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Review and synthesis

A novel causal mechanism for grey squirrel bark stripping: The Calcium Hypothesis ☆

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A B S T R A C T

Grey squirrels, *Sciurus carolinensis*, damage trees in the UK by stripping bark and eating the underlying phloem; squirrel motivation for damage is, however, unknown. Damage can result in deterioration of timber quality and a significant economic toll on the forestry industry. Prediction of severe damage followed by targeted killing of squirrels is the current recommended management option. However, the use of warfarin (an anticoagulant poison) is now restricted in the UK and other more humane methods of killing are labour-intensive, so an alternative solution is needed. A better understanding of what motivates grey squirrels to strip bark may enable a preventive approach to be developed. Whilst the bark stripping literature has explored predictive factors affecting the likelihood of damage, causal understanding is lacking. The aim of this review is to introduce the Calcium Hypothesis as a possible explanation for bark stripping, with a view to informing the prevention of damage. The Calcium Hypothesis states that grey squirrels damage trees to ameliorate a calcium deficiency. The main predictive factors of bark stripping behaviour each inform and lend support to the Calcium Hypothesis. Calcium is stored in tree phloem, and damage increases with phloem width, providing squirrels with more calcium per unit area ingested. Calcium levels increase in trees as active growth resumes after winter dormancy, this occurs immediately prior to the main bark stripping season of May–July, and trees growing most vigorously are at increased risk of damage. It is likely grey squirrels also have a requirement for calcium during the bark stripping season. Adult females will be under post-parturition pressures such as lactation, and juveniles will be going through their main period of bone growth, both of which likely represent a requirement for calcium – which supports an observed positive correlation between juvenile abundance and bark stripping. A high autumnal seed crop increases juvenile recruitment the following spring, and could also induce a requirement for calcium to a population due to the high phosphorus to calcium ratio of seeds. To further investigate the hypothesis, the extent to which grey squirrels can utilise calcium oxalate, as calcium occurs in bark, should be determined, and also the extent to which grey squirrels undergo seasonal periods of calcium deficiency. Increasing our causal understanding of bark stripping could inform the future development of preventive measures to aid forest management.

Contents

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1. Introduction

1.1. Background

The invasive Grey squirrel, *Sciurus carolinensis*, has become well established in the UK since its introduction in the late nineteenth century (Middleton, 1930). Its naturalisation has negatively impacted the UK's native biodiversity, the most well-known example of which is the regional extinction of the red squirrel, *Sciurus vulgaris* (Lloyd, 1983), via resource competition (Gurnell et al., 2015). The grey squirrel also has a negative impact on woodlands by stripping bark from trees. Underlying phloem and sap is ingested, and if an unbroken ring is stripped around the trunk, the tree can die due to an inability to transport nutrients and glucose down to the roots. Wounds created by squirrels can allow fungal infections to enter and can also weaken the tree, leaving it vulnerable to 'wind-snap' during inclement weather (Abbott et al., 1977; Gill, 1992; Gill et al., 1995; Gurnell and Mayle, 2002; Mayle et al., 2007; Mountford, 1997).

The selectivity and rapidity with which damage can occur raises the potential for the loss of vulnerable species from mature woodland, to the concomitant detriment of associated flora and fauna, and alteration of the composition of woodland (Mayle et al., 2007; Mountford, 1997). Grey squirrel damage has grave implications for woodland regeneration (Gill et al., 1995), affecting the conservation of sites with cultural or biological importance (Mountford, 1997), as well as timber production (Gurnell, 1987; Gurnell et al., 1992; Rowe, 1967), both in the UK and potentially in mainland Europe, following the introduction of grey squirrels to Italy (Lurz et al., 2001). Damage in Italy has yet to become serious (Signorile and Evans, 2007), and so careful monitoring is warranted as the grey squirrel range expands in mainland Europe. Damage may become more severe as new forest-types are encountered, similar to that which occurred in the UK as the grey squirrel's range expanded (Rowe and Gill, 1985).

Continued damage will likely lead to reduced timber yield (Mayle et al., 2009), and the cost incurred by the UK forestry industry each year as a result of damage to beech, *Fagus sylvatica*, sycamore, *Acer pseudoplatanus*, and oak, *Quercus* spp., is thought to be £10 million (Mayle and Broome, 2013). Those damaged trees that do not die but recover, are of less value when harvested for timber, due to the internal weakness brought about by wounding, uneven growth in the callous, and decay.

1.2. Preventing bark stripping

Approaches to controlling grey squirrel bark stripping range from minimising the threat of damage, for instance by planting less-susceptible tree species, to removing the threat by directly controlling grey squirrel populations. Research is ongoing into the possibility of using the pine marten, *Martes martes* – a natural predator, as a biocontrol agent, after a grey squirrel population crash in Ireland was found to be linked to pine marten abundance (Sheehy and Lawton, 2014). In the meantime the recommended method of controlling grey squirrel damage by the Forestry Commission requires the prediction of the level of severity likely to be incurred, followed by targeted killing of grey squirrels to remove the threat in these high risk years (Kenward and Dutton, 1996; Kenward and Parish, 1986; Mayle et al., 2007). To date, the most effective way of reducing squirrel populations, and therefore the level of damage, has been to use the anticoagulant poison warfarin (Gurnell and Pepper, 1998; Kenward et al., 1996, 1988; Pepper, 1996). Whilst warfarin is the least labour-intensive method of control, it is considered inhumane (Mason and Littin, 2003). After the certification for the use of warfarin as a pesticide lapsed, no application for renewal was put forward by the manufacturer, and as such, the licence for its use was withdrawn in September 2015. The remaining control options afforded to landowners and foresters, such as live-trapping followed by immediate dispatch (Mayle et al., 2007; Rowe, 1967; Thompson and Peace, 1962), are labour-intensive and expensive, hence the need for an alternative, cost-efficient, solution.

Counter-productively, culling can exacerbate damage, as temporary reduction in grey squirrel densities will likely prompt a compensatory increase in reproductive rate (Rushton et al., 2002), and increased immigration (Gurnell, 1989). Both of which can promote agonistic encounters and may trigger bark stripping, and so for this, and for ethical reasons, it would be advantageous for any proposed solution to the bark stripping problem to avoid the need for lethal control, as such an approach is often unpopular with the public (Barr et al., 2002). The abundance and wide range of the grey squirrel makes complete eradication unlikely (Gurnell and Pepper, 1993), although local removal is possible, as has been achieved notably on Anglesey (Schuchert et al., 2014). However in areas where no red squirrels are present, eradication is likely to be less sustainable.

Bark stripping is best solved by addressing the underlying cause of the problem. Increased understanding of bark stripping behaviour will likely yield improved forecasting of damage, and more appropriate habitat management. Also depending on the underlying motivator, a direct application may be produced if for instance there is a need for a particular dietary facet which can be supplemented. Research into the cause of tree damage by the Barbary macaque, *Macaca sylvanus*, in Morocco, indicated that it was due to a water shortage, and so making water readily available was a potential conservation strategy (Ciani et al., 2001). Similarly by providing supplementary food to Yeso sika deer, *Cervus nippon yesoensis*, in Japan, bark stripping was effectively reduced (Masuko et al., 2011), however this solution is not a panacea for preventing damage in all deer species.

1.3. Predictive factors

Much work has been carried out to identify why grey squirrels strip bark, and many predictive factors have been identified that increase the likelihood that a tree will be damaged. However despite this, just because a tree is likely to be damaged, there is no guarantee that it will be damaged. Certain trees are more vul-