators and parasitoids of the heather beetle, which operate on the adult beetle or larvae, and these include a ladybird predator *Coccinella hieroglyphica* L. (Schrier &

Portier, 1981), a pentatomid bug *Rhacognathus punctatus* L. and two species that parasitize the larvae (a wasp, *Degeeria collaris* Fallén, Cameron *et al.*, 1944; and a fly *Asecodes mento* Walker, Golightly, 1962). *Coccinella hieroglyphica* and *Rhacognathus punctatus* have both been suggested as population regulators of the heather beetle, they are uncommon on heathland and where present are too low in number to be effective as a control measure (Webb, 1989). A small population of the heather beetle in southern England was found to be parasitized by *Asecodes* and by the parasitoid *Degeeria collaris* (Waloff, 1987). These parasitoids can have a high and consistent incidence (35-55%), although this is density independent and so did not control the heather beetles (Scandrett & Gimingham, 1991). Other parasites and predators do not have significant effects on the population (Scandrett & Gimingham, 1991).

Beauveria bassiana (Bals) Vuill is a fungal pathogen that affects heather beetles (Schrier & Portier, 1981). Locally, mortality can be very high, with many corpses detected during an outbreak covered by the fungus (up to 285/m²); the fungus was lethal to both larvae and beetles in the laboratory (Brunsting, 1982). The fungus is density-dependent, causing mortality in high-density populations. In Scotland, this fungus is present but does not seem to have the importance observed in the Netherlands (Scandrett & Gimingham, 1991), affecting up to 8.3% of the population in the largest record.

6.2. Management controls

Burning may help to reduce the impact of an outbreak, but most adult beetles hibernate deep within the litter layer during the burning season and so will be little affected by heather burning, unless the burn removes all above-ground plant material including the litter and bryophyte layers. This almost inevitably means a relatively hot burn (Pakeman *et al.*, 2002). As many prescribed burns are carried out at lower temperatures in an attempt to rejuvenate the *Calluna* without complete destruction of the underlying litter it is possible that heather beetle larvae escape such fires. The suggestion that burning in late-July to early August might kill heather beetles is a possible solution but this is prevented under the current burning restrictions. Cutting and removal of the vegetation would presumably have a similar effect to a hot prescribed burn. Summer burning and cutting plus vegetation removal are techniques that require considerable research in areas where heather beetle attacks are ongoing.

7. Vegetation recovery from heather beetle attack

There is a change in the way that *Calluna* regenerates across the European climatic gradient (Marrs, 1988). In more oceanic climates the principle regenerative method of *Calluna*, at least in the short term, is through layering, and subsequent vegetative growth of older stems (Scandrett & Gimingham, 1991). In the more continental climates of East Anglia and the Netherlands layering is negligible (Marrs, 1988), and regeneration is solely from seeds. Superimposed on this is resprouting from stem

buds, that occurs after burning or cutting (Miller & Miles, 1970). As both the number of stems decline with age, and the number of available buds per stem (Miller & Miles, 1970), recovery through this pathway will decline with plant age.

The response of the vegetation after a heather beetle attack will, therefore, depend on at least two factors at a given site: (a) the relative balance between the two regeneration mechanisms (layering versus seed), which in broad terms is climate dependent (in the UK southern, regeneration is mainly by seed, in upland, northern and western sites regeneration can occur through layering); and (b) the proportion of plants killed outright. Where there is a complete kill regeneration has to occur from seed (Scandrett & Gimingham, 1991) and on sites where regeneration is mainly by layering this can take some time to re-establish vegetation. Where the plants are not killed outright they can recover via resprouting from stem buds, in a similar way to recovery after burning/cutting. This process is most likely to occur in the oceanic areas and where the damaged plants are not too old. If there is no resprouting then the plants must regenerate from seedling germination (Pakeman *et al.*, 2002).

If *Calluna* can regenerate (vegetatively or from seed) to a virtually closed canopy quickly, then establishment and expansion of Wavy hair grass *Deschampsia flexuosa* or other grasses will be prevented (Berdowski & Zeilinga, 1987). During this time land owners should limit the grazing impact of both livestock and grouse by reducing stocking levels, but also by shooting the moor hard, to provide the new plants with opportunity to establish and grow.

Where damaged heather has been replaced by grasses, methods for restoring heather-dominated communities have been developed (e.g. Milligan *et al.*, 1997, 2004; Pakeman *et al.*, 2000a; Pakeman *et al.*, 2000b; Todd *et al.*, 2000), much in conjunction with Geoff Eyre (Reference to his Restoration Company). However, not all situations have been covered by this research, and there is uncertainty as to whether restoration techniques designed for use on dry, lowland heaths will be effective in moorland situations with peaty soils (Milne *et al.*, 2002).

Management post-outbreak has focussed mainly on burning, although there is no obvious reason why cutting would not provide a similar effect. However, this use of burning has not been based on any research, but on the instinct and experience of moorland managers. Where the heather has been previously well managed and competitors are restricted in abundance then burning should serve well as a means of encouraging heather regrowth and seedling regeneration. Nevertheless, experience shows that the effect can be variable; burning the damaged vegetation appears to help recovery in some instances, although not in others. This variability might be related to the age of the heather before the heather beetle damage occurring (Pakeman *et al.*, 2002). If we accept that regeneration declines with stand age then we can predict that only young stands of heather will recover well from stem bases after an affected area has been burnt (Pakeman *et al.*, 2002). If there is little regeneration

from stem bases then regeneration has to come from seed; this can be quite effective but is much slower (Gimingham, 1972)

However, where potential competitors such as Purple moor-grass *Molinia caerulea* are present, then burning may disadvantage the heather (Pakeman *et al.*, 2002). It has been proposed that “the best solution is to shut one’s eyes to the dead and dying heather and to carry out the burning programme of strips and patches in the normal way” (Philips & MacDonald, 2000). In other words, to carry out normal moorland management practices. There is an alternative view that large-scale, even whole-moor burns should be carried out to remove the dead material and allow the heather to recover from seed, and that this approach will re-establish the moorland vegetation faster. If the heather has not been affected too severely, then burning need not be carried out as the plants should recover (MacDonald, 2000). However, all of the information in this debate is rather woolly and both the need for burning, the scale of burning required and follow-up actions in order to restore moorland quickly needs to be researched actively.

It has been suggested that on lowland heaths intervention management by cutting and burning, to maintain large areas of *Calluna* in the building phase, may be the most appropriate long term technique (Marrs, 1986). This approach prevents succession from heathlands to woodlands, i.e. it prevents invasion of taller trees and shrubs, and it short-circuits the *Calluna* regeneration cycle (Miles, 1979); where *Calluna* eventually dies and regenerates mainly from seed. Following invasion by grasses, it has been demonstrated (Diemont *et al.*, 1982) that removal of the grasses including the sod brings back a *Calluna* or *Erica*-dominated heath within two years.

8. Future research

We have some understanding of the biology and life-cycle of heather beetle, however, we do not have enough information at present to fully understand: (1) the processes that shift a natural population of heather beetles, apparently controlled by predators and parasites (Webb, 1989) to one where the population increases rapidly during outbreaks; (2) the extent of the current problem, (3) why some heathlands/moorlands are affected to a greater extent than others: (4) the role of management as a prevention and cure, and (5) are there any other insect herbivores living in moorlands that might cause similar problems in the future.

The difficulty of course is that we are dealing with a natural problem that has the potential to break out anywhere and anytime, hence it is difficult to develop predictive models.

8.1. Natural control processes

Heather Beetles are controlled most of the time by parasites and predators, and our understanding of why this breaks down in outbreak years is limited. For example, the dynamics of outbreaks may be controlled by the behaviour of the parasitoids. Where outbreaks are limited in extent, the conditions may either be inhibiting the growth of the beetle's population or promoting the growth of the parasitoids' populations (or vice versa) (Pakeman *et al.*, 2002). A greater in-depth understanding of the interactions between these populations might help shed light on "outbreak biology".

8.2. The extent of the current problem

The heather beetle was identified in 1853, but usually populations are at a low level with occasional outbreaks (Cameron *et al.*, 1944). All current anecdotal evidence suggests that outbreaks are becoming more frequent and affecting larger areas, although the quantitative evidence to back this up is lacking. The current attempt to collate this information via the Heather Trust's website is a welcome initiative to get some basic information on the potential scale of the problem. To be effective, this initiative needs support from all upland managers.

In order to build on, and to eventually develop, a system for predicting the likelihood of outbreaks in given areas much more data are needed. The obvious way to start collating this information would be to monitor outbreaks, and the easiest way to do this would be to use remote sensing to map damage at a range of scales. This spatial information will be important in helping to predict the areas most likely to be infected from damaged patches. However, any remote sensing approach needs to be linked to damage on the ground. There is, therefore, a need to integrate remotely-sensed data with field based assessments. Hence, there is a need to develop a site-based systematic and standardised method for recording of heather beetle outbreaks and damage (seen only in Scandrett & Gimingham, 1991), so that comparative data can be collected. This would provide much better quantitative data rather than relying on anecdotal accounts.

8.3. Why are some heathlands/moorlands affected to a greater extent than others?

Improved knowledge of both the insect's life-cycle and the ecology of given moors is required. At present, this information is lacking, except in broad generalities. A better understanding of the time course of damage on individual moors should be developed, identifying which plants are affected and why some recover and other do not. Previous data suggest that age is a major factor, but other environmental factors may interact with age (e.g. soil nutrient supply, atmospheric deposition, management applied, exact age structure etc). This information can only be collected by detailed field-based survey.

8.4. The role of management as a prevention and cure

Information is needed for three situations: (1) Prevention, i.e. to try and stop outbreaks occurring in the first place; (2) Control, where the aim is to minimise loss when an outbreak has occurred, and (3) Recovery, where the aim should be to achieve rapid *Calluna* recovery.

The only current management options available for all three of these scenarios are to manipulate the management regime (burning, cutting, and grazing). Development of sound knowledge of the best approach to adopt would be to set up controlled experiments in a range of situations and formally assess the most appropriate methods for given situations. The treatments should include some of the common ones suggested for treating heather beetle (see the Moorland Association website), for example: (1) Burning affected *Calluna*-dominated land in mid-late summer when all the eggs have hatched and the larvae are feeding on the *Calluna* and therefore exposed; (2) Mowing the affected heather to expose the larvae to light and heat and removing their preferred moist conditions; and (3) Burning the grey-coloured dead *Calluna* early in the following year to provide conditions for seed germination and growth of new plants.

We suggest that these proposed methods; along with other combinations of different prescribed burning/cutting regimes need to be tested experimentally for Control and Restoration as defined above. Almost certainly this will involve attempts to compare “hot” *versus* “cool” burns to assess the importance of removal of the litter layer, and also restoration treatments such as re-seeding and perhaps also the use of graminicides if grass invasion is prolific (Todd *et al.*, 2000; Milligan *et al.*, 2004).

This is a medium-term option and would take at least five years.

An alternative approach might be to attempt to develop biological control mechanisms, either using parasites/predators or species-specific myco-pesticides. Whilst this is technically feasible, it would require a considerable investment in research and development to ensure successful control, and would have to go through the standard pesticide regulatory process.

8.5. Any other potential pests?

Whilst the heather beetle is the obvious candidate as an herbivorous pest of *Calluna*, large scale die-back (1-5 ha) of *Calluna* on Orkney from winter moth caterpillars (*Orthoptera brumata* L.) has been reported (Picozzi, 1981). Whilst a localised outbreak, this work highlights that other species could cause problems in the future, especially if climate conditions change. The only possible way to identify these sorts of novel problems is to develop a web-based notification system and encourage estate managers to report “odd problems”. This approach would provide an “early warning system”

that would allow both scale and severity of new “insect problems” to be detected early, and hopefully research implemented to develop appropriate management techniques to deal with them quickly. The development of such an early-warning system for novel insect damage problems would be very difficult to implement as it requires estate managers to be vigilant in damage detection, have sufficient expertise to know that the damage is not caused by heather beetle but something else, and the willingness to take the trouble to log the information. This is particularly difficult because of the problem in separating potentially new serious problems from “one-off” local incidents.

9. References

- Aerts, R. (1993). Competition between dominant plant species in heathlands. In: *Heathlands: Patterns and Process in a Changing Environment* (Aerts, R. & Heil, G.W., eds.). Kluwer Academic Publishers, Dordrecht.
- Aerts, R. & Heil, G.W. (1993). *Heathlands: Patterns and Processes in a Changing Environment*. Kluwer Academic Publishers, Dordrecht.
- Alonso, I. & Hartley, S.E. (1998). Effects of nutrient supply, light availability and herbivory on the growth of heather and three competing grass species. *Plant Ecology*. **137**: 203-212.
- Association of Deer Management Groups (2002). *Deer Management in Scotland*. <http://www.deer-management.co.uk/dmg3.shtml>.
- Blankwaardt, H.F.H. (1968). De heidekever. *Tijdschrift Koninklijke Nederlandsche Heidemaatschappij*. **10**: 477-482.
- Blankwaardt, H.F.H. (1977). The occurrence of the Heather Beetle (*Lochmaea suturalis*) in the Netherlands since 1915. *Entomologische Berichten*. **37**: 33-40.
- Berdowski, J.J.M. (1985). Short-term changes in heathland after Heather Beetle outbreak. 2nd *European Workshop on Heathland Ecology*. Utrecht.
- Berdowski, J.J.M. (1987). Transition from heathland to grassland initiated by the heather beetle. *Vegetatio*. **72**: 167-173.
- Berdowski, J.J.M., & Zeilinga, R. (1983). The effect of the Heather Beetle (*Lochmaea suturalis* Thomson) on heather (*Calluna vulgaris* (L.) Hull) as a cause of mosaic patterns in heathlands. *Acta Botanica Neerlandica*. **32**: 250-251.
- Berdowski, J.J.M. & Zeilinga, R. (1987). Transition from heathland to grassland: damaging effects of the heather beetle. *Journal of Ecology*. **75**: 159-175.
- Berendse, F. (1985). Introduction: Annual report on the Heathland Research Project 1984. *The Utrecht Plant Ecology News Report*. **1**: 3-5.
- Bobbink, R. & Heil, G.W. (1993). Atmospheric deposition of sulphur and nitrogen in heathland ecosystems. In: *Heathlands: Patterns and Processes in a Changing Environment* (Aerts, R. & Heil, G.W., eds.). Kluwer Academic Publishers, Dordrecht.
- Bokdam, J. (2001). Effects of browsing and grazing on cyclical succession in nutrient-limited ecosystems. *Journal of Vegetation Science*. **12**: 875-886.
- Bouček, Z. & Askew, R.R. (1968). *Eulophidae (Tetrastichinae)*. *Index of Entomophagous Insects*. La François, Paris.
- Brunsting, A.M.H. (1982). The influence of the dynamics of a population of herbivorous beetles on the development of vegetational patterns in a heathland system. In: *Proceedings of the 5th International Symposium on Insect-Plant Relationships*, Wageningen. pp. 215-223. Pudoc, Wageningen.
- Brunsting, A.M.H. & Heil, G.W. (1985). The role of nutrients in the interactions between an herbivorous beetle and some competing plant species in heathlands. *Oikos*. **44**: 23-26.
- Cameron, A.E., McHardy, J.W. & Bennet, A.H. (1944). *The Heather Beetle (Lochmaea suturalis)*. *An Inquiry into its Biology and Control*. British Fields Sport Society, Petworth, Sussex. **53**: 69.

- de Smidt, J.T. (1977). Interaction of *Calluna vulgaris* and the Heather Beetle (*Lochmaea suturalis*). In: *Vegetation und Fauna*. (Tüxen, R., ed.) pp.179-186. Cramer, Vaduz, Liechtenstein.
- de Smidt, J.T. (1979). Origin and destruction of Northwest European heath vegetation. *Werden und Vergehen von Pflanzengesellschaften* (Wilmans, O. & Tüxen, R., eds.) pp.411-433. Cramer, Vaduz, Liechtenstein.
- de Smidt, J.T. (1983). Heathland management in the Netherlands, scientific and social aims. *Acta Botanica Neerlandica*. **32**: 248-252.
- den Boer, P.J. (1977). Dispersal power and survival. Carabids in a cultivated countryside. *Miscellany Papers*. **14**: L.H. Wageningen, Veenman & Zn. B.V., Wageningen. pp190.
- den Boer, P.J. (1981). On the survival of populations in a heterogeneous and variable environment. *Oecologia*. **50**: 39-53.
- Diemont, W.H., Blankenburg, F.G. & Kampf, H. (1982). *Blij op de hei?* Arnhem, Rapport Werkgroep Verwerking en Afzet van Heideplaggen.
- Diemont, W.H. & Heil, G.W. (1984). Some long term observations on cyclical and seral processes in Dutch heathlands. *Biological Conservation*. **30**: 283-290.
- Dingle, H. & Arora, G. (1973). Experimental studies of migration in bugs of the genus *Dysdercus*. *Oecologia*. **12**: 119-140.
- Gimingham, C.H. (1972). *Ecology of Heathlands*. Chapman & Hall, London.
- Gimingham, C.H., Chapman, S.B. & Webb, N.R. (1979). European heathlands. In: *Ecosystems of the World 9A: Heathlands and related shrublands* (Specht, R.L., ed.). Elsevier, Amsterdam. pp. 365-413.
- Golightly, W.H. (1962). Biological control of *Lochmaea suturalis* Thomson (Col., Chrysomelidae). *Entomologists Monthly Magazine*. **98**: 196.
- Gordon, C., Woodin, S.J., Alexander, I.J. & Mullins C.E. (1999). Effects of increased temperature, drought and nitrogen supply on two upland perennials of contrasting type: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytologist*. **142**: 243-258.
- Grimshaw, P.H. (1911). The Heather Beetle (*Lochmaea suturalis* Thomson). In: *The Grouse in Health and Disease*, Volume 1. pp. 414-429. Smith Elder, London.
- Heather Trust (2005). *Photographs of Heather Beetle damage*. Dumfries.
- Heil, G.W. & Diemont, W.H. (1983). Raised nutrient levels change heathland into grassland. *Vegetatio*. **53**: 113-120.
- Johnson, C.G. (1969). *Migration and Dispersal of Insects by Flight*. Methuen, London.
- Kristensen, H.L. & McCarty, G.W. (1999). Mineralisation and immobilisation of nitrogen in heath soil under intact *Calluna*, after Heather Beetle infestation and nitrogen fertilisation. *Applied Soil Ecology*. **13**: 187-198.
- Ladekarl, U.L., Nornberg, P., Rasmussen, K.R., Hielsen, K.E. & Hansen, B. (2001). Effects of a Heather Beetle attack on soil moisture and water balance at a Danish heathland. *Plant and Soil*. **229**: 147-158.
- Loach, K. (1966). Relations between soil nutrients and vegetation in wet-heaths. I. Soil nutrient content and the moisture conditions. *Journal of Ecology*. **56**: 117-127.

- MacDonald, A. (2000). *Heather Beetle Outbreaks*. SNH Advice Note, Advisory Services, Scottish National Heritage, Edinburgh.
- Marrs, R.H. (1986). The role of catastrophic death of *Calluna* in heathland dynamics. *Vegetatio*. **66**: 109-115.
- Marrs, R.H. (1988). Vegetation change on lowland heaths and its relevance for conservation management. *Journal of Environmental Management*, **26**, 127-149.
- Marrs, R.H. (1993). An assessment of change in *Calluna* heathlands in Breckland eastern England, between 1983 and 1991. *Biological Conservation*. **65**: 133-139.
- Marrs R.H. & Britton, A.J. (2000). Conservation problems on Breckland heaths: from theory to practice! *Biological Conservation* **95**: 143-151.
- McNeill, S. & Southwood, T.R.E. (1978). The role of nitrogen in the development of insect/plant relationships. In: *Biochemical Aspects of Plant and Animal Co-evolution*. (Harborne, J.B., ed.) Academic Press, London.
- Miles, J. (1979). *Vegetation Dynamics*. Chapman & Hall, London.
- Miller, G.R. & Miles, J. (1970). Regeneration of heath (*Calluna vulgaris*) (L.) Hull) at different ages and seasons in north-east Scotland. *Journal of Applied Ecology*. **7**: 51-60.
- Milligan, A.L., Marrs, R.H. & Putwain, P.D. (1997). Control of *Molinia caerulea* (L.) Moench in upland Britain. *British Crop Protection Conference (Weeds)*. **1997**: 679-680.
- Marrs, R.H., Galtress, K., Tong, C., Blackbird, S. J., Heyes, T.J. Pakeman, R.J. & Le Duc, M.G. (2007). Conflicts between competing conservation goals, biodiversity or ecosystem services: quantification of element losses and species recruitment using a moorland-bracken model system. *Journal of Environmental Management*, **85**, 1034-1047,
- Milligan, A.L., Putwain, P.D., Cox, E.S., Ghorbani, J., Le Duc, M.G. & Marrs, R.H. (2004). Developing an integrated land management strategy for the restoration of moorland vegetation on *Molinia caerulea*-dominated vegetation for conservation purposes in upland Britain. *Biological Conservation* **119**: 371-387.
- Milne, J.A., Pakeman, R.J., Waterhouse, C. & McKeen, M. (2002). Langholm- Newcastleton Hills SSSI. Moorland restoration plan. Report to Scottish Natural Heritage. Macaulay Research Consultancy Service, Aberdeen. April 2002.
- Morison, G.D. (1963). *The Heather Beetle*. pp. 1-16. The North of Scotland College of Agriculture, Aberdeen.
- Pakeman, R.J., Le Duc, M.G. & Marrs, R.H. (2000a). Bracken distribution and control methods: their implications for the sustainable management of marginal land in Great Britain. *Annals of Botany*. **85** Supplement B: 37-46.
- Pakeman, R.J., Thwaites, R.H., Le Duc, M.G. & Marrs, R.H. (2000b). Vegetation restoration on land previously subject to bracken control by herbicide. *Applied Vegetation Science*. **3**: 95-104.
- Pakeman, R., Stolte, A., Malcolm, A. & Marrs, R. (2002). *Heather Beetle outbreaks in Scotland*. The Scottish Executive Environment Group, Edinburgh.
- Philips, J. & MacDonald, A. (2000). Heather Beetle outbreaks. *Looking to the Hills*, 9: 6-7. Joint Nature Conservation Committee.

- Picozzi, N. (1981). Common gull predation on winter moth larvae. *Bird study* **28**: 68-69.
- Pitcairn, C.E.R., Fowler, D. & Grace, J. (1995). Deposition of fixed atmospheric nitrogen and foliar nitrogen-content of bryophytes and *Calluna vulgaris* (L) Hull. *Environmental Pollution*, **88**:193-205
- Rankin, M.A. (1978). Hormonal control of insect migratory behaviour. In: *Evolution of Insect Migration and Diapauses* (Dingle, H., ed.), pp. 5-32. Springer Verlag, New York.
- Riis-Nielsen, T. (1997). Effects of nitrogen on the stability and dynamics of Danish heathland vegetation. *Ph.D. Thesis*, University of Copenhagen.
- Scandrett, E. & Gimingham, C.H. (1991). The effect of Heather Beetle *Lochmaea suturalis* on vegetation in a wet heath in NE Scotland. *Holarctic Ecology*. **14**: 24-30.
- Schaick Zillesen, P.G. van & Brunsting, A.M.H. (1983). Capacity for flight and egg production in *Lochmaea suturalis* (Col. Chrysomelidae). *Netherlands Journal of Zoology*. **33**: 266-275.
- Schrier, A. (1981). The heather beetle. *Natura*. **78**: 322-325.
- Schrier, T. & Portier, A. (1981). Populatie- Oecologie van *Lochmaea suturalis*. Doctoraalverlag, Laboratorium voor Zoologische Oecologie en Taxonomie. *Heidekeverproject rapport no. 6*, 1-52.
- Stegwee, D. (1964). Respiratory chain metabolism in the Colorado potato beetle- II. Respiration and oxidative phosphorylation in sacrosomes from diapausing beetles. *Journal of Insect Physiology*. **10**: 97-102.
- Todd, P.A., Phillips, J.D.P., Putwain, P.D. & Marrs, R.H. (2000). Control of *Molinia caerulea* on moorland. *Grass & Forage Science*. **55**: 181-191.
- University of Strathclyde (2001). *An Economic Study of Scottish Grouse Moors: An Update (2001)*. A report by the Fraser of Allander Institute for Research on the Scottish Economy, University of Strathclyde. Game Conservancy Limited, Fordingbridge.
- Van Heusden, W.R.M. (1983). Monitoring changes in heathland vegetation using sequential aerial photography. *ITC Journal*. **2**: 160-165.
- Waloff, N. (1987). Observations on the Heather Beetle *Lochmaea suturalis* (Thomson) (Coleoptera, Chrysomelidae) and its parasitoids. *Journal of Natural History*. **21**: 545-556.
- Watt, A.S. (1955). Bracken *versus* heather: a study in plant sociology. *Journal of Ecology*. **43**: 490-506.
- Webb, N.R. (1989). The invertebrates of heather and moorland. *Botanical Journal of the Linnaean Society*. **101**: 307-312.
- Wilde, J. de (1969). Diapause and seasonal synchronisation in the adult Colorado beetle (*Leptinotarsa decemlineata* Say.). *Symposium of the Society for Experimental Biology*. pp. 263-284.