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Review and synthesis

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

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ABSTRACT

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.

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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 Yezo 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-

nerable than others: sycamore, beech, and oak are most at risk (Rowe, 1984; Rowe and Gill, 1985), however no direct links have been made between species choice and a motivation for bark stripping (Gill, 1992). Damage generally occurs between late April and Late July (Gurnell, 1987; Shorten, 1957), which coincides with a relative paucity of natural food available to squirrels (Zwahlen, 1975). This has led to speculation that bark is a source of carbohydrate, and tends to be taken when other sources of carbohydrate, for example seeds are in short supply (Kenward, 1982; MacKinnon, 1976). However bark stripping still occurs in enclosures when food is available *ad libitum*, and the sheer quantity of phloem that would need to be ingested per day to meet an individual's energy requirements makes this an unlikely motivation for damage (Kenward, 1982).

The seasonal timing of bark stripping behaviour does however shed light on a key predictor of squirrel damage: sap volume and phloem width. The bark stripping season coincides with seasonal physiological changes to trees during the spring and summer months, which lend themselves to damage (Middleton, 1931). At this time trees are reactivating after winter dormancy, and it is these actively growing trees that suffer the most damage (Kenward, 1982; Rowe and Gill, 1985) in addition to those that are dominant (Mayle et al., 2009). Trees with reduced competition, such as those on the edge of stands or trees remaining after thinning also have increased likelihood of damage due to active, and rapid vigorous growth (Kenward, 1983; Kenward and Parish, 1986; MacKinnon, 1976; Rowe and Gill, 1985). Increased sap volume corresponds with an increased phloem width, a factor which directly correlates with damage (Kenward, 1982; Kenward et al., 1988). Phloem vessels are the tree's sugar transport system, and it has been suggested that the root cause of squirrel damage is a fondness of sugar (Shorten, 1954). Kenward and Parish (1986) however found that damage was not correlated with phloem sugar concentration. Although they admit that whilst sugar concentration *per se* was not being selected for, those preferred trees with increased phloem volume, would provide the greatest weight of sugar per unit area of phloem ingested. The link between phloem width as a predictor of damage, and the underlying cause is still unclear (Gill, 1992).

The availability of seed to a grey squirrel population can be a key factor in determining the severity of damage to vulnerable trees. The percentage of vulnerable woodland judged to be severely damaged increases with the number of nearby mature seed-bearing trees (Kenward et al., 1996). The quantity of seeds produced by these trees plays a role, as a large autumnal seed crop, known as a mast year, increases the likelihood of squirrel damage in the following bark stripping season. Increased food supplies can advance the breeding season and increase juvenile recruitment during this critical period (Gurnell, 1989, 1983; Gurnell and Pepper, 1988). It has been suggested that a trigger cause for damage may be agonistic social encounters brought about by high population densities, especially juveniles (Gurnell, 1989; Taylor, 1966, 1969, 1970). Indeed even the presence of relatively low levels of young squirrels is enough to trigger damage (Kenward et al., 1996; Kenward and Parish, 1986). Some ambiguity exists as to the role of juveniles (Gill, 1992), and the selectivity with which trees are damaged suggests individuals have more of a motivation, and are gaining more from ingesting the phloem tissue, than simply an object on which to vent aggression. Also stripping seems not to be restricted to one age or sex class (MacKinnon, 1976), and quantitative studies providing evidence of social interactions relating to stripping are lacking, as squirrels are usually concealed in the canopy and difficult to observe (Gill, 1992).

Despite these predictive factors, our causal understanding of bark stripping behaviour remains unclear. Other proposed causes have included the bark as a source of water (Taylor, 1970), or nest

lining material (Brown and Yeager, 1945), or as a substrate on which to grind down teeth (Davidson and Adams, 1973), all of which appear unlikely (Kenward, 1983; Kenward et al., 1988). Another hypothesis for the cause of bark stripping is that it is the result of a trace-nutrient deficiency (Allen, 1943). However despite being deemed unlikely, due to its lack of explanatory power for the seasonal and spatial variation typical of bark stripping (Kenward, 1982), it remains a discussion point in the literature (Lawton and Rochford, 1999). A review of the literature, and synthesis of findings, has yielded support for the hypothesis that bark stripping is the result of a trace-nutrient deficiency, namely calcium. The hypothesis that grey squirrels damage trees to ameliorate a calcium deficiency will hereafter be referred to as the Calcium Hypothesis.

1.4. The Calcium Hypothesis

That a trace nutrient deficiency could be the cause of bark stripping was posited as long ago as 1943 (Allen, 1943), however an apparent lack of evidence (Kenward, 1983) has left this an under-investigated topic in the bark stripping literature. Nutrients required in the body in relatively large amounts are calcium, phosphorus, sodium, potassium, magnesium, chlorine, and sulphur (Robbins, 1983). These are not discounted, however calcium was deemed most likely as a candidate nutrient driving bark stripping, due to its role in triggering bark stripping in other mammals (Stephens et al., 2006), including the Malabar giant squirrel, *Ratufa indica* (Borges, 1990).

The concept that squirrels might have a propensity for calcium deficiency is not a new one in the literature. It is well known that red squirrels can encounter metabolic bone disease (MBD) both in the wild (Keymer and Hime, 1977; Sainsbury and Gurnell, 1995), and in captivity (Gurnell et al., 1990; Rings et al., 1969). MBD includes a range of syndromes characterised by bone abnormalities, commonly caused by irregularities relating to minerals such as calcium. It is not unheard of for free-living wild animals to suffer MBD, for instance the arctic fox, *Vulpes lagopus* (Conlogue et al., 1979), and moose, *Alces alces* (Hindelang and Peterson, 1996; Ytrehus et al., 1999). The Calcium Hypothesis does not necessarily imply that grey squirrels are suffering from MBD *per se*, although such a condition is not ruled out. Rather that individuals, or populations, go through “calcium-lean” periods, which result in a “calcium-seeking” urge that is satisfied by ingesting the phloem of trees.

Grey squirrels have previously been linked to “calcium-seeking” behaviour such as the gnawing of calcium carbonate rocks (Gobet and Hattin, 2002), bone, and antlers (Allan, 1935; Coventry, 1940). A preference for de-fatted bone suggests the behaviour is likely to be driven by a need for minerals, rather than lipids (Klippel and Synsteliën, 2007). Grey squirrels may gnaw bones for calcium, but this does not preclude the approach that they may also be eating phloem for calcium, rather it supports the idea that the grey squirrel can self-select for certain nutrients, as many other animals have been shown to do (Borges, 1990). Also the anatomy of the squirrel jaw lends itself to the ability to taste as it gnaws (Davidson and Adams, 1973), suggesting the merit of stripping a given tree can be determined quickly, possibly explaining why so-called “trial” wounds are found on trees that are otherwise undamaged.

1.5. Seasonal diet

Squirrels are opportunists and have a varied diet primarily consisting of tree seeds and fruit (Mollar, 1983). Secondary foods include berries and fungi, and other lesser consumed items are tree bark, buds, shoots, lichen, invertebrates, and birds' eggs (Gurnell,

Table 1

The percentage of calcium (Ca) and phosphorus (P) in food items selected by grey squirrels seasonally. See the referenced papers for fungi and invertebrate species.

Food item	Ca (%)	P (%)	Ca:P	Source	Seasons selected
Acorns	0.041	0.079	0.52	USDA database	Autumn, winter, less so in spring and summer
Hazelnuts	0.114	0.29	0.39	USDA database	
Fungi (average of 14 species)	0.09	0.52	0.17	Grönwall and Pehrson (1984)	Throughout the year, less so in winter
Scots pine (<i>Pinus sylvestris</i>) buds	0.5	0.41	1.22	Grönwall (1982)	Spring and early summer
Norway spruce buds	0.67	0.78	0.86		
Invertebrates (average of 11 species)	0.147	0.797	0.18	Ooninx and Dierenfeld (2011)	Spring and summer when other foods are scarce
Woodlice	14.38	1.22	11.79		
Oak bark (<i>Quercus</i> spp.)	2.7	0.021	128.57	Nichols et al unpublished	Mid-spring to mid-summer
Beech bark	2.13	0.04	53.25		

1987). Quantities of these food items vary depending on time of year and availability, with buds, shoots, flowers and animal foods being taken during spring and early summer as seeds become scarce from the previous autumn (Grönwall, 1982; Gurnell, 1987; Mollar, 1983). They may also be taken in late summer, autumn, and winter if a large seed crop is not produced (Pulliainen and Salonen, 1965; Smith, 1968).

That the grey squirrel diet is at its most varied during the spring and summer, when damage is most likely, has been used as a counterpoint to suggestions that trees are damaged to obtain nutrients in response to a deficiency, including calcium (Kenward, 1982, 1983). However the phosphorus to calcium ratio of certain components of this more diverse diet is likely to be counterproductive in preventing or redressing any calcium deficiency. It is beneficial for the ratio of phosphorus to calcium absorbed into the body of mammals to be at least 1 for appropriate bone health and growth. If more phosphorus than calcium is absorbed, calcium can be mobilised from bone to compensate (Bernard and Allen, 1997).

The Calcium Hypothesis implies that ingesting the underlying phloem of bark is a form of pica – defined as the habitual ingestion of items not commonly considered food (Reid, 1992), as bark stripping by grey squirrels is not a problem in their native North America (Gooden, 1961; Gurnell, 1987), and that phloem is ingested purely as a source of food is deemed unlikely (Kenward, 1982). This suggests grey squirrels may be showing a form of nutritional wisdom, by selecting items to ingest to correct a specific deficiency (Richter, 1936).

Table 1 details the percentage of calcium and phosphorus in food items selected by grey squirrels seasonally. It is clear from these values that not only do primary food items selected by grey squirrels, such as acorns and hazelnuts, have a low calcium to phosphorus ratio (USDA, 2016), but as do other items taken when seeds and nuts are scarce, such as fungi (Grönwall and Pehrson, 1984) and invertebrates, with the notable exception of woodlice, *Porcellio scaber* (Ooninx and Dierenfeld (2011)). Tree buds – predominantly available in the winter and early spring, may be taken in an attempt to compensate for a potentially calcium-draining diet in the run up to the bark stripping season before bark becomes suitable for stripping, as red squirrels are known to do in response to a high phosphorus diet (Shuttleworth, 2000). Factors affecting the suitability of bark for stripping are discussed in the below Synthesis section. However even tree buds may not reliably provide a method of compensation as Norway spruce buds, *Picea abies*, for instance, have a calcium to phosphorus ratio of less than 1 (Grönwall, 1982). Those buds that do provide adequate calcium levels will likely become a less important part of the diet by the time the bark stripping season is underway as budburst can be a temporally exclusive and specific occurrence, especially in some species favoured by the grey squirrel for stripping, for example oak (Visser and Holleman, 2001). Tree bark then becomes a candidate source of calcium for grey squirrels. Table 1 indicates that the bark of some tree species favoured by grey squirrels for bark stripping such as oak and beech have both a high percentage of calcium, and an exceptionally high calcium to phosphorus ratio.

Birds' eggs may also provide a source of calcium and will be available in the spring and summer during the bark stripping season; however the effort of evading parents to acquire these may prove inhibitive to a degree. Also the extent to which eggs are utilised by grey squirrels is unclear (Newson et al., 2010). Diet varies geographically, between individuals, and between sex and age groups (Mollar, 1983), and so what might represent a source of nutrition to some individuals, or populations, may not be utilised by all.

2. Synthesis

The main predictive factors of bark stripping behaviour each link in and lend support to the Calcium Hypothesis (see Fig. 1):

- Increased phloem width: Calcium is stored in the phloem of trees and levels in the phloem of oak (*Quercus robur* and *Quercus petraea*) for instance can be as much as 14 times that of the wood, with an average of 17.6 mg g^{-1} of calcium in the phloem, compared with 1.2 mg g^{-1} in wood (Freer-Smith and Kennedy, 2003). And so increased phloem width equates to an increased level of calcium available to squirrels.
- Actively growing trees: Calcium can increase in the phloem by as much as 40% in trees in Spring and Summer after Winter dormancy, as it is required for growth (Fromm, 2010). Bark is therefore at its peak as a source of calcium during the bark stripping season.
- High juvenile density: The bark stripping season coincides with the first peak in juvenile grey squirrel numbers of the year, as first litters are weaned and become independent. These juveniles are going through their main period of bone growth, and adult females are recovering from the bodily calcium drain of lactation. Both these factors result in an increase requirement for calcium for those individuals concerned.

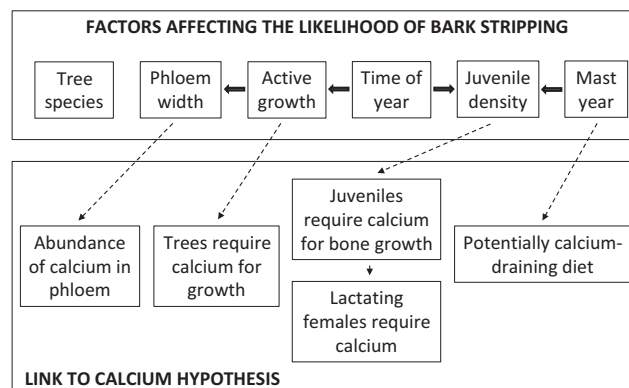


Fig. 1. The link between factors affecting the likelihood of bark stripping and the Calcium Hypothesis that grey squirrels damage trees to ameliorate a seasonal calcium deficiency.

- **Good mast year:** A good autumnal mast year, in which natural food supplies for squirrels are abundant, increases overwinter survival, advances the breeding season and increases juvenile recruitment during the bark stripping season. The diet of such overwintering individuals during a mast year will contain an increase in seeds from specific species such as oak or beech, depending on which species of tree is undergoing a mast year. The high phosphorus to calcium ratio of which could result in a requirement for calcium to be obtained from other food sources such as bark, to ameliorate the potential deficit.

Each predictive factor will now be taken in turn to expand on the arising evidence in support of the Calcium Hypothesis.

2.1. Predictive factor 1: Increased phloem width

Calcium has a number of roles at a cellular level in trees in the regulation of physiology and structure (Lautner and Fromm, 2010). Free calcium is integral as a messenger (Bangerth, 1979), a signalling molecule (Felle, 1988; Hirschi, 2004), and as a membrane stabiliser (White and Broadley, 2003). Calcium is found in high quantities in the bark of trees, and precipitates as calcium oxalate (CaOx) crystals in the cell vacuoles of many species of angiosperm trees (Borchert, 1990), acting as a store as excess calcium is sequestered (Hudgins et al., 2003). Trockenbrodt (1995) showed that CaOx can be found in the phloem section of the bark of oak and poplar, both of which are known to suffer damage from the grey squirrel. Indeed CaOx crystals occur in most plant families and can comprise a large amount of the total calcium in plants (Franceschi and Nakata, 2005), and so it is likely to be widely present as a potential source of calcium for the grey squirrel. Phloem is one of the most nutritionally rich tissues in plants (Linhart et al., 2001), and calcium is found in greater quantities than any other inorganic element in plants (McLaughlin and Wimmer, 1999). Several studies have found strong correlations between severe damage, and the sap volume and concomitantly the phloem width of trees (Kenward, 1982; Kenward and Parish, 1986; Kenward et al., 1988). Kenward (1982) first indicated this relationship in beech and sycamore by collecting the sappy tissue under the outer bark and showing that the sap volume correlated with increasing severity of damage on individual trees. This was then confirmed by Kenward and Parish (1986), in which despite the influence of other factors such as an increased presence of juvenile individuals, serious damage was not found to occur unless trees were “suitable” and had a high phloem width. An increased phloem width gives the capacity for increased levels of calcium that can be obtained by squirrels that are ingesting this tissue. It is likely that those squirrels that damage trees with a large phloem volume will therefore also be ingesting a higher quantity of calcium. Trees can vary in their calcium levels both between individuals and within an

individual tree, with branches often containing a higher concentration (McLaughlin and Wimmer, 1999). This could explain why not all trees get damaged to the same extent, and why often it is the branches that get stripped preferentially, although this has also been attributed to convenience of position for the squirrel. Regardless, the source of calcium in phloem could be one of, or perhaps even the main incentive to damage trees.

2.2. Predictive factor 2: Actively growing trees

A tree with a wide phloem layer indicates it is actively growing (Pallardy, 2008). Damage risk is increased on trees that are growing vigorously (Mountford, 2006; Mountford and Peterken, 1999), especially if they are of a high yield class (Mayle and Broome, 2013). For example, trees on the edge of forests or stands with increased light, less competition and generally favourable conditions are more likely to get damaged (MacKinnon, 1976) due to their increased phloem layer and “sappiness” (Kenward et al., 1988), whereas trees in naturally regenerated woodland with more competition have lower phloem volumes (Kenward, 1989) and so are less likely to suffer damage. Not only will actively growing trees have a wide phloem layer and therefore increased calcium levels as a result, calcium levels also increase in these trees due to reactivation after winter dormancy. Calcium levels increase in the cambium and phloem during spring reactivation (Follet-Gueye et al., 1998), by as much as 40% (Fromm, 2010). This is because calcium plays a key role in tree development and wood formation (Dünisch and Bauch, 1994; Eklund and Eliasson, 1990), as new wood is produced from the cambium of trees (Pallardy, 2008). Calcium supply rates influence wood formation (McLaughlin and Wimmer, 1999), and in the absence of calcium, reduced lignification is observed, and a greatly reduced cambial zone (Lautner et al., 2007). Therefore it is those actively growing trees with increased phloem widths, which have increased susceptibility to damage, that are likely to provide the highest calcium content for grey squirrels. Moreover, the peak of these seasonally increased calcium levels likely coincide with the time at which the majority of bark stripping occurs: between May and July (Kenward, 1982). Fig. 2 indicates the timing of the gradual spring reactivation of growth prior to the bark stripping season. The Calcium Hypothesis predicts bark will be stripped once adequate calcium levels have amassed, making trees suitable for stripping. In some species even, calcium oxalate crystals seem to be prevalent during the bark stripping season and then decline thereafter throughout the year (Itoh and Kang, 1993).

2.3. Predictive factor 3: High juvenile density

Calcium may be available during the bark stripping season, but for the Calcium Hypothesis to gain credence, squirrels must also

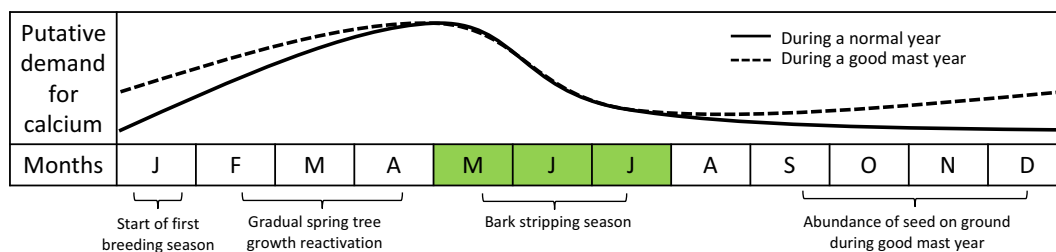


Fig. 2. A qualitative and theoretical look at seasonal change in putative demand for calcium at the population level in grey squirrels throughout the year, inferred from predictions arising from the Calcium Hypothesis, in both a normal year (black line), and as a result of a good mast-year (dotted line). The Calcium Hypothesis predicts that juvenile bone growth and adult female lactation will increase the average demand for calcium in a population from the first breeding season, during which time calcium levels gradually increase in trees during spring reactivation. These factors come to a head during the bark stripping season (shaded green), in which demand for calcium putatively decreases due to ingesting calcium-rich phloem. Demand for calcium starts to increase earlier in a mast-year due to ingestion of a diet with a high phosphorus to calcium ratio. See text for references. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

have a need for it. There are a number of reasons as to why grey squirrels may be in need of calcium during the bark stripping season. Juveniles from the first breeding season of the year will have just undergone their main period of bone growth. Calcium intake during bone growth has been shown to be a key factor in determining peak bone mass (Matkovic, 1991). Despite the influence of juvenile density being ambiguous (Gill, 1992), at least hand-sized patches of damage are very likely to occur if more than one juvenile is recorded per 2 hectares of forest (Kenward et al., 1996; Kenward and Parish, 1986), and damage generally increases with population abundance, especially juveniles (Gurnell, 1989; Kenward et al., 1996; Mayle and Broome, 2013).

Whilst the Calcium Hypothesis supports the approach that juveniles could be responsible for damage, it does not exclude adult individuals from the behaviour. Adult females especially could also be responsible for damage as they could have a requirement for calcium supplementation due to the rigours of reproduction and lactation. Lactating mammals, and even squirrels, needing calcium is not a new concept. Calcium seeking behaviour has been documented during pregnancy and lactation in laboratory rats (Woodside and Millelire, 1987). Carlson (1940) reports lactating squirrels gnawing bone for calcium and phosphorus, and it has since become well known that squirrels – particularly breeding females, will gnaw bones and antlers for calcium (Klippel and Synsteliën, 2007). Near daily gnawing of a dry clavicle was observed in March, coinciding with the first lactation period for squirrels (Gurnell, 1987). The main damage period would usually occur just after this, starting in April, and so it could be that squirrels in woods are more likely to damage trees if bones and antlers are in short supply. In rats, bone turnover is increased throughout lactation (Ellinger et al., 1952; Warnock and Duckworth, 1944) and the composition of both rat and mouse bones can decline by up to 35% (Kovacs, 2005; Thakker et al., 2013; Vanhouten and Wysolmerski, 2003), and is more intense in small mammals than in humans (Ofstedal, 1984), with a larger toll on skeletal maintenance (Hood et al., 2006). The contribution of the maternal skeleton to her young is increased through bone resorption, leading to demineralization, if stresses are put on dietary calcium intake (Garel, 1987; Van Soest, 1987), such as those that may be experienced after a good mast year the previous autumn.

Grey squirrels have two breeding seasons per year, in winter and summer (Gurnell, 1987). While numbers of weaned juveniles from the first breeding season will be peaking during the bark stripping season, weaned juveniles from the second breeding season will be peaking in autumn, along with adult females that have finished lactating. It is therefore curious that bark is not usually stripped in autumn, especially as this coincides with a new seed crop, presenting a low-calcium diet (Havera and Smith, 1979; Robbins, 1983). It is likely that the second cohort of juveniles and mothers have a similar requirement for calcium to the first cohort; however trees cease to be a viable source of calcium for amelioration. During autumn, trees stop active growth and begin senescence in preparation for winter dormancy (Keskitalo et al., 2005). So despite stripping occasionally extending to September (Mayle et al., 2009), the second breeding cohort must have to find calcium elsewhere, or subsist with bones of lower mineral density.

2.4. Predictive factor 4: Good mast year

In certain populations, all individuals could be in need of calcium during the bark stripping season, not just juveniles and adult females. A good mast year increases the likelihood of damage, and high population densities in the spring and summer can be the result of a good seed crop, or mast year, the previous autumn (Gurnell, 1983; McShea, 2000). Grey squirrel population densities fluctuate annually, in accordance with both tree seed crops and

winter temperatures (Gurnell, 1996). Thus a large population is promoted due to high overwinter survival rates, based on a diet of large amounts of acorns or beechnuts for instance. It is possible that these ‘mast-year beneficiaries’ will also be calcium deficient as a result of a diet rich in seeds containing a high phosphorus to calcium ratio, leading to calcium bone mobilisation, and subsequent calcium deficiency (Brot et al., 1999). Seeds are known to be low in calcium (Robbins, 1983), supported by Havera and Smith (1979) who found low calcium levels in an analysis of mast diet. The consumption of bones and other rich calcium sources is essential for fox squirrels because nuts and seeds commonly consumed are inadequate in calcium (Havera, 1978). It is already known that red squirrels will modify their diets to include buds and other calcium-rich foods depending on levels of phosphorus ingested (Shuttleworth, 2000), and grey squirrels may also attempt to compensate any calcium-strain imposed by a mast-year by doing the same prior to the bark stripping season. However the deluge of primary food resource with high phosphorus to calcium ratio that comes with a mast year would make it difficult to fully compensate. Those individuals sustained throughout the winter on such a diet may still have a higher requirement for calcium by the bark stripping season compared with individuals in other years in which there is not a large mast crop.

Seeds and nuts are also high in unsaturated fatty acids (Chen and Blumberg, 2008), especially common in mast seeds such as acorns (Dodd et al., 1993; Ferreira-Dias et al., 2003; Meziante and Mameri, 2005; Ozcan, 2007), and beechnuts (Ratajczak and Pukacka, 2005). This can have the effect of reducing calcium availability in these food resources (Sainsbury, 2003). Indeed metabolic bone disease has been recorded in wild red squirrels – possibly caused by excessive seed ingestion (Keymer and Hime, 1977). So a mast year could have not only the effect of increasing overwinter survival, but also the urge to replace calcium lost from an inadequate diet. The predicted effect of a mast-year on calcium-demand compared with a non-mast-year is illustrated qualitatively in Fig. 2, in which demand for calcium increases as seed becomes abundant in autumn and winter, and continues to be higher up until the bark stripping season in late spring.

A trace nutrient deficiency has previously been deemed an unlikely explanation for bark stripping due to its lack of explanatory power for the local and annual variation of the behaviour (Kenward, 1982). However mast years are not locally or annually consistent and provide squirrels with a potentially calcium-draining diet. So mast years could be a potential trigger for calcium-seeking behaviour culminating in bark stripping, providing evidence to the contrary of this claim.

3. Further work

Whilst the Calcium Hypothesis is eminently plausible, it is based on assumptions that further work should seek to investigate. The hypothesis assumes that grey squirrels undergo seasonal periods of calcium deficiency. This has been shown in other non-hibernating rodents such as the northern red-backed vole, *Myodes rutilus*, in Alaska (Stevenson et al., 2009), and is therefore possible in squirrels. Linking such a deficiency to damage will be a challenge however due to our lack of knowledge of which individuals actually commit damage. This should therefore be a priority for research in to bark stripping by grey squirrels to add credence to the hypothesis.

The Calcium Hypothesis also assumes that grey squirrels can utilise calcium in the form it takes in trees – calcium oxalate. Not all mammals can utilise calcium oxalate however, as the complex is inert and poorly absorbed (Hossain et al., 2003) unless it can be broken down into its constituent parts. Degrading the resultant

oxalate then becomes a problem as oxalate is a dietary deterrent for grey squirrels (Schmidt et al., 1998). Oxalic acid can poison squirrels as they are absorbed by the gut and react with calcium to form calcium oxalate in the blood, which is insoluble and can cause renal damage and decreased blood coagulation (Blackwell, 1990). The CaOx complex would need to be broken down in the gut prior to absorption. This feat can be achieved by some mammals, for instance the pack rat, *Neotoma albigula*, and the fat sand rat, *Psammomys obesus*, (Shirley and Schmidt-Nielsen, 1967) which can degrade oxalate with symbiotic microbes such as *Oxalobacter* species (Palgi et al., 2008). It is possible that grey squirrels could also harbour such bacteria to aid the utilisation of calcium from CaOx in bark.

Other next steps should include analysis of bark to determine if those trees that have been damaged contain high levels of calcium. The painted ringtail possum, *Pseudochirulus forbesi* (Stephens et al., 2006), has already been shown to damage bark with higher levels of calcium, so this is a possibility for grey squirrels. Also, as squirrels show a clear preference for certain tree species, it should be investigated if these species have higher levels of calcium as a rule, whilst also taking into account the geographical location of damage to account for any potential effect of calcareous soils on damage distribution.

The Calcium Hypothesis offers an exciting new avenue for bark stripping research. If a better causal understanding of grey squirrel motivations for damage can be found through ecological studies, this may inform the production of non-lethal, humane, low-effort alternatives to current grey squirrel control methods. This has the potential to increase timber revenue, and reduce forest management costs through reduced need to control squirrels.

Conflict of interest

The authors declare that they have no conflict of interest.

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