



A desk review of the ecology of heather beetle (NEER008)

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A desk review of the ecology of heather beetle

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Cover photograph

Heather beetle, © Christoph Benisch - kerbtier.de.

Executive summary

The heather beetle *Lochmaea suturalis* is a naturally occurring species in the heather dominated landscapes of the United Kingdom. When the heather beetle population density increases dramatically it can cause significant damage to heather plants. It has been suggested that burning heather outside the permitted heather-burning season will promote the regeneration of heather following heather beetle damage. There is also some discussion as to whether burning outside the permitted season might also help control heather beetle. For these reasons Natural England regularly receives applications for licences to burn outside the permitted season. However, burning at this time of year may have effects on a wide range of biodiversity. Therefore, Natural England commissioned this report, and (NEER009 - *Desk review of burning and other management options for the control for heather beetle*) to ensure the best available evidence is being used.

This report is based on an extensive literature review to determine the current state of knowledge of the ecology of the heather beetle. Some of the older references, which appear to form the basis for much current thinking on the subject, are now out of print and were not accessible for this review. A flurry of work was published in the 1980s and early 1990s, but much of this was either:

- based at the same experimental plots;
- involved relatively low levels of replication; or
- did not report heather beetle damage as a central focus of the work.

More recently, there have been some PhDs quantifying the ecology of heather beetles in more detail, but these have rarely been published in the peer-reviewed literature. Therefore, current thinking may be influenced by out-of-date information and experimental work that does not truly back up the conclusions of authors. This makes it difficult both to confidently discern patterns over time in frequency and severity of attacks (such as might be caused by climate change or changing nutrient deposition loads) and to be certain which factors control population levels in most years at most heather-dominated sites. Much more, and higher quality, monitoring and experimental work needs to be carried out to be able to predict the likely population dynamics of this species under different scenarios. The potential for parasites and parasitoids to control population numbers is particularly worthwhile. More detailed spatial analyses based on citizen science records, combined with carefully designed laboratory studies, might also be used to more clearly elucidate the relationship between beetle numbers and climatic conditions, enabling prediction of the relative likelihood of outbreaks occurring in the future.

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1 Introduction

Background

- 1.1 The heather beetle *Lochmaea suturalis* is a naturally occurring species in the heather dominated landscapes of the United Kingdom. It is recognised that population density can vary dramatically at the local level, giving rise to ‘outbreaks’ which can lead to damage to heather plants, with damage appearing in late June through to September.
- 1.2 The Heather and Grass Burning regulations (2007) stipulate that burning (in Upland areas) can only be done from 1st October to 15th April inclusive, unless under licence from Natural England. In lowland habitats managed burning is permitted from 1st November to 31st March. Natural England regularly receives applications for licences to burn outside this permitted season in order to promote effective regeneration of heather following “heather beetle” damage. There is also some discussion on whether summer burning might help ‘control’ heather beetle. Burning outside of the season may have effects on a wide range of biodiversity, such as breeding birds.
- 1.3 In order to inform their advice and decision-making on this issue, Natural England commissioned this report to ensure they are drawing on the best available evidence.

Aims and objectives

- 1.4 The aim of this review was to provide an overview of what is known about the life cycle and population dynamics of the heather beetle. This is to facilitate the prediction of the likely response of heather beetles to different management options, in the event that information is lacking on impacts from published material (see Evidence Review NEER009 - *Desk review of burning and other management options for the control for heather beetle*). In addition, we aimed to assess the quality of published analyses, and highlight knowledge gaps where these occurred.

Approach

- 1.5 In order to be confident that knowledge gaps are true and not just perceived, it was necessary to complete a systematic review of the literature. The search terms, dates of search and databases searched are given in Table 1. Initial searches were performed by a librarian, with titles being screened for relevance. The papers chosen for inclusion in the study were found. The outcomes (inclusion, rejection and at which stage) along with availability were noted in Appendices 1, 2 & 3. The information in the spreadsheet produced by the librarian was screened by the lead author. Many discrepancies were found in initial tests between the papers marked for inclusion and rejection by the librarian and the lead author (kappa value 0.0394 for all sources returned by mySearch, 0.2435 for all sources considered for this report), so all papers returned in the searches were consequently screened by the lead author. Papers were rejected if the title was clearly not relevant, or if the source was clearly not reliable (ie a press release or news source). If there was any uncertainty with the title then papers were screened at the abstract level. After screening at the abstract level, if the relevance of a paper was still unclear then a full text search was performed to determine relevance.
- 1.6 The chosen papers were then read in more detail and synthesised to produce this report. We made all possible efforts to track down papers that were not immediately available, with some being provided directly by the authors via ResearchGate (<http://www.researchgate.net/>), others being provided by Moors for the Future and some theses being requested via EThOS. However, two particularly influential texts (Cameron *et al.* 1944 and Morison 1963) were only available as abstracts, both are currently out of print and were not held by our library.

Table 1 Searches performed by librarian to generate source articles for this report

Date	Search String	Database	No. of results
08/10/13	Heather Beetle AND Life Cycle	mySearch ¹	1
	Heather Beetle AND Behaviour		4
	Heather Beetle AND Pop*		14
	Heather Beetle AND Dynamic*		8
	Heather Beetle AND Outbreak		14
	<i>Lochmaea suturalis</i> AND Life Cycle		2
	<i>Lochmaea suturalis</i> AND Behaviour		3
	<i>Lochmaea suturalis</i> AND Pop*		20
	<i>Lochmaea suturalis</i> AND Dynamic*		8
09/10/13	Heather Beetle	mySearch ¹	140
	<i>Lochmaea suturalis</i>		82
09/10/13	<i>Lochmaea suturalis</i> AND Life Cycle	Google Scholar	59
16/10/13	<i>Lochmaea suturalis</i> AND Population	Google Scholar	215
	Heather Beetle AND Outbreak		101
	<i>Lochmaea suturalis</i> AND Behaviour		105
12/11/13	<i>Lochmaea suturalis</i> AND Dynamic	Google Scholar	79

¹ mySearch is BU's resource discovery tool, which is hosted in EBSCO's Discovery Service. mySearch surfaces bibliographic data from all the traditional bibliographic databases to which BU subscribes, in addition to extensive journal publisher feeds and peer-reviewed open access sources. Times cited linking for Web of Knowledge and Scopus is also incorporated to aid forward cascading of searching to pinpoint the most contemporary studies.

A typical search using mySearch in the field of ecology would produce results derived from Scopus, Web of Knowledge (including Science Citation Index), Environment Complete, CAB Abstracts, Academic Search Complete, MEDLINE Complete, GreenFILE, ScienceDirect, JSTOR, Hospitality and Tourism Complete, Business Source Complete, Publisher provided full text searching file, BioOne Online journals, OAlster, British Library Inside Serials & Conference Proceedings and British Library EThOS.

mySearch also has the capacity to include selected non peer-reviewed sources. Additionally full text searching of extensive academic e-book collections, such as Ebrary Academic Complete, MyiLibrary and EBSCO Academic Complete can be conducted. Rare and unique research material held by over 70 of the UK's national, research and specialist libraries can be exposed by searching using the Copac catalogue.

1.7 The search terms Heather Beetle AND Life Cycle, Heather Beetle AND Behaviour, Heather Beetle AND Pop* Dynamic*, Heather Beetle AND Outbreak were found to return mostly irrelevant papers when entered into Google Scholar, which returned any papers with the words heather and beetle included in the full text. The subject of most of these was other beetle groups (for example, Carabidae) that are regularly studied on heather. For this reason, we did not include these search terms in the google scholar section of the systematic review.

1.8 In total:

Appendix 1

- 29 references were rejected at the title level;
- 75 were rejected at the abstract level;
- 64 were rejected after a full-text search; and
- 11 were found to be repeats.

Appendix 2

- 38 sources were either not available, or were only available as an abstract.

Appendix 3

- The remaining sources were synthesised and their quality was assessed.

2 Autecology and population dynamics

- 2.1 The heather beetle *Lochmaea suturalis* is closely related to the genus *Galerucella* and to *Tricholochmaea decora* (Borghuis *et al.* 2009). It was first recognised in 1876 and the first record of an outbreak (in Germany) comes from Cornelius (1858, reported in Berdowski 1993). It is present in the fossil record in the UK, being recorded in the late-glacial, then not again until the Holocene, but this could be due to the patchy nature of the fossil record (Buckland 2005). It is regularly reported from the whole of North West Europe (Webb 1986), where its distribution is closely correlated with Ling heather *Calluna vulgaris* (Berdowski 1993). Both larvae and adults eat the leaves, stem apices and bark of heather shoots (Cameron *et al.* 1944 cited in Gimingham 1972). Many sources state that heather beetles are monophagous on *C. vulgaris* (for example, Berdowski 1993), although others have reported feeding to a lesser extent on bell heather *Erica cinerea* and cross-leaved heather *Erica tetralix* in the UK (Morison 1938, Pakeman *et al.* 2002) and it has been recorded feeding on *Erica multiflora* in Spain (Peñuelas *et al.* 2004). A small study found that there is no effect of the hairiness of the *Calluna* variety *hirsuta* on herbivory and that *Calluna* was preferred to *Erica tetralix* and *Empetrum nigrum* (Scandrett & Gimingham 1991). Laboratory and field experiments in the UK confirmed that adult survival is reduced on other plants relative to survival on *Calluna*, but that larvae were able to develop to adults on three of the four *Erica* species tested (Syrett *et al.* 2000).

Life cycle

- 2.2 An overview of the life cycle is given in Figure 1. *Lochmaea suturalis* has one generation per year, and laboratory studies revealed that there is no obligatory diapause (Cameron *et al.* 1944). The winter is spent in hibernation, which is carried out by the adult phase and these adults become active once the temperature reaches 9 °C (Cameron *et al.* 1944). From one study in the Netherlands, adult dispersal occurred during April and May, on days where the temperature reached a minimum of 16 °C (Brunsting 1982) and beetles have been observed to land whenever clouds obscure the sun or wind speed increases (van Schaick Zillesen & Brunsting 1983), although this last observation is based on casual observations rather than quantified behavioural studies. During the dispersal phase, beetles can travel several kilometres (Morison 1963, cited in Rosenburgh & Marrs 2010), although their flight is usually fairly weak and determined by the wind (Berdowski 1993). Despite this, studies from Denmark have estimated that gene flow between populations corresponds to 3 - 4 individuals per generation (Simonsen *et al.* 1999). Copulation occurs during the flight (dispersal) stage (Berdowski 1993). Following dispersal, flight muscles degenerate in females during oviposition, although males retain their capacity for flight throughout their life cycle (van Schaick Zillesen & Brunsting 1983). Sweep netting in Scotland in June 1983 - 85 revealed a female-biased sex ratio (Scandrett & Gimingham 1991), with up to 90 % of individuals at one site being female. Staley (2001) also found a female-biased sex ratio in the field, this time in the River Tyne catchment. However, lab-reared beetles from this site and the Surrey Heaths were not biased, and Waloff (1987) found a slight bias towards males in a population near Silwood Park. In Denmark, Riis-Nielsen (1997) found female biases in many experimental plots that became infested, with the most biased ratios being found on plots showing the most damage. He interpreted this as males being more food-demanding, with the potential for higher mortality during hibernation, but this was speculation and he did not test whether the males had died or simply moved to another site, as they retain their capacity for flight (potentially to mate with other females).
- 2.3 Within the New Forest, the heather beetle is considered to be a wet heath specialist (Carpenter *et al.* 2012). It has also been reported from coniferous forests in the Netherlands (Moraal & Jagers op Akkerhuis 2011) and boreal forests with shrub and grass understory in

Southern Norway (Amundsen 2012), which is a newly recorded area for it (Bobbink *et al.* 1998). Although heath sites with *Calluna* occur in Central Norway, up to 2004 it had not been recorded on them (Nilsen 2004). In New Zealand, where *Calluna* is considered to be a pest species, heather beetle has been trialled as a bio-control agent (Syrett *et al.* 2000, Peterson *et al.* 2004). It has recently been assessed as providing moderate benefit in this role (measurable benefit to local plant and animal communities, Suckling 2013).

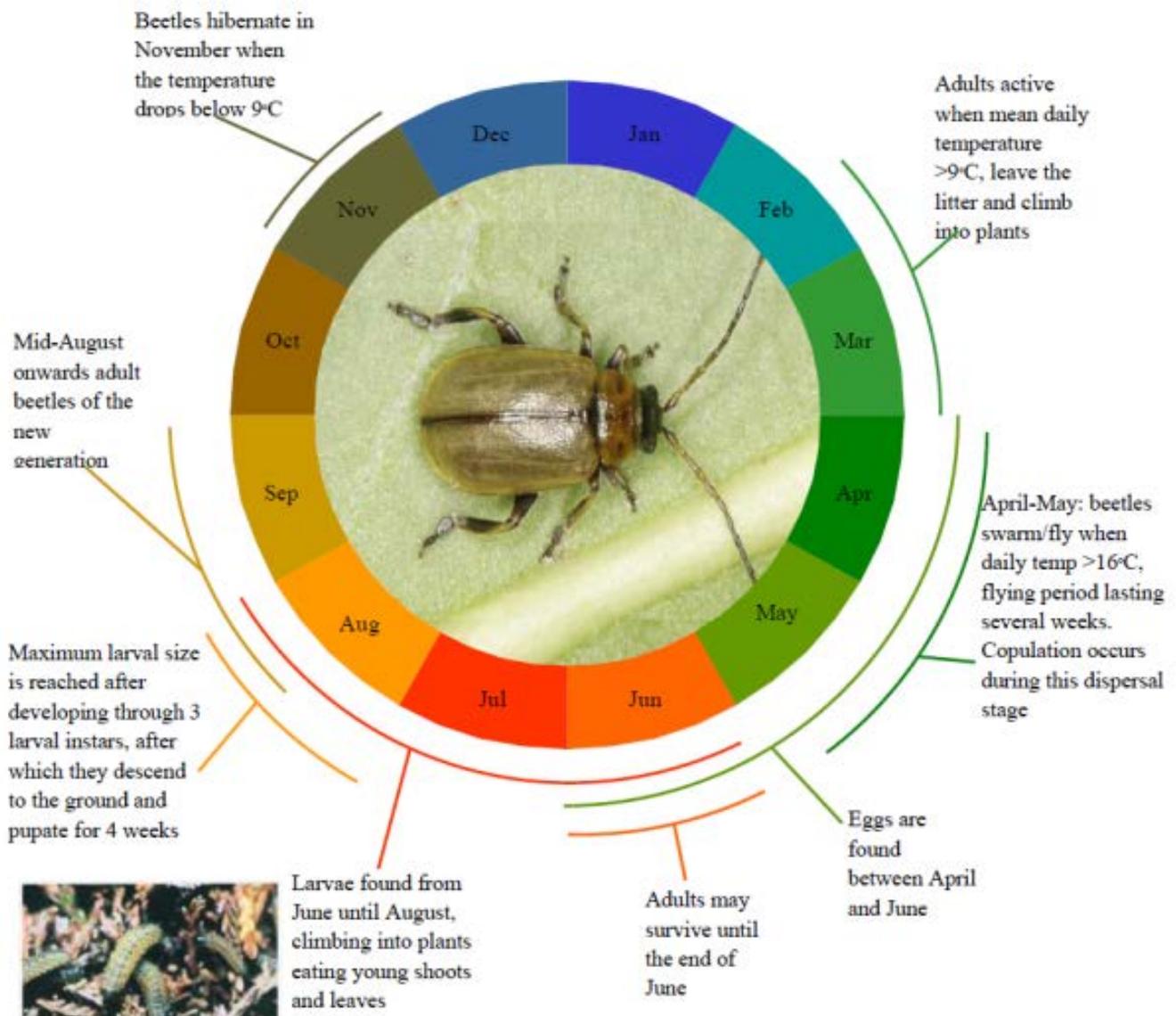


Figure 1 The life cycle of *Lochmaea suturalis* (From Rosenburgh & Marrs 2010)

2.4 Eggs are laid onto damp moss or litter (Berdowski 1993). Bunce (1989) stated that the eggs need 70% humidity to hatch, but did not cite a source or provide experimental evidence for this. Both eggs and larvae have been found to contain anthraquinones and dithranol, which may give some protection from predators; ants, given a choice between feeding on ground up heather beetle eggs, larvae and *Drosophila* eggs, tended to prefer the latter (Hilker *et al.* 1992). In the lab, mean fecundity at ambient conditions was recorded as 35 - 37 eggs per pair (Staley 2001). The beetles go through three larval instars and a pupal stage, before emerging as adults from mid-August (Rosenburgh & Marrs 2010). High rates of food consumption occur during oviposition in June, at the end of the third instar stage in July and once adults emerge in September, coinciding with egg production or fast growth rates, with 1.51 mg (dry weight) of food being required per beetle between hatching from the egg and becoming sexually mature (Brunsting 1982). In the autumn, some dispersal flights may also occur once flight muscles have developed and where conditions are suitable (van Schaick Zillesen & Brunsting 1983)

and beetles remain active to around 13 °C, with a higher proportion becoming inactive in the soil and those already in the soil moving lower down with decreasing temperatures (Staley 2001), although Berdowski (1993) states that beetles retreat into the litter to hibernate when the temperature reaches 9 °C. From modelling work by the same author (Staley 2001), fecundity, pupal mortality and egg mortality have all been identified as potentially being important factors in determining population dynamics.

Natural enemies of *Lochmaea suturalis*

- 2.5 The heather beetle has several natural enemies, which each affect different stages of its life cycle. A summary of these are given in Table 2. Predators include the Hieroglyphic Ladybird *Coccinella hieroglyphica* (Cameron 1944, in Scandrett & Gimingham 1991), which attacks the larvae. The shield bug *Rhacognathus punctatus* also preys on larvae (Webb 1986). However, Fielding and Haworth (2002) state (without any evidence either way) that predators such as these are unable to prevent the outbreak of heather beetle plagues. This statement may have been based on Webb (1986), who found no evidence for a controlling influence of either *Coccinella hieroglyphica* or *Rhacognathus punctatus* on population counts in England, although the work that led to this conclusion is not described.
- 2.6 A study in Scotland in the 1980s found a high incidence (around 35 % of adults) of infestation by parasitoids, probably the tachynid fly *Degeeria collaris* (Scandrett & Gimingham 1991), also known as *Medina collaris*. Wardlaw *et al.* (2000) also found this species parasitising adults in Dorset, with incidence varying from 7 – 65 % of newly emerged adults across five sites and double parasitism in some cases. In both cases, *Medina collaris* larvae were found in adults surviving until June (Scandrett & Gimingham 1991, Wardlaw *et al.* 2000), which would probably already have laid eggs, so any effect of the natural enemy would have been to limit the number laid due to decreased energy being available for reproduction. Waloff (1987) also found this species parasitising adults near Silwood Park in Southern England, with parasitised adults being recognisable by their distended abdomens. He recorded two generations of the fly, with parasitism in newly emerged adults being low at 3.5 % of individuals, whilst during the next spring the peak incidence of parasitism of this species was 30 %. In addition, *Asecodes mento* has been recorded as parasitising larvae (Golightly 1962, in Scandrett & Gimingham 1991, Waloff 1987), which causes the larval cuticle to become black, hard and brittle (Waloff 1987). Incidence of parasitism by *Asecodes mento* ranged from 24.1 % to 53.2 %, depending on year, with the number of parasites present per larvae ranging from 1 to 18 (mean 7.35, Waloff 1987). Riis-Nielsen (1997) reports a personal communication from Nigel Webb that the scarcity of large scale attacks in Britain compared to the Netherlands is likely to be due to control factors such as parasitic insects, and this possibility deserves further study.

Table 2 Natural enemies of heather beetle (not including enemies within its introduced range)

Enemy	Taxonomic group	Life stage affected	Density dependence	Reference
<i>Coccinella hieroglyphica</i>	Coleoptera	Larvae	N	Cameron 1944 Webb 1986
<i>Rhacognathus punctatus</i>	Hemiptera	Larvae	N	Webb 1986
<i>Medina collaris</i> Synonym <i>Degeeria collaris</i>	Diptera	Adults	N	Scandrett & Gimingham 1991 Wardlaw <i>et al.</i> 2000
<i>Asecodes mento</i>	Hymenoptera	Larvae	?	Golightly 1962 Waloff 1987
Unknown microsporidian	Microsporidia (Eukaryote)	Not recorded	?	Peterson <i>et al.</i> 2004 Fowler <i>et al.</i> 2010
<i>Beauvaria bassiana</i>	Fungus	Adults and Larvae	Y	Brunsting 1982 Webb 1986
Black grouse	Bird	Adults	?	Grimshaw 1911
Trout	Fish	Adults	?	Fahy 1985

- 2.7 Some heather beetles imported to New Zealand from Southern England have also been found to be infected by an unnamed microsporidian (Peterson *et al.* 2004, Fowler *et al.* 2010), with presence of the disease agent being detected in a population in Scotland as well, whilst other populations appear to be disease free (Wigley 1997). Additionally, mortality during winter and the spring dispersal phase can be caused by the fungus *Beauvaria bassiana*, which is lethal to both adults and larvae under laboratory conditions (Brunsting 1982), although this appears to be more important in the Netherlands than the UK (Webb 1986). In New Zealand, egg predation has been observed by native carabid larvae and larvae have occasionally been seen to be attacked by the pentatomid bug *Cermatulus nasalis* (Peterson *et al.* 2004).
- 2.8 *Lochmaea suturalis* may also make up part of the diet of moorland birds; Buchanan *et al.* (2006) found that leaf beetles (Chrysomelidae, to which family the heather beetle belongs) were part of the diet of a range of moorland birds. Black grouse in particular have been confirmed as having consumed them, with one blackcock being recorded with over 300 adult heather beetles in its crop (Grimshaw 1911). In addition, adult heather beetles have been identified from the guts of trout in the Irish Sea (Fahy 1985) although in these cases it is not clear how important a component of the diet the beetles are.

Effects of external factors

Heather age

- 2.9 Earlier works stated that heather beetle was not found in younger heather (Richards 1926), although Grimshaw (1911) anecdotally records attacks in both young and older heather. This is thought to be due to a requirement for more than 50 % of the canopy to be *Calluna* (Bakema *et al.* 1994, although no evidence was given for this statement). Indeed, Marrs (1986) found that at a site in Breckland, areas with degenerate heather were more susceptible to attack than areas with mature heather. Furthermore, in areas with building or pioneer heather, only the oldest stems were killed and some younger stems survived, indicating factors at play beyond simply canopy cover. Where there is differential survival of different age classes of heather, it is unknown whether this is due to the initial infestation rate, growth

and survival of larvae, or differential ability of the heather to regenerate vegetatively. More recently, infestations have been reported from pioneer heather on Danish (Riis-Nielsen 1997) and Dutch heathland (Bokdam & Gleichman 2000). In Scotland, Pakeman *et al.* (2002) found 22 reports of damage by heather beetle on very young or pioneer heather (< 5 years old) and over 30 reports of damage on heather between 6 and 10 years old. What is not clear is whether this infestation of younger heather is a new phenomenon, as Richards (1926) noted that his observations may not have been complete enough to rule out the use of pioneer and building phase plants. If it is a true pattern, we do not know why this should be the case. Richards (1926) observed that younger heather lacks the moist moss carpet found under older heather, which might be expected to negatively impact egg incubation given the requirement for humidity, but Syrett *et al.* (2000) found that heather beetles laid eggs which successfully hatched on all four substrates tested (three moss species and heather litter). Bakema *et al.* (1994) state that > 3500 kg per hectare (dry weight) of litter is needed for heather beetles to hide from drought, but they do not give evidence for this and acknowledge that there is no data to describe the relationship between amount of litter and survival.

Nutrient deposition

- 2.10 There is a fairly well-established link between levels of certain nutrients (particularly nitrogen) and the growth rate of *Lochmaea suturalis*. Krupa (2003) describes two studies (Van der Eerden *et al.* 1990 and 1991) which studied this but were unavailable to be assessed for quality for this review. When fed on leaves from plants exposed to NH₃, the number of beetle larvae reaching the third (most injurious) instar increased with increasing exposure of the *Calluna* plants to NH₃. Similarly, in field experiments, the percentage of third instar larvae shed from plants exposed to artificial rain increased with increasing (NH₄)₂SO₄ concentrations (compared to second instar larvae, indicating a faster growth rate). Additionally, Brunsting & Heil (1985) found higher larval growth rates, adult weights and growth per unit of food consumed on *Calluna* plants treated with 400 kg per hectare of NPK fertiliser than on a control plot. This positive response was reduced (although still higher than the control) on the plot treated with 800 kg per hectare. Caution should be used interpreting this result as there was no replication, with only one experimental plot per treatment. In a more carefully designed experiment with slightly higher levels of replication, Power *et al.* (1998) found that mean larval growth rate and adult weight at emergence was higher when reared on *Calluna* with higher shoot nitrogen content. However, they also included a treatment where control conditions and high nitrogen conditions were alternated, and on this treatment larval growth rate and adult weight was almost identical to the control treatment. In another relatively carefully designed experiment, Uren (1992) found increased growth rate of second instar larvae fed on plants fumigated with ammonia under laboratory conditions. However, she also found no effect of fumigation in two experiments designed to more closely replicate field conditions in the UK, where the levels of deposition were lower but continued for a longer time period. Berdowski (1993) provides some evidence (from a personal communication, so quality could not be assessed) that heather beetle mean growth rate increased during a 12 hour fumigation experiment with SO₂.

Climate change

- 2.11 There is some suggestion that climate change may have positive effects on heather beetle grazing rates. Beier *et al.* (2000) found in a field experiment in Denmark which became infested by heather beetle that plots that were warmed or subjected to drought had a higher ratio of grazed to ungrazed *Calluna* shoots than control plots. Whilst these ratios were not significantly different, this was likely to be due to the low number of replicates within the study as the magnitude of the difference was high. However, given the uncontrolled nature of the infestation in this case, there remains the possibility that initial infestation rates were higher by chance in the treatment plots. More recently, Peñuelas *et al.* (2004), in a similar experiment with opportunistic infestation but with additional sites in Wales, The Netherlands and Spain, found that warming in particular, but also drought, led to increased grazing (measured by the % of leaves damaged). Staley (2001) also found an increase in weight per unit time at higher temperatures, particularly for larvae. Fagundez (2013) postulated that this might have been

due to the depletion of phenolic compounds within the leaves, which are used in defence against herbivores, but this link has yet to be made experimentally. Mean fecundity in the lab was also found to increase with temperature (up to a maximum temperature of 25°C, Staley 2001). However, a well-designed experiment in Denmark (Gladbach 2010, reported in the scientific literature as Scherber *et al.* 2013) found that larval growth and survival were significantly reduced by elevated CO₂ and drought. These negative effects were most apparent at week 3, which is when larvae under ambient conditions showed the fastest growth rate. Subsequent analyses of leaf carbon and nitrogen content indicated that elevated CO₂ increased the C/N ratios of *Calluna vulgaris* leaves, which reduced food plant quality. Further lab analysis showed that the heather plants growing under elevated CO₂ contained higher concentrations of leaf tannins than those in ambient CO₂, which may have increased mortality, particularly for smaller larvae (Gladbach 2010).

- 2.12 Climate change is expected to lead to increased winter survival of *Lochmaea suturalis* (Sinnaduri 2011). Although no experimental work has yet been done to quantify its environmental tolerances, Fowler *et al.* (2007) did find that heather beetle establishment in New Zealand (where it is used to control heather) was more successful at lower altitude sites and at the one successful higher altitude site there was a population crash following fluctuating winter temperatures. Because lower altitude sites are warmer, this suggests a role for temperature in survival of heather beetle. However, Staley (2001) found that adult winter survival was higher at 3 °C than at 0 °C, 6 °C or 9 °C. There has been an increasing frequency of attacks in the Netherlands since 1980, coinciding with a period of climate warming but also increased nitrogen deposition (Heil & Bobbink 1993), so the relative effects may be difficult to tease apart. Other authors have also suggested that outbreaks have become more frequent and severe in more recent years (Melber & Heimbach 1984, Berdowski 1993) and that warm dry summers favour outbreaks (Morison 1963, in Miles 1981). This would account for what Miles (1981) describes (without formal analysis) as a greater frequency of catastrophic damage in Southern England, Holland and North Germany than in Scotland. However, in coniferous forests in The Netherlands, numbers have been decreasing since the 1980s, in common with the 9 other pest beetle species found in these habitats (Moraal & Jagers op Akkerhuis 2011). This is possibly due to a move away from clear-cut monocultures, as it is in contrast to increases on Dutch heaths (Berdowski 1993). Modelling work (Staley 2001) has predicted that the currently observed pattern of population cycles, where numbers decline after an outbreak, may change with increasing temperatures. At low levels of temperature increase (up to 4 °C), the decline in numbers is predicted to take longer, and above 4 °C an increase in population size is predicted.
- 2.13 Climate change may also affect the natural enemies of heather beetle. Wardlaw *et al.* (2000) found that both larval development time and pupal senescence of *Medina collaris* were affected by temperature. Survival from pupa to adult decreased from 87 % at 15 °C to 25 % at 24 °C and the duration of their adult life was also temperature dependent. If temperature warming has a negative effect on this natural enemy, then it is possible that warmer temperatures could lead to release of heather beetle from parasitism.
- 2.14 Some lessons can be learned from the failure of heather beetle to establish as a biocontrol agent in many areas of New Zealand. Fowler *et al.* (2010) highlighted very low organic nitrogen levels (around 1 % dry weight) in some areas of New Zealand as a possible contributory factor to poor establishment, possibly due to an interaction between body size and winter survival and fecundity (Fowler *et al.* 2007). An increased occurrence of warm periods in winter and spring at the Tongariro National Park is thought to have led to premature emergence of overwintering adults from diapause (Gerard *et al.* 2010), suggesting that more variable weather may in fact lead to fewer outbreaks (although there is only anecdotal evidence for this). However, failure to establish is likely to be partly due to severe bottlenecks since all the introduced individuals are descended from only two females collected in Northern England (Gerard *et al.* 2013).

3 Density and dependence

- 3.1 Many processes appear to be density independent in heather beetles, for example, Scandrett and Gimingham (1991) found a density independent female biased sex ratio, with parasitism (probably by *Medina collaris*) that was neither sex-biased nor density dependent. There are very few reports of density dependent processes occurring in populations of heather beetles. Brunsting (1982) described an outbreak in the Netherlands, and found that during dispersal a 'front' develops of high densities (2000 per m²) at the edge of the previous year's focus, where damage had occurred in the previous summer and autumn. Beetles then dispersed by flight and colonised the area surrounding this focus relatively evenly, although there was high mortality (285 corpses per m²) due to the fungus *Beauveria bassiana*. There were also fewer eggs and higher larval mortality in the former front due to this fungus. In this area the heather coverage recovered over time, rather than being replaced by wavy hair grass *Deschampsia flexuosa* (see Figure 2). However, Scandrett & Gimingham (1991) only observed *Beauveria bassiana* in a maximum of 8.3 % of the adult population, so this fungus does not appear to have the same importance in Scotland, although this was based on a small number of sites.
- 3.2 Webb (1986) also noted that beetles may swarm in years when they are abundant. Dispersal can cause mortality directly if individuals do not land on a suitable food source (Blankwaardt 1968, cited in Rosenburgh & Marrs 2010). However, in New Zealand it has been observed that lack of food is not the primary cause of population collapses, as plenty of heather is usually available nearby (Peterson *et al.* 2004). In laboratory experiments, larvae have been shown to migrate as the heather sprig they were feeding on became depleted, but never further than the nearest fresh sprig (Scandrett & Gimingham 1991).

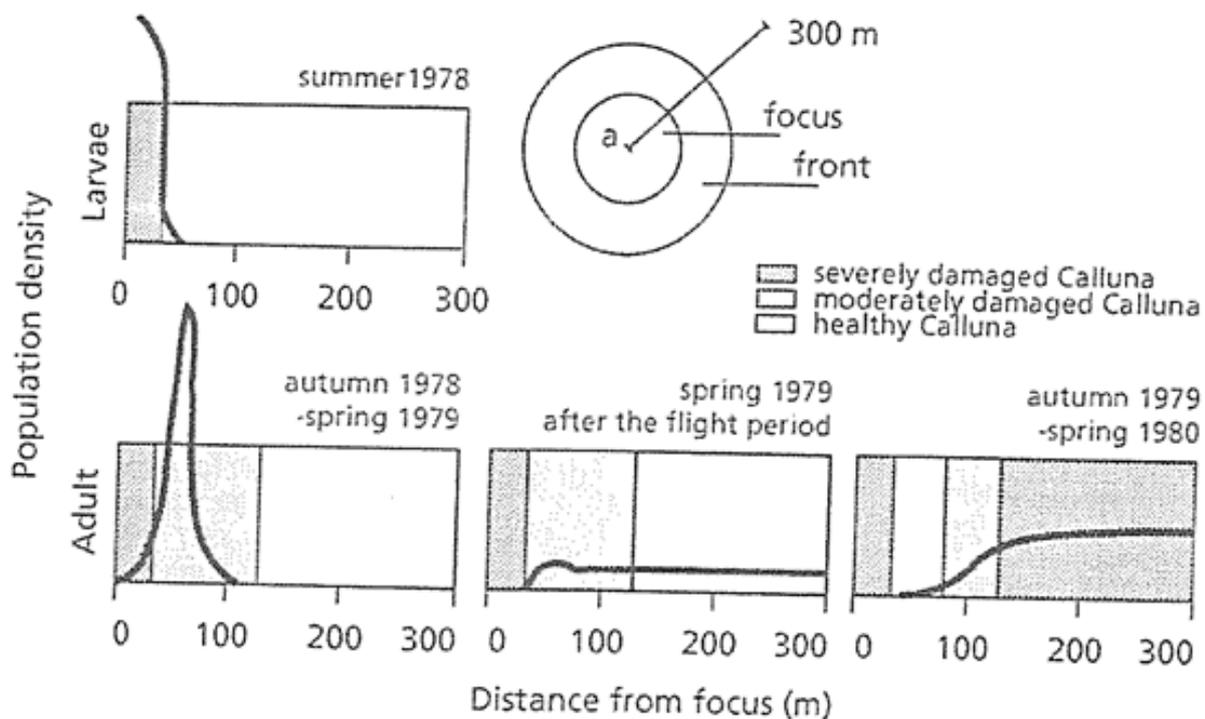


Figure 2 Population density (on a relative scale) and the dispersion pattern of *Lochmaea suturalis* on the Dutch heathland area Oud Reemsterveld in relation to vegetation damage at four time periods. Distance from focus refers to a transect through dry heath vegetation from the initial location of the outbreak (From Berdowski 1993).

4 Behavioural responses to threats

- 4.1 Several authors state that heather beetle larvae have a habit of dropping to the ground at the first sign of disturbance (for example, Taylor 1996, Laurie 2013). However, it is not clear whether these are repeating anecdotes from each other or whether these statements are based on observations in the field. There is also no information as to whether this is true for all types of disturbance, or more or less likely at different stages within the life cycle. Another unknown is whether heather beetles have any behavioural responses to the natural enemies mentioned in the previous section.
- 4.2 A shortage of food (as might occur for adults emerging in an area where an outbreak occurred in the previous year, and which could be considered a threat to survival) has been found to encourage flight. Beetles kept without food for 12 days in laboratory conditions flew frequently, whereas those that were fed rarely flew (Van Schaick Zillesen & Brunsting 1983). The same authors also found that lack of food delayed the onset of oviposition and the related breakdown of flight muscles in females. In combination, these responses would be expected to maximise the chances of beetles dispersing away from areas where the heather has already been depleted to an area with enough food for the next generation of larvae. Riis-Nielsen (1997) hypothesised that, when faced with a shortage of food, larvae will pupate earlier, whilst when food availability is high they will continue to grow and reach a higher weight before pupation. Again this deserves further study, as heavier individuals would be expected to be more likely to survive the winter and would also be expected to be more fecund in the subsequent spring.

5 Effects of outbreaks

Damage to heather

- 5.1 Consumption of heather in outbreak areas can exceed that of sheep at normal (0.8 per hectare) stocking rates (Brunsting 1982). Heather beetles damage heather both directly, by consuming the leaves, and indirectly via the physiological consequences of leaf damage due to their habit of scraping and fraying leaves, shredding the protective layer and causing dehydration (Laurie 2013). This latter mechanism in particular can lead to plant death (Pakeman *et al.* 2002). De Smidt *et al.* (1984, cited in Berdowski 1993) found that mimicking heather beetle damage to leaves resulted in increased water loss due to transpiration. This effect disappeared within two days, and Berdowski *et al.* (1985, cited in Berdowski 1993) found that as leaf removal results in less leaf area for the same water supply, healthy plants actually have more negative water potential in the long run. There is some evidence from an experiment with a low number of replicates to suggest that evapotranspiration is reduced after an outbreak (Ladekarl *et al.* 2001). This is presumably due to a lower surface area of leaves, although it is also possible that dead heather on the soil surface may act as a barrier to evapotranspiration. Part defoliation has been found to result in increased rates of photosynthesis in the remaining leaves, although this does not compensate fully for the losses caused by having a lower surface area to photosynthesise (Berdowski 1987, cited in Berdowski 1993). In the longer term, leaf damage and loss leads to less build-up of carbohydrate reserves in the fine roots and correspondingly lower weights of these, which could affect plant performance in the growing season following an outbreak (Berdowski 1993). However, no research has been carried out to date to quantify whether plants of different age classes, under different environmental conditions, will die or recover given a certain amount of defoliation.

Factors affecting the severity of damage

- 5.2 A variety of factors could affect the severity of damage by heather beetle outbreaks. Staley (2001), reanalysing historical data, found a negative relationship between altitude and damage in 1959, which suggests a role of temperature since this decreases with altitude. Webb (1987, pers comm in Waloff 1987) observed that outbreaks in the Dorset Heaths seemed to coincide with absence of parasitoids in heather beetle larvae, but this was not tested formally.
- 5.3 There is some evidence from field experiments to suggest that nitrogen fertilisation can lead to higher numbers and more severe damage by heather beetles. Heil and Diemont (1983) found higher abundances in older heather that was fertilised, although this was more of an observation than an experimental result and they did not test the relationship statistically. Cuesta *et al.* (2008) similarly found higher abundances of larvae in pitfalls placed within fertilised plots than unfertilised controls. This was statistically significant on a short timescale, although pitfall traps just 5 m apart appear to have been used as independent replicates in their statistical analysis, which is not good practise. Over a longer timescale (15 months), although there were more larvae on the fertilised plots, this difference was no longer significant. McNeill *et al.* (1988, reported in Berdowski 1993) found an increasing grazing pressure of herbivorous insects, including heather beetles, with increasing fertiliser supply on several British sites, with the largest proportional increase on mature heather. Bobbink *et al.* (2003) cited three further sources, two from Denmark and one from the UK, which apparently all found more severe damage to *Calluna* in nitrogen-fertilised vegetation. However, none of the sources they cited are from the peer-reviewed literature and they are not readily available, so it has not been possible to assess their quality. Cawley (2000, reported in Price 2003) found significantly heavier damage in plots in the UK fertilised with 60 and 120 kg per hectare of ammonium nitrate compared to 20 kg per hectare and control areas. However, Wilson (2003), in subsequent experiments on the same plots, discovered that during the second year

of the infestation there was less damage than in the previous year on the high nitrogen plot and the differences observed were no longer significant. In Denmark, Riis-Nielsen (1997) found more damage on more heavily fertilised plots at one site, with another site having equally severe damage on all plots (including controls), but higher abundances of adults being trapped by emergence traps in the plots with higher levels of fertilisation. However, the levels of replication in this study were fairly low and it appears that replicates from the same plot were considered to be independent measurements in the statistical analyses, highlighting a potential problem with pseudoreplication. Lastly, Power *et al.* (1998) found that feeding beetles with shoots containing a higher nitrogen content led to faster development and higher adult weights, which would be expected to increase survival rates since exposure to predators and parasites is minimised by shorter development time, and higher body weight would be expected to result in increased winter survival as well as higher fecundity the following spring. Dise *et al.* (2011) claimed that there is a clear link between nitrogen deposition and the frequency and severity of heather beetle attack on dry lowland heaths, but the evidence they cite in their review is only that which is mentioned here, most of which is based on studies with limited geographical extent or low levels of replication. Others have claimed that damage is especially severe on wetter habitats (Allen *et al.* 2004), although with no experimental work to back up these claims.

Physical effects of heather damage

- 5.4 As well as potentially being influenced by the nutrient status of plants, outbreaks can change the nutrient balance of the soils they occur on. Although not directly involving heather beetles, Chapman *et al.* (1989) found that death of heather in Dorset following the summer drought of 1976 resulted in enhanced levels of phosphate and other nutrients in drainage waters, and hypothesized that similar results might be expected following heather death caused by infestations of *Lochmaea suturalis*. At a site in the Netherlands, infestation led to increased mobilisation of dissolved organic carbon and nitrogen from the organic soil layer (Beier *et al.* 2004) but not below the root zone. In Denmark, an outbreak was found to lead to a decrease in the ability of *Calluna* to immobilise NH_4^+ , resulting in net ammonification (Kristensen & McCarty 1999) although this experiment involved pseudoreplication and had only 4 true plots, one with each treatment. In the same system, Nielsen *et al.* (2000) found that an outbreak led to approximately double the leaching of soluble organic matter below the mor layer, regardless of the level of fertilisation. Nitrate, ammonium and aluminium leaching also all increased after the attack. All these effects were seen after a time lag of two years, with no increase immediately following the outbreak. Brunsting (1982) found that the amount of nitrogen returned to the soil via faeces and corpses in a Dutch site was of the same order of magnitude as the yearly deposition from the air. Increased nitrogen and phosphorus has been shown to increase the growth rate of *Molinia* more than *Calluna* (Heil & Bruggink, 1987), so that release of nutrients caused by heather beetle infestation could result in a competitive advantage for this grass species. Increased phosphorus availability has also been linked to invasion by *Betula* scrub (Manning *et al.* 2006), and such invasions have been observed in Breckland where *Calluna* death due to both drought and infestation was most severe (Marrs 1986). Low levels of nitrogen application can result in large positive effects on the growth and flowering of *Calluna* in the short-term (Uren *et al.* 1997), and at this site grasses were not present so there was no other species to out-compete the heather.
- 5.5 Changes in vegetation structure following heather beetle attack have been found to increase the amount of Photosynthetically Active Radiation reaching ground level from 8 % in intact vegetation to 27 % in infested vegetation (Berdowski 1993). Work from Denmark, The Netherlands and Norway has shown that once the canopy has been opened following infestation, grasses such as *Deschampsia flexuosa* and *Molinia caerulea* can invade (Beier *et al.* 2004, Berdowski 1987, Berendse 1990, Berendse *et al.* 1994, Bobbink *et al.* 1998, Bobbink *et al.* 2003, Bokdam 2001, Heil & Bobbink 1993). Although there is a high level of agreement between these studies, one is a modelling exercise, many involved relatively few replicates, several were performed on the same sites and some remain unpublished, so it is unknown to what extent this is a more general phenomenon. The dispersal rate of many

moorland grasses is low (3-5 m for *Deschampsia flexuosa*, De Smidt 1985, cited in Berdowski 1993) and likelihood of conversion to grass-dominated vegetation following infestation is strongly affected by the neighbouring presence of grass species (Berdowski 1987, see also Diemont & Heil 1984 for an observational study), although the extent of heather beetle damage could also be a factor (Berdowski 1993). Similar increases in *Deschampsia flexuosa* were observed following an outbreak in England (Cawley 2000), although they were temporary in nature as the coverage of *Calluna* increased again in the following three years despite a lack of management of the affected area (Wilson 2003). In Scotland, Scandrett and Gimingham (1991) found that decreased *Calluna* cover following an outbreak led to increases in *Sphagnum plumulosum* and *Hypnum jutlandicum*, although again there was no real replication in this study. There was no evidence of an increase in grass cover, which they attributed to lower nutrient status, lower pH, poor drainage and the different climate experienced in Scotland compared to the studies mentioned above. Using simulation models including a stochastic chance of heather beetle outbreak, Ashmore and Terry (2007) showed that historical management was more important than historical nitrogen deposition in determining the balance of heather and grass species on four lowland heaths in England.

Economic effects of heather damage

- 5.6 Morison (1963, cited in Waloff 1987) claimed that grouse will desert a badly attacked moor. The loss of heather associated with heather beetle outbreaks has more recently been cited as a likely pressure on red grouse in Ireland (Allen *et al.* 2004) and indeed the economic impact of outbreaks in Scotland has been estimated at 0.7 - 3.1 % (depending on assumptions used in calculations) of grouse-related revenue and 0.2 - 0.7 % of deer-related revenue (Pakeman *et al.* 2002). On the Langholm Moor demonstration project, a high grass to heather ratio resulted in lower survival of red grouse broods, and distance to mature heather showed a negative trend with brood survival (Hazelwood 2013). If infestation leads to invasion of the heather canopy by grasses (see above), this could result in lower survival and therefore abundances of red grouse in the longer term as well. However, black grouse have been shown to use heather beetles as a food source (Grimshaw 1911) and if red grouse could do the same then it is possible the negative effect of loss of heather could be offset by the availability of a new, high protein food source. The loss of *Calluna* in flower could also reduce heather honey production and van der Spek (2012) recommended avoiding placing hives in areas with low flowering due to beetle attack because of the potential effects of honeybees on wild bees, although the economic effects of this have not yet been calculated (Rosenburgh & Marrs 2010).

6 Knowledge gaps

- 6.1 Much of the work done on the heather beetle consists of opportunistic or observational studies, with very few controlled experiments. Some of the more reliable quantitative work has been completed in recent decades by PhD students, (for example, Gladbach 2010, Staley 2001, Uren 1999) and much of this work has never been formally published. Although a substantial amount of fieldwork has been completed in the UK in recent years (for example, O'Hanrahan 2005, MacGillivray 2004), very little attention has been paid to proper experimental design in many cases, and there have been few attempts to carry out formal data analysis. Many of the studies that have been carried out in the past in the field involve very low levels of replication (for example, Beier *et al.* 2004, Bokdam 2001) and many published sources come from the same field sites (for example, Kristensen & McCarty 1999, Ladekarl *et al.* 2001, Nielsen *et al.* 2000) and so proper statistical analysis of the data is not possible.
- 6.2 We currently do not know what causes a natural population of heather beetles to rapidly increase in size, leading to an outbreak (Rosenburgh & Marrs 2010). Melber and Heimbach (1984) state (rather specifically) that outbreaks can be expected if there are 3 years with more than 43 days during the period of larval development with more than 0.1 mm of precipitation. Cameron *et al.* (1944) stated that abnormally dry weather during oviposition in spring and early summer is unfavourable for oviposition and egg development. However, both these sources were only available as abstracts and therefore their quality has not been assessed. Nielsen (1986) also found a relationship between wet weather from May to July and outbreaks, although this was not assessed statistically and he did find that at five sites outbreaks coincided with a very dry period for the entirety of April to October.
- 6.3 We also do not know what causes outbreaks to end. Of particular importance, very little is known about the relationship between heather beetle and its natural enemies. For example, despite the UK ladybird survey stating that numbers of the hieroglyphic ladybird vary year on year according to the availability of heather beetle ([UK ladybird survey hieroglyphic ladybird](#)) there do not appear to be any articles published in the scientific literature that examine how predators, parasites and pathogens affect population densities. Berdowski (1993) states that outbreaks can be ended by lack of food, fungal or parasite infestation of the beetles or unfavourable weather conditions, but unfortunately the sources he cited for this information were not available and so cannot be assessed for quality. In New Zealand, lack of food has not been found to be a factor as yet, because populations have declined even in the presence of plentiful supplies of *Calluna* (Peterson *et al.* 2004).
- 6.4 Rosenburgh & Marrs (2010) also highlighted further knowledge gaps, stating that there is no information currently available on the relative risk of different areas of the UK. This risk encompasses;
- 1) the chance of an outbreak occurring;
 - 2) the percentage of the vegetation that is impacted if an outbreak does occur; and
 - 3) the likelihood that heather will recover following attack.
- 6.5 The role of geographical location, climate, weather, atmospheric pollution and management as both prevention and cure is largely unknown. Current work is underway in what might be called a citizen science project to attempt to map all known outbreaks within the UK each year ([Google maps heather beetle records 2013](#)), and if properly analysed this information could provide a good starting point in understanding the relative risk of different areas.

Recommendations for future studies

- Assessment of behavioural responses to threats, specifically to test whether beetles pupate earlier in response to lack of food and the extent to which this affects overwintering survival and subsequent fecundity.
- Inclusion of control plots in any subsequent field studies, and control groups in any laboratory studies.
- Laboratory/controlled field studies to determine the effects of raised temperature and changes in humidity on survival and fecundity.
- Assessment of the impact of natural enemies on survival and fecundity.
- Controlled field studies to determine the importance of wet flushes and moss cover in the reproductive cycle.
- A combination of laboratory preference tests and controlled field studies to determine preferences and ability to feed on heather plants of different ages.
- Determination of the importance of heather beetles as food source for grouse and any associated economic effects of this.

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Appendices 1 - 3 Outcome (inclusion, rejection and at which stage) and availability of the papers chosen for inclusion in the study

Appendices 1 - 3 are available in the form of an excel spreadsheet and supplement this report.



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