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Original article

Factors affecting beech *Fagus sylvatica* bark stripping by red deer *Cervus elaphus* in a mixed forest

Christine Saint-Andrieux, Christophe Bonenfant, Carole Toïgo, Mathieu Basille & François Klein

Bark stripping by large herbivores is widespread, yet poorly understood. Our study was carried out in a 2000-ha area situated in the Vosges Mountains, France, where beech *Fagus sylvatica* bark is heavily bark stripped by red deer *Cervus elaphus*. We tested whether the seasonal variation in the frequency of beech bark stripping by red deer was correlated with bark nutritive value or bark mechanical properties (using an index of bark detachability). We also evaluated whether red deer selected beech trees based on the chemical composition of their bark (e.g. carbohydrates and minerals). Bark-stripped trees had slightly higher carbohydrate contents than non-stripped trees, but this difference resulted from a physiological reaction of the tree to bark stripping. Bark composition was similar between stripped and non-stripped trees spring and summer, but was easier to detach during these periods than during autumn and winter. Therefore, beech bark stripping by red deer in the Vosges Mountains does not appear to be driven by nutritional needs, but it may help deer in improving digestion efficiency.

Key words: carbohydrates, chemical composition, damage, deer, ENFA, tree selection

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Large herbivores can influence their environment by affecting plant and animal biodiversity, as well as the community structure (Hobbs 1996, Côté et al. 2004). In a forest exploitative context, impacts of large herbivores on the environment can translate into a reduction of forest productivity (Waller & Alverson 1997, Shimoda et al. 1994, Vila et al. 2001) since herbivores can lower tree growth and quality through seed predation, shoot consumption or bark stripping (Gill 1992, 2006). Across the northern hemisphere, many large mammalian species engage in bark stripping (browsers and mixed-feeders mainly; Gill 2006). Moose *Alces alces* (Faber & Edenius 1998), sika deer *Cervus nippon* (Yokoyama et al. 2001, Ando et al. 2003), white-tailed deer *Odocoileus virginianus* (Michael 1987), sheep *Ovis aries* (Anderson et al. 1985), horse *Equus caballus* (Kuiters et al. 2006), goat *Capra hircus* (Scogings & Macanda

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2005) and red deer *Cervus elaphus* (Putman & Moore 1998) were shown to consume bark; however, this behaviour is not limited to ungulates (Lutz 1951, Kenward & Parish 1986, Ménard & Qarro 1998).

Numerous hypotheses have been proposed to explain bark stripping by herbivores and although many studies investigated the underlying causes of this behaviour (DeCrombrugghe & Louis 1981, Husak 1985, Reimoser & Gossow 1996, Putman & Moore 1998, Ando et al. 2003, Kuiters et al. 2006), it remains poorly understood (Verheyden et al. 2006). The nutritional value hypothesis (NVH; Miquelle & Van Ballenberghe 1989), which posits that bark is selected for its nutritive value, has frequently been put forward. By eating bark, herbivores could benefit from finding specific minerals (DeCrombrugghe 1965, Ernst 1975, Husak 1985), carbohydrates (Faber 1996, Randveer & Heikkilä 1996), or water (König 1968). However, recent studies have reported that the nutritive value of bark was similar in stripped and non-stripped trees of the same species (e.g. Ando et al. 2003, Kuiters et al. 2006).

Alternatively, bark stripping may improve digestion or provide protection from parasites ('Digestion Benefit Hypothesis' or DBH; Hutchings et al. 2006). Herbivores may ingest bark as a ballast bulk to promote digestion efficiency when the diet has a low fiber content (Keenan 1986, Gill 1992, Reimoser & Gossow 1996). Ingesting bark could slow down digestive transit thereby increasing nutrient and water absorption. Because bark has high concentrations of tannins, it could also have antiparasitic properties (Dearing 1997, Lason et al. 1996, Meissner & Paulsmeier 1995) as repeatedly shown in many experiments (see Hoste et al. 2006). For instance, Min et al. (2004) reported that feeding on rich condensed-tannins forage by goat lowered the number of faecal eggs of the wire worm *Haemonchus contortus* by 70%. If parasites lower deer fitness, then the evolution of anti-parasitic behaviour (Møller et al. 1993), such as eating bark, is expected.

In southern Europe, red deer is responsible for most damage linked to bark stripping (Verheyden et al. 2006) which can cause important technical problems to foresters, leading to serious economic losses (Gill et al. 2000, Ward et al. 2004). Our study aimed at assessing whether bark stripping on beech *Fagus sylvatica* by red deer in the Vosges Mountains was linked to nutritional factors, digestion improvement or to gaining protection against parasites. We focused on beech because it is the main deciduous species in our study area (Saint-Andrieux & Klein 1995). We used temporal changes in the chemical composition of beech bark and in the frequency of bark stripping to test two predictions. The NVH predicts that consumed bark has a higher appetence than other available resources (Miquelle & Van Ballenberghe 1989, Gill 1992). We thus tested whether carbohydrate and nutrient content in bark was higher in stripped than in unstripped beeches. If deer consume bark to improve digestion or to protect themselves against parasites (DBH), a specific temporal pattern of bark stripping frequency should arise at times of highest energy demand. Under the DBH, bark stripping should peak in late spring-early summer. During spring, deer also gather in meadows to forage in large groups and hence, are at the highest risk of parasite infection (Altizer et al. 2003). We thus assessed how bark-stripping frequency matched with the timing of deer energy need to test the DBH.

Material and methods

Study site

Our study was carried out in a 2,000-ha area (N 48°26'-E 7°19'). In the Vosges Mountains, the elevation varies from 650 to 1,000 m a.s.l. The climate is continental with relatively cool summers and cold, snowy winters (average annual rainfall: 850 mm; average annual temperature: 5°C). The soils are acid and the forest consists mostly of beech (≈20%), Norway spruce *Picea abies* (≈40%), fir *Abies* sp. (≈20%), Douglas fir *Pseudotsuga menziesii* (≈10%) and sycomore *Acer pseudoplatanus* stands (≈5%). Ash *Fraxinus excelsior* stands are found occasionally (≈5%). Stem density was 1,780 stems/ha. Professional foresters (from National Forest Service, ONF) measured the average tree diameter with a calliper which, for the different tree species, varied between 7 and 15 cm at 1.3 m height. Forest management is a traditional timber tree growth above a coppiced woodland where natural regeneration and plantation occur. Forest covers 80% of the area, but vineyards and meadows for cattle breeding follow the mountain foot to the east. For all species confounded, 11% of all trees were bark stripped in the area. Stripped beech averaged 26%, but marked spatial variation in bark stripping frequency occurred, ranging from 1% to 83%. Coniferous trees were also subjected to bark stripping with 22, 42 and 11% of damaged trees for Norway spruce, Douglas fir and fir, respectively.

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Red deer inhabit the whole Vosges Mountains (Milner et al. 2006). Rut occurs during September - October, peaking around 19 September (Malgras & Maillard 1996). Females give birth to a single calf from early May to mid-June with 80% of births taking place between 4 May and 10 June (Loe et al. 2005). Females feed their young until the following November (Clutton-Brock et al. 1982), but the peak of lactation occurs during the first three months after calf birth (Loudon 1985, Clutton-Brock et al. 1989). Both sexes are strongly sedentary (Hamann et al. 1997). Red deer is hunted from late October to the end of January (see Bonenfant et al. 2002 for details). Stalking is the main hunting method with an annual harvest of 1.73-3.22 deer/100 ha over 12 years. Being forbidden by French laws, no supplementary feeding was supplied for red deer.

Sampling and analyses of bark quality

Sampling

Censuses of bark-stripped beeches lasted from May 1998 to September 2001 (Fig. 1A). Once a week, the same observer (CSA) walked a unique transect, 5 km long and 25 m wide (12.5 m on each side) and thus sampled a total area of 12.5 ha. The transect was designed to cross all beech stands where bark stripping could have occurred in the study area. The observer recorded every beech tree showing evidence of bark stripping along the transect. For each stripped tree, we recorded tree diameter at ca 1.3 m height, signs of recent bark stripping, and whether the tree had previously been bark stripped or not. Thus, the frequency of bark stripping per week that we reported (see Fig. 1A) is the number of newly bark-stripped trees that occurred within seven days.

We only sampled trees stripped < 24 hours before collection based on the wound aspect after bark stripping (i.e. showing moist and highly glistening wounds; see Vasisiauskas & Stenlid 1998 for an example on ash). For each recent stripped beech, we sampled the bark of the wounded tree and of the closest non-stripped beech that had a similar diameter (bark-stripped trees: 11.14 ± 2.74 cm; non-bark-stripped trees: 10.09 ± 2.71 cm; $N = 23$, $t = 1.060$, $P = 0.150$). For each tree, we collected 10 g of bark beside the wounded parts (i.e. not above or below the wound) of the tree to prevent changes in composition following bark stripping. Outside the bark stripping period (autumn-winter), we randomly selected beech having a similar diameter as stripped trees along the transect. Because of logistic limitations, sampling for bark composition was carried out from May 1998 to September 1999 only.

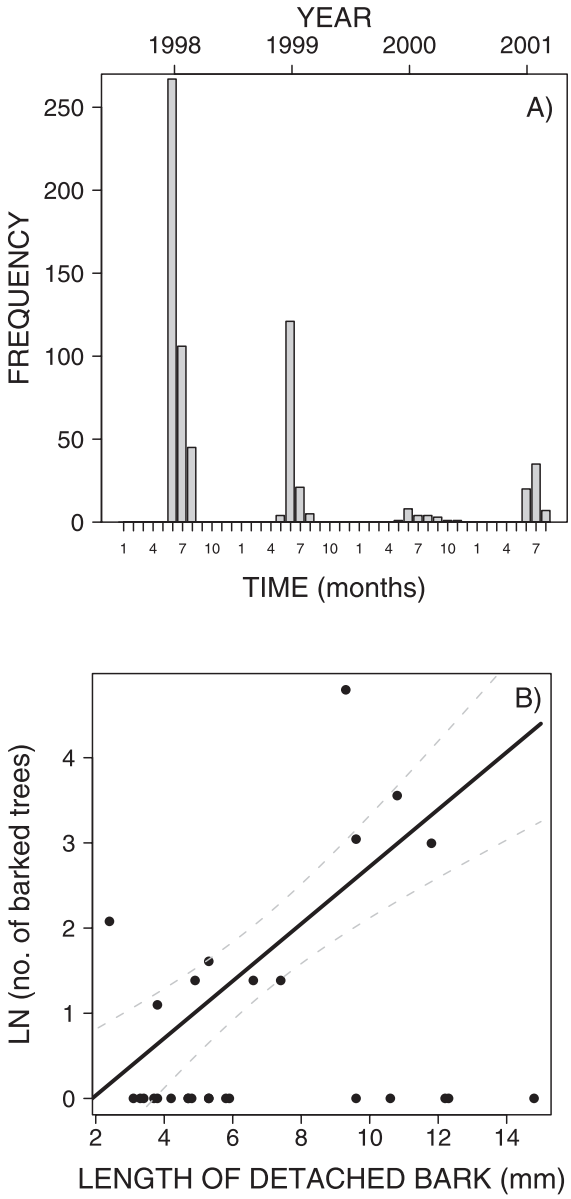


Figure 1. Temporal variation in bark-stripping frequency of beech trees per month in the Vosges Mountains, France, during May 1998 - October 2001 (A), and the relationship between the number of bark-stripped beeches per month (log-transformed; during April 1999 - September 2001) and debarking easiness as assessed by the length of pealed off bark with a chisel (B) (on average per month; $N = 26$). The equation is ln(number of bark-stripped trees) $= 0.637 + 0.335(\pm 0.130) \times$ length of detached bark (negative binomial regression).

Bark composition

All bark samples were placed in -185°C liquid nitrogen and stored at -18°C before chemical analyses.

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Using weight differences between fresh and dried weight (after 48 hours at 70°C), we assessed bark water content. Chemical analyses were carried out at the Laboratory of Cellular Plant Biology of the University of Limoges in France. We quantified macro (Na, Ca, Mg and K) and trace elements (Mn, Fe, Cu, Zn, Co, Pb, Cc and Ni), i.e. the mineral contents (Hoenig & vander Strappen 1978). We also determined crude protein content using total nitrogen dosage, the amount of soluble carbohydrates (glucose, fructose and saccharose; Bergmeyer et al. 1974, Rocklin & Pohl 1983) and starch. A total of N = 63 samples were analysed. Moreover, the chemical composition of bark at the time of sampling may differ from that at the time of debarking. We therefore investigated whether beech responded to bark stripping by comparing bark composition of 20 trees at the time of the manual removal of bark, and five hours later (N = 40).

Ease of bark detachment

To remove bark, red deer pull the bark upwards between the incisors of the lower jaw and the hard fold of the upper jaw. Gill (1992) proposed the ease of bark detachment as a proximate cause of bark stripping. To test this hypothesis, we made a cut in the bark with a wood chisel, and we pulled the scrap upwards until it broke off. We repeated the operation five times per tree. We used the length of the detached bark as an index of bark detachment easiness. These measurements were carried out on 203 randomly sampled trees along the transect from April 1999 to September 2001 (eight trees per month).

Statistical analyses

Bark composition is likely to change markedly between seasons. We thus defined three time periods according to the photosynthesis activity of trees and the temporal pattern of bark stripping frequency (see Fig. 1A). Periods of intense photosynthetic activity of trees and occurrence of bark stripping corresponded to late spring and summer in year 1998 ('summer 1998' during May-August 1998; N = 26, 13 bark-stripped trees) and 1999 ('summer 1999' during May-August 1999; N = 24, 12 bark-stripped trees). A third period, corresponding to the time of lowest photosynthetic activity (the sapless period) and lack of bark stripping on beech, started in September 1998 and ended in April 1999 ('winter 1998'; N = 13, 13 non-stripped trees). A between-class Principle Component Analysis (PCA) was used to assess the change in bark composition according to season and year (three periods), and we tested the difference using a Monte Carlo procedure (Manly 2005).

If, as predicted by the NVH, deer choose particular trees because of bark chemical content, then tree selectivity should occur based on bark composition. We used the Ecological-Niche Factor Analysis (ENFA; Hirzel et al. 2002) to assess whether deer selected particular trees among those available ('adehabitat' package for R; Calenge 2006). Availability is thus defined as the chemical content of all bark-stripped and non-bark-stripped beeches. The use of ENFA was motivated by: 1) the multivariate nature of our data (15 variables) requiring to account for correlations among variables; the multivariate approach also avoids the problem of multiple comparison tests; 2) the ability of the ENFA to detect selection on the mean and variance of a variable. The ENFA summarises beech selection into two components, the marginality (M) and the specialisation (S). The marginality (M) is the difference between the mean composition of bark-stripped trees as compared to all trees. M detects whether consumed bark has, on average, greater or smaller content in one or several compounds than unconsumed bark. The specialisation is the ratio of the variances of the composition of bark of stripped trees as compared to all trees. S detects whether deer consumed bark within a restricted range of values in one or several compounds (restriction around the mean). We tested the extent to which the overall chemical compounds of bark of stripped trees differed from the neighbouring available trees using a Monte Carlo test (Manly 2005).

To test the prediction that bark stripping of beech occurred at the time of calving or rutting (i.e. DBH), we compared the number of bark-stripping events from May to July (calving) with the number of bark-stripping recorded events during the rest of the year using a Generalised Linear Model (GLM; log-link and negative binomial distribution; Venables & Ripley 1999: 233). Finally, to test whether deer ease of bark detachment accounted for beech bark stripping (Gill 1992), we regressed the number of bark-stripped trees found along the transect in a month (count data) against the average length of pealed bark using a GLM (log-link and negative binomial distribution; Venables & Ripley 1999). All statistical analyses were conducted using R (R Development Core Team 2007).

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Results

Short-term effect of stripping on bark composition

The comparison of bark composition of 20 healthy beech trees before and after the manual removal of bark (one sample was taken at the time of bark removal and a second sample five hours later; N = 40) revealed a significant increase in glucose ($+2.24 \pm 0.91$ mg/g; paired t-test: $z = 2.464$, $P = 0.013$) and fructose ($+3.00 \pm 1.01$ mg/g; paired t-test: $z = 3.020$, $P = 0.025$) caused by the simulated bark stripping.

Seasonal variation in bark composition

Three principal components of the between-class PCA were retained, explaining 50% of the total variance. We observed clear seasonal variations in the chemical composition of bark (Fig. 2A). Bark contained more carbohydrates (Glc and Frc), less macro-elements (Na, Ca, Mg and K) and more water in the summer of 1998 and the summer of 1999 than in the winter of 1998. Bark composition also changed between summers: in 1999, it contained less potassium (K), proteins and starch, but more iron (Fe) than in the summer of 1998. Seasonal and between-summer differences in chemical composition of the bark were highly significant (Monte Carlo simulation: $P = 0.001$) and accounted for 19% of the total variance.

Beech selection and timing of bark stripping

Contrary to the predictions of the NVH, red deer did not select particular chemical compounds in bark during late spring and summer. Marginality (M) was slightly related to glucose content in selected trees, but neither marginality ($M = 0.229$, $P = 0.844$) nor specialisation ($S = 5.660$, $P = 0.713$) was significant, which means that the mean and the variance of the chemical components of bark was similar in stripped and non-stripped beech.

We found marked annual variations in average occurrence of bark stripping in summer ($\chi^2 = 11.98$, $df = 3$, $P = 0.007$) and bark-stripping frequency differed according to the season ($\chi^2 = 76.59$, $df = 2$, $P < 0.001$). In agreement with the DBH, bark stripping occurred during the calving season, i.e. during May-August, peaking in June in the years of 1998, 1999 and 2000 and in July in 2001 (see Fig. 1A). No bark-stripped trees were recorded in other months except in 2000 where limited bark stripping occurred until November (see Fig. 1A). We found that 10% of new bark-stripping events were made on previously stripped trees, which is significantly lower than the observed 26% of wounded trees in the beech population (Binomial test: $P < 0.001$).

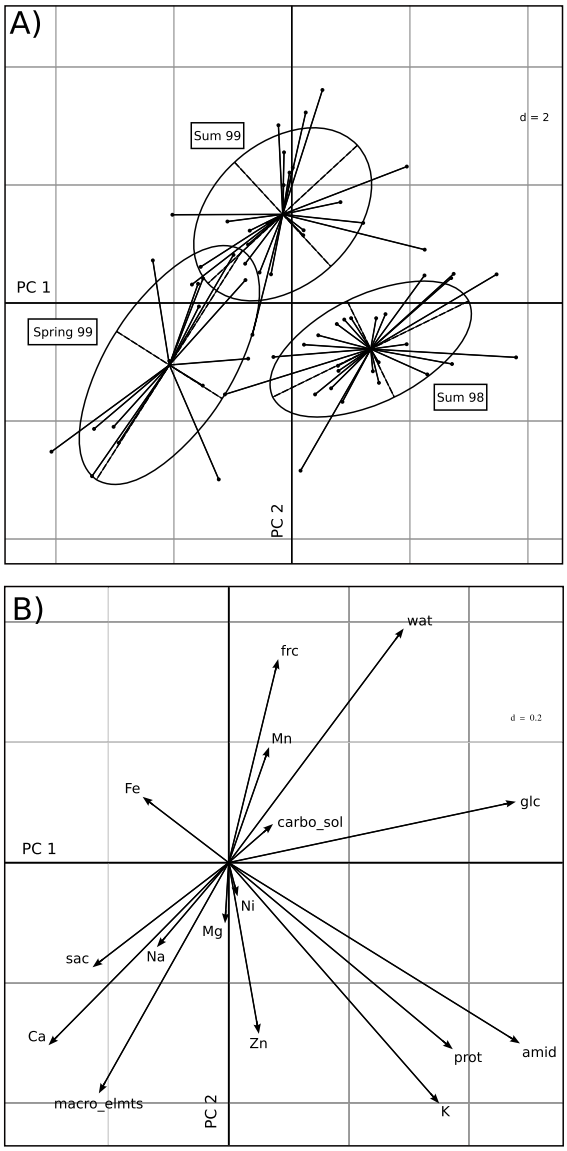


Figure 2. Projection of the beech bark composition onto the two first principal components (PC 1 and PC 2) of the between-class PCA (A) according to the season (winter vs summer) and year (1998-1999), and B) the correlation circle of the between-class PCA showing which variables are associated with PC 1 and PC2 in A) to explain the between-group variation in bark composition. From B), we found evidence of a change in water (wat) and calcium (Ca) content in beech bark, but potassium (K), proteins (prot) and starch (amid) explain most of the observed variation in chemical composition between the summers of 1998 and 1999. In winter, high content of calcium (Ca) and macro-elements (macro_elmts) characterised bark chemical composition. In summer, photosynthetic activity leads to higher water (wat), manganese (Mg) and carbohydrates (fructose (frc), glucose (glc)) content than in spring.

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Ease of bark detachment

The length of manually removed bark was on average 5.07 cm longer in late spring and summer ('summer 1998' and 'summer 1999'; $N = 96, 9.56 \pm 3.94$ cm) than during autumn and winter ('winter 1998'; $N = 107$, 4.49 ± 1.62 cm; $t = 13.207$, $P < 0.001$). The average number of bark-stripped trees per month was positively related to the average length of removed bark ($\chi^2 = 4.775$, $df = 1$, $P = 0.029$; see Fig. 1B).

Discussion

Bark stripping of beech was strongly seasonal and only occurred during summer. Bark contained more water and carbohydrates, and less macroelements in late spring and summer than during autumn and winter (see Fig. 2), reflecting the higher tree metabolism in summer than in winter. Beech bark was easier to peel off in summer than in the sapless period in autumn and winter, correlating with stripping frequency. Furthermore, bark composition was apparently similar in stripped and non-stripped trees suggesting a random selection of beech for bark consumption by red deer in summer.

Resource selection occurs at several spatial and temporal scales (Johnson 1980). Selection for beech bark by red deer was found at the seasonal scale only, and no selection was found at the tree scale within a season. Despite high glucose or fructose levels having been proposed as an explanation for bark stripping (König 1968, Faber 1996, Tamura & Ohara 2005), consumed and unused bark had similar carbohydrates content in our study site. Moreover, most damaged trees were recorded in summer (May-August; see Fig. 1A) when grass provides much higher food quality and quantity than bark as reported by Gill (1992). Finally, bark is a marginal component of red deer diet in summer representing, all year round, only 1% of rumen content weight in the Vosges Mountains (Storms et al. 2008). That bark of stripped trees is richer in nutrients than non-stripped trees (NVH) appears weakly supported by our data. At this point, we acknowledge our small sample size and limited statistical power to reject the NVH definitely. On the other hand, if only slight variations in nutritional value occur among trees, there is no point in devoting time to be selective to get benefits from a specific nutrient. Such behaviour would really hamper our ability to understand bark stripping, especially since factors triggering bark consumption seem highly site-specific. For instance, bark may serve as a food surrogate under difficult environmental conditions like harsh winters (Ueda et al. 2002) or high population densities (Hutchings et al. 2006), but such extreme conditions are unlikely in our population. Hunting pressure indeed keeps population density lower than the carrying capacity (Bonenfant et al. 2002).

We show that beech bark contained 2.24 mg/g more glucose and 3 mg/g more fructose five hours later than at the time of bark stripping. Higher carbohydrate contents in the bark of stripped trees may result from a response of the tree to scarification, as part of the healing process or because carbohydrates accumulate above the wound after phloem cells are broken and sap transport is interrupted (Salisbury & Ross 1992). Hence, any preferences for higher carbohydrate levels in consumed bark previously reported (e.g. Faber 1996, Reynolds et al. 1998, Tamura & Ohara 2005) should be interpreted cautiously since when measured at the time of stripping, the chemical composition of the bark may not differ between stripped and non-stripped beeches. Several previous studies (Randveer & Heikkilä 1996, Tamura & Ohara 2005, Kuiters et al. 2006) also failed to identify any specificity in the composition of bark stripped trees, comparing trees within or among species (but see Welch et al. 1997 for a selection of Sitka spruce by deer according to stem girth). This apparent random choice of tree may be explained by deer not having the ability to discriminate among bark showing slight differences in chemical composition.

The seasonal pattern of bark consumption (see Fig. 1A) is partly accounted for by the positive relationship between bark-stripping frequency and water content of beech bark (see Fig. 1B). Our results agree with the suggestion that a mechanistic property of bark could facilitate stripping by red deer (DeCrombrugghe 1965, Gill 1992, Kuiters et al. 2006). Bark is probably much easier to peel off from the stem in summer, when the increased plant metabolism (involving carbohydrate production, sap transport, higher water content and radial growth) may weaken the bark-sapwood cohesiveness, than in autumn or winter. The role of bark mechanistic property is consistent with the fact that previously stripped beech were consumed less than expected from their availability (10 vs 26%). This is because regrown bark is much harder than pristine bark. A long-term observation assessing yearly variation in bark water content with bark-stripping

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frequency would, however, strengthen this interpretation.

Over three years, we observed that the pattern of bark-stripping frequency matched with the birth season and the peak of energy need linked to lactation. The DBH predicts that terpens and tannins could act as parasite repellent for deer (Hoste et al. 2006). As parasites affect females reproductive success and body condition (Mulvey et al. 1994), females should avoid parasite infection particularly during lactation (Møller et al. 1993), which is the most energetically demanding (Loudon 1985) and critical stage in a deer life cycle. Better protection against internal parasites could improve the mother's condition and could limit the risks of calf infection. Similarly, males and females could benefit from the property of condensed-tannins to form complexes with proteins which increases body growth rate through a better protein absorption (Min et al. 2003). Eating bark could also improve food comminution and digestion by favouring mixing and augmenting transit time. By eating bark, we hypothesise that males of dimorphic and polygynous species could achieve a higher body mass in early autumn and eventually, a higher reproductive success (Clutton-Brock et al. 1982, Clutton-Brock 1988). Moreover, if males consume bark to improve digestion or to protect themselves against parasites, we predict that bark stripping by males should also increase during the rut because of a decreased immune system efficiency (Pelletier et al. 2005).

Conclusion and application

Although we did not measure tannin content and based our conclusion on the temporal pattern of bark-stripping frequency, the DBH predicting protection from parasites and improved digestion (Hoste et al. 2006) seems to have more support in the Vosges Mountains than the NVH. Ultimate causes of bark stripping could be enhanced food digestion or improved parasite protection, but we cannot disentangle both processes from the observed pattern of bark stripping. The easiness of bark detachment may facilitate stripping of beeches in summer. Accordingly, a way to lower the intensity of bark stripping would be to promote bramble *Rubus* sp. production by creating patches of clearings in the forest. Bramble could offer the same level of protection against parasites to deer owning to its very high tannin contents (González-Hernández et al. 2003) while contributing to increasing the extent of food availability. The efficiency of increased availability of tannin-rich plants to reduce bark stripping, however, remains to be experimentally tested. We suggest that addressing the problem of bark stripping from an evolutionary perspective could be a promising way to better understand this behaviour.

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