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White bark in birch species as a warning signal for bark-stripping mammals

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Abstract

Background: Birch species such as *Betula pendula* have conspicuous white bark and the evolutionary drivers for this colouration remain unresolved.

Aims: We evaluated our hypothesis that the white bark is a visual warning signal to deter mammals from bark-stripping. Many species of deer (Cervidae) and multiple other mammals consume bark. White birch species' bark contains betulin and other compounds which likely make the bark unprofitable for herbivores. The white bark has features consistent with a visual signal for mammalian herbivores and could act as a visual aposematic signal of chemical defence.

Methods: We compared deer bark-stripping between tree species in Scottish woodlands. For *Betula pendula*, we compared stripping of juvenile brown bark with mature white bark. We also reviewed existing literature to find the tree-species preference for a wide-range of bark-stripping mammals.

Results: In Scotland, we found that white-barked birch bark was less preferred. We also found mature white birch bark was avoided compared to juvenile brown bark. Existing literature for multiple herbivores showed that white birch species' bark was often either not preferred or avoided.

Conclusion: We suggest that the conspicuous white colouration of birch bark may act as an aposematic visual signal to deter bark-stripping mammals.

Keywords: bark-stripping; birch; *Betula*; white bark; aposematic; betulin; signal; extinct megafauna

Introduction

Background and hypothesis

White-barked birch species such as silver birch *Betula pendula* Roth are common in the Northern Hemisphere in temperate and boreal climates (Vakkari 2009). Protection against sunscald bark damage due to refreezing of cambium tissue after sun thawing (Karels and Boonstra 2003) was initially hypothesised as the evolutionary driver of their unusual conspicuous colouration. Recently Lev-Yadun (2019) challenged this hypothesis and suggested five alternative functional explanations for the white bark, including camouflage during snowy winters and visual aposematic signalling during summer seasons. Our hypothesis is that an important non-exclusive driver for the white bark of these species is a year-round visual aposematic signal to deter mammals from bark-stripping; and the signal is a warning of chemical defence from betulin (see below).

As bark is difficult to harvest and often of lower nutrition than other plant material, it can be avoided by mammalian herbivores in fertile areas (or seasons) with alternative forage (Gerhardt et al. 2013). In colder northern regions, where white-barked birch species (silver birch, downy birch *Betula pubescens* Ehrh., Japanese white birch *Betula platyphylla* Suk. and paper birch *Betula papyrifera* Marsh.) are found, there is often reduced potential forage for herbivores, particularly in winter when ground foliage is snow-covered; this makes trees more vulnerable to bark-stripping (Verheyden et al. 2006; Kiffner et al. 2008). Tree bark is consumed by many mammalian species in northern temperate and boreal regions, but currently mainly by deer (Cervidae, e.g. red deer *Cervus elaphus*)(Gill 1992a). As bark is

slow to heal (Welch et al. 1997), trees are more likely to adopt a defensive rather than a compensatory regrowth strategy (Agrawal 2007). The bark of white-barked birch species (henceforth white birch) contain high levels of betulin and other compounds (Krasutsky 2006), which could make the bark unprofitable for mammalian herbivores. The white bark could act as a warning signal of this chemical defence. Visual aposematic signalling has been described in plants only relatively recently, examples include colourful thorns in cacti (Lev-Yadun 2001) and leaf and branch spots advertising spines and thorns (Lev-Yadun 2001; Kavanagh et al. 2016; Lev-Yadun 2016). Aposematism has been studied extensively in animals where usually a conspicuous visual signal is paired with an antipredator defence (Caro and Ruxton 2019).

We describe the diverse mammalian species that strip bark and the bark defences of white birch species. We then assess whether the white bark makes a plausible visual warning signal. We describe predictions regarding which trees might signal, the form of the signal and the mammalian response. We then examine existing literature and present new data to assess whether white birch is avoided by bark-stripping mammals.

Bark-stripping mammals

Within white birch habitat, many deer species strip bark; these include red deer, moose/Eurasian elk *Alces alces*, American elk/wapiti *Cervus canadensis*, previously thought to be a subspecies of red deer (Ludt et al. 2004), and species which less commonly strip bark such as European roe deer *Capreolus capreolus* and fallow deer *Dama dama* (Gill 1992a). High stem and branch bark is stripped by North American porcupines *Erethizon dorsatum* (Tenneson and Oring 1985) and squirrels (*e.g.* Eastern grey and red squirrels *Sciurus carolinensis* and *S. vulgaris*) (Springthorpe and Myhill 1994). At the stem base, bark is stripped by voles (*e.g.* *Microtus agrestis*) and rabbits and hares (*e.g.* European rabbit

Oryctolagus cuniculus and snowshoe hare *Lepus americanus*) (Gill 1992b). Beavers *Castor canadensis*/*C. fiber* also consume bark (Harrington et al. 2015).

Historically, megafauna including proboscideans, rhinocerotids and large bovids such as bison (*e.g. Bison bonasus*) consumed bark in these habitats (Rivals et al. 2012; Rivals and Lister 2016).

White birch bark defences

Most plants have multiple complex chemical and mechanical defences against herbivory. Organic compounds produced for defence are known as plant secondary metabolites (PSMs) (Freeland and Janzen 1974; Bennett and Wallsgrave 1994). Birch species produce many PSMs to protect leaves, buds, twigs and bark (Palo 1984; Laitinen et al. 2005; Krasutsky 2006). Triterpenoids are a common secondary metabolite in plants and white birch bark contains the highest concentration of triterpenoids of all plants investigated (Krasutsky 2006). Betulin is the most abundant triterpenoid in birch bark (also betulinic acid, lupeol and oleanolic acid); the highest levels of betulin are in the outer layer of bark, the phellem, where 20% dry weight is betulin, with a lower concentration in the inner phellogen/phelloderm layer (Alonso-Serra et al. 2019). Betulin is responsible for the white colour of mature bark (Bergvall et al. 2013; Lev-Yadun, 2019). Immature brown birch bark has lower levels of betulin (Yin et al. 2012; Alonso-Serra et al. 2019; Räsänen et al. 2019). Betulin and other secondary metabolites can be toxic or can inhibit herbivore digestion through antimicrobial properties (Bergvall et al. 2013). Betulin and derivatives have antibacterial, antiviral, antiprotozoan and antifungal properties (Alakurtti et al. 2006; Krasutsky 2006; Meira et al. 2016).

Birch bark also has mechanical defences. The bark of most tree species is more adherent in winter making it harder to strip (Mitchell et al. 1977), birch bark has added protection:

superficial layers will strip while retaining more adherent deeper bark. Additionally, cervids strip bark vertically upwards (Springthorpe and Myhill 1994) and birch bark is resistant to vertical stripping and will only strip in a horizontal direction (Lutz 1956).

White bark as a plausible visual warning signal for mammalian herbivores

The key features of a visual signal include detectability (visibility, contrast and conspicuousness), discriminability, memorability, redundancy, degeneracy and pluripotentiality (Guilford and Dawkins 1991; Wiley 2006; Chen and Crilly 2014; Hebets et al. 2016). White birch bark is highly visible as the white bark is highly reflective of ambient light (Campbell and Borden 2005). The black bark markings provide high internal luminance contrast (figure 1). The branches are unusually dark compared to the branches of sympatric species and provide further contrast. Conspicuousness is a property of an object itself and of the object relative to its surroundings (Wertheim 2010) and the white open stem contrasts with branches and most backgrounds – often shaded darker backgrounds. The signal has high discriminability as it is clearly different from sympatric trees even from distance (apart from quaking aspen *Populus tremuloides*, see below). Memorability is enhanced by contrast with background and repeated patterns (Guilford and Dawkins 1991); the white bark and black markings make a recognisable and memorable repeated pattern. For unpalatability signals, the consistency of unpalatability enhances memorability (Guilford and Dawkins 1991) and white birch bark will always be unpalatable, or unprofitable to consume, as betulin is white. Redundancy, degeneracy and pluripotentiality are systems concepts (Chen and Crilly 2014; Hebets et al. 2016). The white colouration over the vertical height of the stem provides redundancy if only part of the stem is visible. The dark brown branches, tree shape and leaf shape (in summer) can provide degeneracy if the stem is hidden. If the signal deters multiple

diverse species of bark-strippers, this is a form of pluripotentiality. So overall, white birch bark has the expected features of an effective aposematic visual signal.

Predictions regarding which tree species would likely select a warning signal, the form of the signal and the mammalian response

Tree species which have an antiherbivore defence might select a warning signal and signal selection more likely if the defence is covert, for example, chemical defence rather than visible thorns (Caro and Ruxton 2019). Also, trees expected to signal would have relatively more vulnerable bark by sharing habitat with bark-stripping mammals with low levels of alternative forage. Trees can be further vulnerable in terms of stem habit: shade-intolerant deciduous trees have a more vulnerable stem in the early pole stage as they prioritise growth to access sunlight and to allow leaves to escape herbivores; this requires a thin-barked flexible stem as thick bark reduces flexibility and wind tolerance (Niklas 1999). Pioneer early successional species are particularly vulnerable to wind due to their open positions (Quine and Gardiner 2007). When bark is thin during the early pole stage, between approximately 6-15 years, trees are particularly vulnerable to bark stripping (Mitchell et al. 1977; Gill 1992a; Vospernik 2006). Short-lived species are relatively more vulnerable to bark-stripping as a larger proportion of their lifespan is in the early pole stage whereas long-lived species have a longer period of protection in maturity from thick woody bark. White birch are a shade-intolerant fast-growing short-lived early successional pioneer deciduous species (Fischer et al. 2002; Hynynen et al. 2010) that grow in habitats where there are numerous bark-stripping mammals with low alternative forage. Therefore, white birch species are more vulnerable and they also have a hidden chemical defence.

The form of the signal would most likely be white with contrasting black. White birch bark maximises reflection of ambient light; black bark markings and black branches provide

contrast. Bark-stripping mammals have strong reliance on vision, most obviously in predator detection. The open white stem is easily recognisable by bark-stripping mammals such as cervids which have relatively low visual acuity (in comparison with humans) and are dichromatic meaning a bright colour, such as red, would be less powerful (D'Angelo et al. 2008). Deer, cows, horses, elephants, squirrels, porcupines, rabbits and hares all have dichromatic vision (Jacobs 1993). White is also a common colour for the described examples of plant aposematism (Lev-Yadun 2014; Lev-Yadun 2016). The signal would ideally be over the majority of stem and large branches to improve conspicuousness from distance and to provide warning at the actual bark-stripping point for a wide range of mammals. Red deer strip bark up to 1.7m (Mitchell et al. 1977) while higher branch bark is stripped by squirrels and porcupines. Historically proboscideans would also strip and remove high branches. The signal would be particularly required during the vulnerable middle years of the lifespan of a tree and this is when birch bark is white; the bark is brown or grey when young and has dark woody patches in older age (figure 1). The response of mammalian herbivores to the signal should be relative avoidance of signalling trees compared to alternative bark/forage based on the advertised unprofitability of white birch bark.

In this paper we aimed to answer these questions:

1. Does existing evidence across the Northern Hemisphere show that white birch bark is avoided by known bark-stripping mammals?
2. In a survey in Scotland (presented here for the first time):
 - a. Is white birch avoided by deer in comparison to adjacent tree species?
 - b. Is birch bark avoided by deer when the bark is white in comparison to juvenile brown bark?

3. Is a visual warning signal more plausible than alternative functional explanations for white birch bark?

To further assess whether white birch bark is avoided in comparison with other tree species we reviewed existing world-wide literature to assess the tree-species bark preference for a wide range of bark-stripping mammals that are currently or were previously sympatric with white birch species. We also directly compared the incidence of deer bark-stripping between tree species in a survey in Scottish woodlands. In the survey, we also assessed the incidence of bark-stripping in relation to stem diameter and for birch in relation to stem whiteness.

Material and methods

Literature review

Existing literature was systematically reviewed for evidence regarding bark-stripping for a wide range of bark-stripping mammals. Using Google Scholar and Web of Science, ‘bark-stripping’, ‘debarking’ and ‘browsing’ were used as search terms in conjunction with each appropriate mammal species. The tree-species preference for bark-stripping, proportion of white birch species in the geographical location, diameter of stripped stems, stem height of stripped bark and season of damage were noted if recorded. Experimental evidence for herbivore avoidance of white birch bark extracts was also reviewed.

Assessment of deer bark-stripping by tree species and by birch bark whiteness

Two mixed-species woodlands in Scotland were assessed to measure the incidence of deer bark-stripping and compare vulnerability between tree species. Sites selected were Pressmennan Wood (Woodland Trust) and Woodhall Dean (Scottish Wildlife Trust), both in East Lothian, Scotland, UK at latitude 55.950; longitude -2.594 and lat. 55.952; long. -2.505. Both are mixed deciduous woodlands of sessile oak *Quercus petraea*, ash *Fraxinus excelsior*,

rowan *Sorbus aucuparia*, silver birch, downy birch, hazel *Corylus avellana*, alder *Alnus glutinosa*, wild cherry *Prunus avium* and European larch *Larix decidua*. European roe deer are common and are the only deer species present at these sites. Roe deer bark-stripping is relatively mild, hence they are not excluded from these woodlands. Assessment made during the winters of 2017/18, 2018/19 and 2019/20.

Stem assessment. Trees up to 15cm stem dbh (diameter at breast height) were assessed. Stems over 15cm dbh were excluded as rarely stripped in these woodlands. Trees were sampled in multiple random blocks of 15 trees within stands containing young trees. Stems were excluded if situated on a $>45^\circ$ slope, stem inaccessible to herbivores or heavily covered with climbing plants. Typical vertical deer stripping wounds were visually graded as 0, 1, 2 or 3 by severity. For results, 0 or 1 were counted as no stripping to reduce false positives. As only roe deer present in these areas, we knew which deer species had stripped each stem. For birch, the stem colour was recorded as brown, transitional (partly white) or white; the stem diameter of transformation to white bark was assessed and the incidence of bark-stripping was measured in relation to stem diameter and stem whiteness.

Results

Literature review

Tree species preference for multiple bark-stripping mammals is summarised below.

Deer. Many species of deer share habitat with white birch species. Deer bark-stripping is summarised in Table 1. Red deer bark-stripping in Europe is well-documented due to commercial forest damage and red deer preferred species such as Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, willow (*Salix* spp.) and ash (*Fraxinus* spp.) while white birch were among the species least preferred (Mitchell et al. 1977; Gill 1992a; Verheyden et al. 2006). Stems stripped were mainly in the 5-20 cm dbh range and red deer strip up to 1.7m in

stem height. Bark was stripped mainly in winter but red deer targeted beech *Fagus sylvatica* and Norway spruce in summer when bark is less adherent (Gill 1992a; Hahn and Vospernik 2022). Moose are known for browsing twigs in winter, but when bark-stripping they preferred aspen *e.g.* *Populus tremula* and willow.

Climbing mammals. Tree-climbing mammals (porcupines and squirrels) bark-stripping is summarised in Table 2. In Minnesota, USA, the American porcupine preferred white pine *Pinus strobus* (66% of trees had bark damage), bigtooth aspen *Populus grandidentata* and Northern red oak *Quercus rubra*; paper birch was completely avoided despite representing 26% of the trees (Tenneson and Oring 1985). Various species of squirrel strip bark, the red squirrel in the Pacific north-west of USA preferred conifers such as lodgepole pine *Pinus contorta* and western larch *Larix occidentalis* (Sullivan 1992). American grey squirrels *Sciurus carolinensis* are common in the UK following introduction and prefer beech and sycamore *Acer pseudoplatanus* (Rayden and Savill 2004). Squirrel bark-stripping is worst in summer from May to July and larger trees (>5cm dbh) of 10-40 years old are preferred (Springthorpe and Myhill 1994; Mayle et al. 2007).

Small non-climbing mammals. At the base of the stem, voles, rabbits and hares strip bark (see Table 3). When snow is deep, rabbits and hares can reach further up the stem, while voles remain in the subniveal space. Voles mainly eat bark at the base of young saplings in winter (Gill 1992b). Snowshoe hares browse twigs, shoots and bark. For the snowshoe hare in Finland, the tree bark preference was ranked as Eurasian aspen, goat willow *Salix caprea*, other *Salix* species then downy birch (downy birch was the commonest species in sample but less preferred) (Pulliainen and Tunkkari 1987). In the UK, European rabbits preferred the bark of beech and ash. Voles preferred bark and buds of young seedlings, birch was avoided except in high vole population density (Harju 1996).

Beavers. Multiple papers have described the trees utilised by the North American beaver and the Eurasian beaver (Table 3). In two areas of North America, quaking aspen was preferred, then ash (Müller-Schwarze et al. 1994; Johnston and Johnston 2017). In Scotland, Eurasian beavers preferred willows and ash despite downy birch being the commonest tree at 60% (Harrington et al. 2015). Beavers preferred stems less than 5cm.

Large ruminants and horses. The American bison *Bison bison* is mainly a grazer but the European bison *Bison bonasus* is a browser that often debarks trees, particularly in winter (Table 3). European bison in Poland preferred oak, ash, hornbeam *Carpinus betulus*, goat willow and silver fir *Abies alba* (Borowski and Kossak 1972; Baraniewicz and Perzanowski 2015). Modern cattle *Bos taurus*, which are descendants of the recently extinct (seventeenth century) auroch *Bos taurus primigenius*, can strip bark and in Scotland preferred rowan, Norway spruce and willow and avoided silver birch (Kinnaird et al. 1979). Przewalski's horses *Equus ferus przewalskii* and wild horses *Equus ferus* in the Netherlands, Poland and Germany preferred beech, ash and willow and avoided silver birch despite it being common (Kuiters et al. 2006; Klich 2017; Zielke et al. 2019).

Experimental evidence for white birch bark avoidance by bark-stripping herbivores

Experimentally, white birch bark extract (from mature *B. pendula* and *B. pubescens*) added to food has been found to be repellent to fallow deer (Bergvall et al. 2013). The repellent effect was persistent rather than transitory, consistent with a post-ingestive effect in addition to unpleasant taste (Bergvall et al., 2013). Also, white birch bark extract (from mature *B. pendula* and *B. pubescens*) applied to Scots pine seedlings significantly reduced herbivory by red deer and moose (Stutz et al. 2017a). Further, birch bark extract (from *B. pendula* twigs) caused weight loss for voles at low concentrations and mortality at high concentrations (Harju 1996).

Assessment of deer bark-stripping by tree species and by birch bark whiteness

Pressmennan Wood. Six hundred and fourteen stems were assessed (see Table 4). Hazel and rowan were the preferred species for roe deer bark-stripping. Young, brown-barked silver birch had 45% of stems stripped. White-barked silver and downy birch were rarely stripped at 7% and 5% respectively, and within this figure are old wounds (thick edge callus with central xylem exposed) that could possibly pre-date the white colouration.

Woodhall Dean. Two hundred and sixty-six stems were assessed (see Table 5). Less tree regeneration was evident than in Pressmennan Wood, likely due to higher numbers of deer, and so brown/transitional birch were not assessed due to low numbers. Stems of 4-15cm dbh were assessed. Again, rowan and hazel were the preferred species for deer bark-stripping. Silver birch stems were rarely stripped. Again, white-barked silver birch wounds appeared old.

Between both woodlands, 6% of silver birch stems were stripped compared to 45% of non-birch (oak+ash+rowan+hazel) stems between 5-15cm dbh. Mean stem height of non-birch stripping wounds was between 29cm to 81cm. Silver birch diameter for transitioning to white bark is variable but at approximately 5-7cm dbh.

Discussion

Evidence for mammalian white-birch bark avoidance

Evidence from across the Northern Hemisphere for a wide range of bark-stripping mammals confirms that white birch bark is either not preferred or avoided in a variety of studies using a diversity of assessment techniques. In many of these areas, white birch species were abundant and stripped in lower proportion to other species. For multiple herbivore species, stems were targeted between 5 and 20 cm and white birch bark would be white within these diameters.

Beavers and voles prefer smaller stems; at this size white birch bark would be brown meaning a white bark signal may be less relevant for these species. Bark-stripping was mainly in winter; however, squirrel bark-stripping in summer and European red deer targeting beech and Norway spruce in summer suggests a year-round signal could be beneficial.

In our assessment, roe deer bark-stripping of white birch was rare. In these woodlands, deer prefer to strip relatively small stems (<5cm dbh) including brown-barked silver birch. Silver birch bark starts to transition to white at about 5cm diameter and stripping was less on transitional coloured trees and then rare on white stems. When species were compared in the greater than 5cm dbh category, white birch was stripped less than rowan, ash, hazel and oak. However, our own assessment was limited, as only one deer species was assessed in one region.

The non-preference or avoidance of white-birch bark could be for various potential reasons: chemical defence; mechanical difficulty harvesting bark; lower nutrition; or factors affecting accessibility of birch stems such as marsh or predation risk. The only potential reason suggested in the assessed literature is chemical defence (Palo, 1984). We have no reason to suspect that white birch bark is less nutritious and when herbivores live at high density or alternative food is scarce, white birch bark will be stripped, which can be seen as evidence that it has intrinsic nutritional value (Verheyden et al. 2006; Harrington et al. 2015). Further, there is no reason to expect white birch stems to be less accessible to herbivores and in many studied areas, white birch trees were numerous.

If it is assumed all different species of tree have equally nutritious bark and if white birch bark has more powerful defences than other tree bark, then with or without a signal, one would expect white birch bark to be less preferred by bark-stripping herbivores. A functioning visual signal could provide further advantage through deterrence from greater

distance, less risk of accidental stripping through misidentification, and accelerated learning regarding unpalatability.

In winter, a warning signal would be important as the risk of bark-stripping is greatest.

Signalling would be enhanced by the absence of obscuring leaves in line-of-sight and improved signal illumination day and night from reduced shading. It could be argued that the signal would be less conspicuous against snow; however, white birch stems remain conspicuous due to black bark markings, particularly at the stem base, and dark branches. In addition, most bark-stripping herbivores are active in low-light when from their perspective the stem background is as likely to be dark sky or other trees.

The signal and chemical defence would be most important during the vulnerable middle years of tree maturity and this is when the bark is white. The juvenile brown bark of white birch is consistent with the aposematic signalling hypothesis as smaller trees need to prioritise protection of leaves, buds and twigs that are within browsers reach. When birch are small, these are the structures most protected with secondary metabolites (Palo 1984; Bryant and Julkunen-tiitto 1995; Laitinen et al. 2005). It can be also argued that small birch would ideally be inconspicuous to avoid advertising their accessible leaves/buds/twigs. It is only when these structures are out of reach that the defence strategy should change to prioritise protection of the stem.

Existing white birch bark hypotheses and ideas

Sunscauld or southwest injury has been suggested as the evolutionary driver for white-barked northern deciduous trees such as birch (Karels and Boonstra 2003). Freeze-thaw conditions can cause vertical cracks on the lower stem on the southwest aspect of trees. However, sunscauld is a problem for urban or cultivated trees and is rarely seen in undisturbed forests (Roppolo and Miller 2001). White bark could potentially reduce this damage, but only the

lower stem and southwestern aspect would need to be white. Also, if sunscald was the driver to this colouration, why are sympatric trees stems not white? Finally, sunscald would not explain why birch bark is brown when the tree is young.

Several alternative non-exclusive explanations for white birch bark have been suggested by Lev-Yadun (2019). These included undermining herbivorous insect camouflage when non-white insects move on white bark; camouflaging trees from extinct megafauna and current mammals that consume bark during snowy winters; being a visual aposematic signal when combined with chemical defence or low palatability (in spring, summer and autumn); reducing activity of herbivorous arthropods by lowering bark temperatures, especially in the morning; and helping predators detect the movement of insects on white bark because of the darker horizontal lenticels common in white bark (Lev-Yadun 2019).

These explanations are largely undermined by the combination of white and black bark markings in white birch species. Dark-coloured insects could be cryptic on black patches; camouflage against snow would be compromised by black bark patches and dark branches; insects could warm faster on black bark patches and also move inconspicuously. However, the contrasting white and black bark would enhance visual signalling. In addition, specific white birch features such as the open stem habit, thin contrasting dark branches and white bark only in mid-life cycle are consistent with visual signalling and not compatible with protection from sunscald, tree camouflage or compromising insect warming/crypsis.

If white bark is beneficial, potential reasons why all sympatric tree species are not white-barked

If white birch bark is an effective strategy to deter bark-stripping, there should be a strong adaptive pressure for sympatric trees to be white or to mimic birch. However, there are costs of producing secondary metabolites and costs of signalling itself. Other species, perhaps less

vulnerable due to habitat, may benefit by avoiding these costs. Even white birch do not invest in white bark and increased betulin until they are approximately 5-7cm diameter or 8 years old (Yin et al. 2012).

The bark colour of Quaking aspen varies but it can closely resemble white birch in terms of white bark colour, contrasting bark markings, tree shape and leaf shape. As a result, the two species can be difficult to differentiate. This could represent a Batesian mimic of white birch which could allow aspen to experience lower rates of bark-stripping without expending the cost of producing secondary metabolites. However, there are still costs to signal production including reduced stem photosynthesis; the cost of producing white colouration; the cost of maintaining white colouration by bark-peeling (birch) or bark-shedding (aspen); perhaps reduced tree crypsis; the cost of not having a stem-obstructing habit (such as low branches in conifers) and the inability to have thick woody bark to provide protection and fire resistance (Lawes et al. 2013). These costs borne by aspen and white birch could make signal production unattractive to other species.

Insect herbivores as an alternative or additional target for a visual signal

Insects that target bark, the bark beetles/borers (Coleoptera: Curculionidae: Scolytinae), are mainly influenced by scent (plant volatiles and beetle pheromones) (Moeck et al. 1981; Raffa et al. 2016) and to a lesser extent by visual cues (Campbell and Borden 2005). However, bark beetles are usually adapted to target a specific host species or are oligophagous selecting between several possible hosts (Raffa et al. 2015). Therefore, if birch was the potential host of a beetle species, conspicuous white bark would only assist visual identification cues.

However, these insects are also vulnerable to PSMs and whether white bark could also act as a deterrence signal to bark beetles is not excluded.

Factors favouring a visual signal rather than odour or taste to advertise chemical defence

Using pre-ingestive (*i.e.* before swallowing) cues, herbivores can assess potential food on basis of appearance, odour, taste or a combination of these methods. Mammals use scent and visual cues when foraging (Stutz et al. 2017b; Schmitt et al. 2018) and both senses can function at distance. Would an olfactory signal be better? All plants emit volatile organic compounds (VOCs), a subclass of PSMs, which have roles in plant protection (Niinemets et al. 2004). These VOCs are commonly monoterpenes (molecular formula $C_{10}H_{16}$) or sesquiterpenes ($C_{15}H_{24}$) and are small molecules with strong odours which are known to deter mammal herbivory (Vourc'h et al. 2002; Nolte et al. 2004; Iason 2005). VOCs are mainly emitted through leaves but also from bark (Özgenç et al. 2017). Olfactory signalling can have advantages over visual signalling in terms of distance and is not affected by visual obstruction (Stutz et al. 2015) or darkness. However, spatial information is imprecise and is affected by wind. Visual signals are spatially more precise, and due to the inherent spacing of trees are less vulnerable to visual obstruction. VOC production is affected by light and temperature (Niinemets et al. 2004) whereas visual signals are unaffected by temperature, important for winter in northern latitudes. Visual signals are more permanent allowing protection throughout all seasons. Visual signalling can be less effective at night, but as nocturnal herbivores have good night vision and the signal is large and white, this could be less of a disadvantage. Additionally, in this case, the principal secondary metabolite is betulin which is a large pentacyclic triterpene ($C_{30}H_{50}O_2$) with a high melting point of 255 °C (Šiman et al. 2016). This means that it is not volatile. It exists in the superficial bark of white birch in a crystalloid state (Patočka 2012) and is therefore not effective for olfactory signalling. However, its white colour means it can act as a visual signal.

A taste-based signal would require damage to the chosen stem which would be disadvantageous to tree and browser. However, white birch bark is also distasteful (Bergvall

et al. 2013). Unpleasant taste can directly communicate unpalatability and can also provide immediate reinforcement of a signalled unpalatability, before any later post-ingestive effects of PSMs, and this could improve herbivore avoidance learning and strengthen association with the signal (Bryant et al. 1991).

Paleoecological perspective

Another important consideration is the number of recently extinct bark-stripping mammalian megaherbivores. The extant white birch species were present from the mid-Miocene epoch (Chen et al. 1999; Stults and Axsmith 2009; Bina et al. 2016). Megaherbivores such as proboscideans can readily strip bark, remove tops or push over trees with their tusks and trunk and were likely formidable bark and tree consumers during the Miocene, Pliocene and Pleistocene when white birch species became widespread. Extant African elephants *Loxodonta africana* are ecosystem engineers and create a mosaic of woodland and savanna (Haynes 2012). In the Pleistocene, the American mastodon *Mammuth americanum*, straight-tusked elephant *Palaeoloxodon antiquus* and various species of Gomphotheriidae were browsers eating leaves and bark (Lambert 1992; Rivals et al. 2012; Yansa and Adams 2012). Other non-proboscidean tree-browsing extinct late-Miocene to Pleistocene megafauna include several species of Rhinocerotidae and large cervids such as giant elk *Megaloceros giganteus* (Rivals and Lister 2016).

Furthermore, as proboscideans and rhinocerotids were hindgut fermenters, their digestive physiology and large size could allow a larger proportion of their diet to be low-nutrition high-fibre bark (Demment and Van Soest 1985; Clauss et al. 2003) and they would have been of greater value for trees to deter. Their hindgut digestion could make them more vulnerable to PSMs (Mackie 2002; Hummel et al. 2006) such as betulin. White birch species also appear adapted to co-exist with these large herbivores as they bear the cost of producing large

quantities of PSMs and of signalling. White birch also likely benefitted when large herbivores predated other tree species creating open spaces for regeneration - white birch are shade-intolerant and incapable of regenerating in closed-canopy woodland (Atkinson 1992; Hynynen et al. 2010). The life cycle of these birches appears suited to a high predation environment with rapid colonisation of open ground, fast growth and a relatively short lifespan.

Conclusion

White birch species have been shown to be not preferred or avoided by multiple bark-stripping mammals. Their bark contains a large quantity of secondary metabolites and experimentally birch bark extract deters herbivory. This is strong evidence to support a non-exclusive function of these secondary metabolites as a deterrent to mammalian bark herbivory. The white bark fulfils logical expectations for a visual signal to deter bark-stripping mammals. It could function as a warning signal of chemical defence and also as a signal for younger trees to show their defensive strategy has changed and differentiate signallers from undefended stems of the same species. Whether the white bark of birch represents a warning signal is not proven but the arguments above suggest that the white bark of birch could have an important, but non-exclusive, function as a year-round visual aposematic signal to deter mammalian bark-stripping. In the recent past, large herbivores such as proboscideans were likely potent tree predators and would have been important to deter. If a visual signal combined with secondary metabolites reduced bark herbivory during epochs where bark-stripping mammals were larger and more numerous, the relative benefit to white birch species would have been greater. However, broad deterrence to a wide range of bark-stripping mammals would likely enhance the success of white birch in multiple geographical habitats.

The relative avoidance of white birch species by bark-stripping mammals means white birch species can tolerate a relatively higher density of bark-stripping mammals and could be favoured by forest managers in such areas, for example, rewilding environments. However young trees remain vulnerable until they develop white bark and may still need protection. The transition to white bark can be used as a sign to managers that the stem is now less vulnerable to bark-stripping.

More evidence for signalling could be obtained by further assessing white birch stripping relative to young birch and other species in areas with bark-stripping herbivores. This can be difficult in our manipulated forest environments where bark-stripping species are often excluded or controlled. The absence of extant proboscideans in white birch habitats also prevents study of their interaction with white birch. More challenging manipulative experiments where non-birch stems were painted white to mimic birch (ideally without odour) and compared with unaltered controls would be a more direct way to assess whether there is a working deterrence signal.

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No conflict of interest for either author. HI carried out this research in his own time.

Author contributions

HI Conceptualisation, Investigation, Writing – original draft, Writing – review and editing

GR Writing – review and editing.

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Table 1. Evidence for deer bark-stripping

Reference	Mammal species	Region	Tree species' bark preferred (in rank order) or avoided	Stem diameter affected (dbh)	Stem height of bark-stripping	Season
Mitchell et al. (1977)	Red deer (<i>Cervus elaphus</i>)	Europe (review data various sites)	A, Salix spp. and LP preferred AG, birch and SS avoided	5-15cm	0.3-1.7m	Winter
Gill (1992a)	Red deer	Europe (review data various sites)	Salix spp., Quercus spp., A, NS, SP, EA preferred	-	0.5-1.0m	Winter and spring
Jamrozy (1980)	Red deer	Poland	SF, Salix spp. NS, preferred, also EA, A	-	-	Winter
Fehér et al. (2016)	Red (and roe deer, boar, mouflon)	Hungary	A preferred then Tilia spp. and maple	12-21cm	-	-
Nevřelová and Ruzickova (2015)	Red deer (and roe deer)	Slovak republic	A preferred then HB	20cm	0.4-1.6m	Winter
Gacic et al. (2012)	Red deer	Serbia	B (86% stripped), HB (10%) SB avoided	20-39cm	-	Beech stripped May-August
Verheyden et al. (2006)	Red deer	Europe (review of data from various sites)	NS, DF, Abies spp. SP, EL, Salix spp. DB avoided	-	-	Mainly winter
Vospěrník (2006)	Red deer	Austria	NS, A, SC and Sorbus spp. preferred	5cm	0.8-1.7m	Winter
Hahn and Vospěrník (2022)	Red deer	Austria	Only NS assessed	-	0.6-1.8m	Winter 79.5% Summer 20.5%
Baker et al. (1997)	American elk (<i>Cervus canadensis</i>)	Colorado USA	QA bark preferred locally and only species assessed	-	1.75-2.25m	Winter
Morow (1976)	Moose	Poland	EA, SP bark preferred, DB bark avoided	-	-	Winter
Renecker and Hudson (1985)	Moose	Alberta, Canada	QA, BP bark preferred	-	-	In April, bark 39% of diet
Miquelle and Van Ballenberghe (1989)	Moose	Alaska, USA	BW, QA, BP bark preferred	5-10cm and greater	-	Spring, May/June

Table 1: key for tree species (white birch species in bold)

A Ash *Fraxinus excelsior* AG Alder *Alnus glutinosa* B Beech *Fagus sylvatica* BP Balsam poplar *Populus balsamifera* BS Basswood *Tilia glabra* BW Bebb's willow *Salix bebbiana* DB Downy birch *Betula pubescens* DF Douglas fir *Pseudotsuga menziesii* EA Eurasian aspen *Populus tremula* EL European larch *Larix decidua* GF Grand fir *Abies grandis* GW Goat willow *Salix caprea* HB Hornbeam *Carpinus betulus* LP Lodgepole pine *Pinus contorta* NRO Northern red oak *Quercus rubra* NS Norway spruce *Picea abies*, O Common oak *Quercus robur* PB Paper birch *Betula papyrifera* QA Quaking aspen *Populus tremuloides* S Sycamore *Acer pseudoplatanus* SB Silver birch *Betula pendula* SC Sweet chestnut *Castanea sativa* SF Silver fir *Abies alba* SP Scots pine *Pinus sylvestris* SS Sitka spruce *Picea sitchensis*

References for Table 1: (Morow 1976; Mitchell et al. 1977; Jamrozy 1980; Renecker and Hudson 1985; Miquelle and Van Ballenberghe 1989; Gill 1992a; Baker et al. 1997; Verheyden et al. 2006; Vospěrník 2006; Hahn and Vospěrník 2022; Gacic et al. 2012; Nevřelová and Ruzickova 2015; Fehér et al. 2016)

Table 2. Evidence for climbing mammals bark-stripping

Reference	Herbivore species	World region	Tree species preference for bark, in order of preference	Tree species present, birch proportion (%) or species ranked by abundance	Dbh of bark-stripped trees
Tenneson and Oring (1985)	Porcupine	NW Minnesota, USA	WP (66% damaged), BA, NRO	PB 26% of total sample, none had bark damaged	> 33cm. None less than 15 cm
Curtis (1944)	Porcupine	Maine, USA	NWC, H, B	BF, RS, WS, NWC, PB , WP, H, BA, NP, RM, B, YB	-
Curtis (1944)	Porcupine	Mass. USA	SM, BW	-	-
Curtis (1944)	Porcupine	Southwest USA	PP	-	-
Curtis (1944)	Porcupine	Lake states, USA	WP	-	-
Mountford (1997)	Grey squirrel	England, UK	B preferred	B, A, SB , DB , FM, LM, SO, WE	10-25 cm
Rowe (1985)	Grey squirrel	UK	S, B, O, A	-	-
Mayle (2007)	Grey Squirrel	England, UK	S, B, O, SC, SP, EL, NS preferred	-	>5cm, 10-40 years old
Rayden and Savill (2004)	Grey squirrel	England, UK	B preferred- 55% stripped; S 43% stripped	SB 12% stripped	10-35 cm
Sullivan (1992)	Red squirrel	USA, pacific NW	LP, WL, PP, WP, DF, GF, PB	-	-
Springthorpe and Myhill (1994)	Red squirrel	UK	SP preferred, also EL, LP and NS	-	-

Table 2: key for tree species (white birch species in bold)

A Ash *Fraxinus excelsior* BA Bigtooth aspen *Populus grandidentata* B Beech *Fagus grandifolia/sylvatica* BF Balsam fir *Abies balsamea*, BW Basswood *Tilia glabra* **DB** Downy birch *Betula pubescens* DF Douglas fir *Pseudotsuga menziesii* EL European larch *Larix decidua* FM Field maple *Acer campestre* GF Grand fir *Abies grandis* H Hemlock *Tsuga canadensis* LM Lime *Tilia cordata* and *T. platyphyllos*, LP Lodgepole pine *Pinus contorta* NP Norway pine *Pinus resinosa* NRO Northern red oak *Quercus rubra* NS Norway spruce *Picea abies* NWC Northern white cedar *Thuja occidentalis* **PB** Paper birch *Betula papyrifera* PP Ponderosa pine *Pinus ponderosa* RM Red maple *Acer rubrum* S Sycamore *Acer pseudoplatanus* **SB** Silver birch *Betula pendula* SC Sweet chestnut *Castanea sativa*, SM Sugar maple *Acer saccharum* SO Sessile oak *Quercus petraea* SP Scots pine *Pinus sylvestris* RS Red spruce *Picea rubra*, WE Wych elm *Ulmus glabra* WL Western larch *Larix occidentalis* WP White pine *Pinus strobus* WS White spruce *Picea glauca*, YB Yellow birch *Betula lutea*

References for Table 2: (Curtis 1944, Rowe 1985, Tenneson and Oring 1985, Sullivan 1992, Springthorpe and Myhill 1994, Mountford 1997, Rayden and Savill 2004, Mayle 2007)

Table 3. Evidence for rabbit/hare, beaver, large ruminant and horse bark-stripping.

Reference	Mammal	Region	Bark preferred (in rank order)	Birch in sample area	Stem dbh	Stripping height	Season
Pulliainen and Tunkkari (1987)	Snowshoe hare	Finland	EA, Salix spp. and DB (DB commonest in sample but less preferred)	DB 95% of deciduous trees	-	-	Winter (March peak)
Pepper (1998)	Rabbit (<i>Oryctolagus cuniculus</i>)	UK	Beech and ash bark preferred	-	-	Up to 54cm	Winter
Bergman et al. (2005)	Rabbit	UK	SP preferred over GW and GW over SB/DB in choice of three	SB/DB mix in test plots	-	Up to 42cm	-
Harrington et al. (2014)	Eurasian beaver (<i>Castor fiber</i>)	Scotland, UK	Salix spp., A, R, H, DB , AG	DB commonest tree at about 60%	2-6cm	-	-
Müller-Schwarze et al. (1994)	Beaver (<i>Castor canadensis</i>)	New York State, USA	A and QA preferred	Proportion of birch not specified	-	-	-
Johnston and Johnston (2017)	Beaver	Minnesota, USA	QA clearly preferred	PB 34% (but only 17% of browsed stems)	<5cm	-	-
Henker (2009)	Beaver	USA +Canada	QA and C preferred, also Salix spp. and AG	<i>Betula</i> spp. less preferred	5-25cm	-	Winter
Fryxell and Doucet (1993)	Beaver	USA	QA preferred in choice of three between AS, GA and RM	-	-	-	-
Zielke et al. (2019)	Przewalski's horse	Germany	O preferred	SB 34%	-	-	Winter and spring
Klich (2017)	Horse (<i>Equus ferus</i>)	Poland	Salix spp. preferred	Birch commonest species but avoided by horses and red deer	Worst at 5-7cm	-	-
Kinnaird et al. (1979)	Cattle (<i>Bos taurus</i>)	Scotland, UK	R preferred. NS and Salix spp. less preferred. A,B, SB ,S,SP,WC and EL avoided	-	-	-	Winter
Borowski and Kossak (1967)	Bison (<i>Bison bonasus</i>)	Poland	O, HB, A (bark 26% of diet)	DB common (shoots browsed but not bark)	4-15cm	-	-
Baraniewicz and Perzanowski (2015)	Bison	Poland	A, SF, GW	Birch rare	10-20cm	-	-
Zielke et al. (2019)	Bison	Germany	Bark and foliage: O and BL preferred, birch avoided	SB 34%, DB 2%	-	-	Winter and spring

Table 3: key for tree species (white birch species in bold)

A Ash *Fraxinus excelsior* AG Alder *Alnus glutinosa* B Beech *Fagus sylvatica* BL Black locust *Robinia pseudoacacia* C Cottonwood *Populus deltoides* **DB** Downy birch *Betula pubescens* EA Eurasian aspen *Populus tremula* EL European larch *Larix decidua* Mill. GW Goat willow *Salix caprea* H Hemlock *Tsuga canadensis* HB Hornbeam *Carpinus betulus* NS Norway spruce *Picea abies* O Common oak *Quercus robur* **PB** Paper birch *Betula papyrifera* QA Quaking aspen *Populus tremuloides* R Rowan *Sorbus aucuparia* RM Red maple *Acer rubrum* S Sycamore *Acer pseudoplatanus* **SB** Silver birch *Betula pendula* SF Silver fir *Abies alba* SP Scots pine *Pinus sylvestris* WC Wild cherry *Prunus avium*

References for Table 3: (Borowski and Kossak 1972; Kinnaird et al. 1979; Pulliainen and Tunkkari 1987; Fryxell and Doucet 1993; Müller-Schwarze et al. 1994; Pepper 1998; Bergman et al. 2005; Henker 2009; Harrington et al. 2014; Baraniewicz and Perzanowski 2015; Johnston and Johnston 2017; Klich 2017; Zielke et al. 2019)

Table 4. Bark-stripping observed in Pressmennan Wood, East Lothian, Scotland (stripped / total stems)

Tree species	1-3 cm dbh	3-5 cm dbh	5-7 cm dbh	7-10 cm dbh	10-15 cm dbh	Total (all diameters)	Total stripped (%)
Total stems (all species)	75/107	77/165	44/135	23/136	12/71	231/614	37
Silver birch	32/52	23/58	2/14	0/4	0	57/128	45
Brown							
Silver birch	0/1	7/20	6/18	2/15	0/4	15/58	26
Transitional							
Silver birch	0	4/9	1/15	0/32	0/16	5/72	7
White							
Downy birch	0/1	2/11	1/11	0/4	0	3/27	11
(<i>B. pubescens</i>)							
Grey/brown							
Downy birch	0	0/5	1/10	0/4	0/1	1/20	5
Transitional							
Downy birch	0	0/2	1/11	0/28	2/22	3/63	5
White							
Oak	0	5/8	11/19	6/18	2/12	24/57	42
Ash	15/20	10/17	2/9	4/8	0/2	31/56	55
Rowan	4/4	9/11	8/13	9/17	6/9	36/54	73
Hazel	14/15	14/15	10/10	2/2	1/1	41/43	95
Larch	5/6	3/7	1/3	0/2	0	9/18	50
Wild cherry	5/8	0/2	0/2	0/2	1/4	6/18	33

Table 5. Bark-stripping observed in Woodhall Dean, East Lothian, Scotland (stripped / total stems)

Tree species	4-5 cm dbh	5-7 cm dbh	7-10 cm dbh	10-15 cm dbh	Total all diameters	Total stripping (%)
Total stems (all species)	37/40	50/72	23/78	3/76	113/266	42
Silver birch (white)	1/1	4/10	1/32	0/55	6/98	6
Oak	1/3	5/12	4/15	0/9	10/39	26
Rowan	22/22	22/24	9/14	0/3	53/63	84
Ash	11/12	12/19	4/12	3/9	30/52	58
Hazel	2/2	7/7	5/5	0	14/14	100

Figure 1 captions

- (a) Silver birch *Betula pendula* showing open conspicuous stems and discriminability from distance
- (b) Silver birch sapling with dark brown bark (3 cm dbh)
- (c) Silver birch with transitional bark (6 cm dbh)
- (d) Silver birch with white bark (8 cm dbh)
- (e) Silver birch showing black bark markings beginning from base and dark branches (12 cm dbh)
- (f) Silver birch with more extensive black bark markings (13 cm dbh)
- (g) Silver birch mature stem with black stem base and black bark markings (17 cm dbh)

White bark in birch species: a warning signal for bark-stripping mammals?

Highlights

- White-barked birch species' bark contains betulin, a plant secondary metabolite, and white birch bark extract has been shown to be repellent to deer
- White birch bark has the expected features of a visual signal
- White birch bark is avoided by multiple bark-stripping herbivores across the Northern Hemisphere
- In a survey in Scotland, white birch bark was stripped less than other trees' bark and mature white birch was avoided in comparison to juvenile brown birch bark
- We propose that white birch bark is a visual aposematic signal for bark-stripping mammals to advertise chemical defence

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Figure 1