



RESEARCH PAPER

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Position, size, and spatial patterns of bark stripping wounds inflicted by red deer (*Cervus elavus* L.) on Norway spruce using generalized additive models in Austria

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Abstract

Key message: Bark stripping wounds by red deer (*Cervus elavus* L.) were assessed on 9026 Norway spruce trees. Wound variables (length, width, area, relative width, height above ground, and angle) were analysed using generalized additive models with spatial soap film smoothers. Wounds located at the uphill side of trees were larger in summer than winter, and wound size depended on the diameter at breast height (DBH) and was spatially clustered.

Context: In Austria, red deer (*Cervus elaphus* L.) is the main species causing bark stripping wounds. In winter, they often gnaw at the bark because of food scarcity; in summer, large pieces of bark are detached to help digestion, water, and nutrient uptake or as social behaviour.

Aims: The aim of this study was to analyse wound size (length, width, area, relative width (i.e., width divided by stem circumference)) and wound position (height above ground, angle (i.e., deviation between wound azimuth from slope line)) for winter and summer bark stripping wounds by red deer depending on stand attributes and to describe the spatial patterns of wound size within stands.

Methods: A total of 3832 wounds on 9026 trees in nine experimental stands of Norway spruce (*Picea abies* (L.) Karst.) located at 47° 19' N and 14° 46' E at an elevation of 1009–1622 m were analysed. A linear regression model was fit for wound length over wound width for each season. For all wound variables (wound length, width, area, relative width, position, height above ground, and angle) generalized additive models (GAM) with soap film smoothers, which predict spatial patterns, were fitted.

Handling Editor: Marco Ferretti

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Results: Of all wounds, 79.5 % were inflicted in winter and 20.5 % in summer. Wound length ($31.9 \text{ cm} \pm 31.2 \text{ SD}$), width ($11.7 \text{ cm} \pm 6.0 \text{ SD}$), area ($446.5 \text{ cm}^2 \pm 558.1 \text{ SD}$), and relative wound width ($0.177 \text{ cm} \pm 0.098 \text{ SD}$) were modelled depending on summer or winter bark peeling, DBH, and tree coordinates. For wound height above ground ($119.4 \text{ cm} \pm 26.8 \text{ SD}$) and angle ($-1.9 \pm 97.3 \text{ SD}$), no meaningful GAM could be calculated. Seasonal differences between wound length and area were more pronounced than for wound width; differences in height above ground were minimal, but significant. Analyses further showed that wounds were mainly located at the uphill side of the trees.

Conclusion: The spatial clustering of wound sizes might reduce the efficiency of thinning to remove heavily damaged trees in bark-peeled stands and might increase the number of sample points required to assess deer impact in forest inventories. Also, the uphill location of damages is an important information in inventories.

Keywords: Cervidae, Wound sizes, Wound position, Spatial distribution, Soap film smoother, *Picea abies*

1 Introduction

1.1 Bark stripping damage on Norway spruce (*Picea abies* L. Karst.)

Many European *Cervidae*s are known to strip bark. Bark stripping damage is reported for red deer (*Cervus elavus* L.), moose (*Alces alces* L.) (Vasiliauskas 1998; Arhipova et al. 2015), sika deer (*Cervus nippon* L.) (Welch et al., 1988), and fallow deer (*Dama dama* L.) (Gill, 1992). Roe deer (*Capreolus capreolus* L.) and reindeer (*Rangifer tarandus* L.) do not strip bark in winter, but forage small trees and grass or lichens, respectively (Gill, 1992).

The red deer is the most widespread bark stripping cervid in Europe, resident in all countries, absent only in northern Fennoscandia (Lovari, et al., 2019). Similarly, the moose is common, but is restricted to the northern part of Europe (Hundertmark, 2016). Sika deer and fallow deer have been introduced from Japan and Turkey, respectively (European Mammal Assessment Team, 2007), and the sika deer is now resident in Great Britain, Czech Republic, and other Central European countries. Populations of all *Cervidae*s, native or introduced, are stable or increasing in Europe (European Mammal Assessment Team, 2007; Harris, 2015). In particular, populations of red deer (Côté et al., 2004; Burneviča et al., 2016; Candaele et al., 2021) and sika deer (Vacek et al., 2020) have been reported to increase rapidly in many areas, causing severe damage to forest stands (Čermák & Strejček, 2007; Vacek et al., 2020), with sika deer causing more severe damage than the native red deer in some areas (Vacek et al., 2020).

Moose is the largest of the *Cervidae*s with a shoulder height of 150–220 cm; shoulder height for red deer varies between 84 and 110 cm and is considerably smaller than that of moose. The other cervids only grow up to 100 cm (sika deer: 65–95 cm; fallow deer: 80–100 cm) (Flamm et al., 1992). Accordingly, the wound height, width, and length inflicted by different cervid species also differ significantly with wound heights above ground and sizes being higher and larger for the larger

animals (Gill, 1992; Månsson and Jarnemo, 2013; Arhipova et al., 2015; Vacek et al., 2020). Bark stripping wounds by red deer were found at a height above ground of 97–110 cm (Arhipova et al., 2015), corresponding to red deer shoulder height. In scientific literature, wound direction was reported to be arbitrary (Welch et al., 1988) however, in steep terrain wounds, seem to be mostly found on the uphill side of the stem, but wound position in steep terrain has not been documented before.

Preferred species are Norway spruce (*Picea abies* (L.) Karst.) (Čermák et al., 2004; Vospernik, 2006; Cukor et al., 2019a, b; Vacek et al., 2020; Candaele et al., 2021), lodge pole pine (*Pinus contorta* Douglas ex Loudon) (Arhipova et al., 2015), Douglas fir (*Pseudotsuga menziesii*) (Candaele et al., 2021), European ash (*Fraxinus excelsior* L.) (Vasiliauskas & Stenlid, 1998; Vospernik, 2006; Candaele et al., 2021), linden (*Tilia* spp.) (Fehér et al., 2016), maple (*Acer* spp.) (Fehér et al., 2016), sweet chestnut (*Castanea sativa* Mill.) (Vospernik, 2006), and *Sorbus* spp. (Vospernik, 2006), whereas thick-barked species are often avoided (Gill, 1992; Vospernik, 2006; Candaele et al., 2021). Open wounds exposed 4–4355 cm² of sapwood (Čermák & Strejček, 2007; Arhipova et al., 2015), and repeated assessment or dendrochronological analysis showed that the same tree was debarked several times (Gill, 1992; Arhipova et al., 2015; White, 2019; Nagaike, 2020), with an average of 1.8–2 wounds per tree (Arhipova et al., 2015). Wounds were inflicted in stands aged 8–10 to 40–60 years (Čermák et al., 2004; Fehér et al., 2016; Cukor et al., 2019a, b; Vacek et al., 2020; Candaele et al., 2021) depending on site productivity and deer abundance (Candaele et al., 2021), with the age of vulnerability corresponding to mean diameters of 6–24 cm for thin-barked species (Vasiliauskas & Stenlid, 1998; Arhipova et al., 2015; Vacek et al., 2020) and a considerably shorter period of sensitivity and smaller diameters for thick-barked species (Gill, 1992; Vospernik, 2006; Candaele et al., 2021). Wound size increases with

diameter at breast height (DBH) (Arhipova et al., 2015; Vacek et al., 2020), and wounds inflicted in summer are reported to be larger than winter wounds (Månsson & Jarnemo, 2013; Candaele et al., 2021).

Food scarcity in winter is thought to be the main reason for winter bark stripping (Gill, 1992). The phloem of trees provides a nutrient-rich food that lacks toxins and feeding deterrents, and bark stripping often occurs in late winter and early spring, when the phloem is more nutrient rich (White, 2019). Reasons for summer bark peeling are less clear. Summer bark peeling has a beneficial effect for the digestion in the rumen (Månsson & Jarnemo, 2013) and has also been related to water scarcity (König, 1968). The two types of wounds can be easily distinguished, since winter bark stripping wounds show teeth marks. In winter, the bark is firmly attached to the stem, whereas in summer, the bark is more loosely attached, and thus, large stripes of bark can be removed from the trees (Gill, 1992; Candaele et al., 2021).

Bark stripping greatly damages saplings and trees by destroying water conductivity and increasing fungal infection (Nagaike, 2020; Vacek et al., 2020). Wounds with more than 65% of stem circumference resulted in increased tree mortality (Nagaike, 2020), and recent studies have also evidenced a significantly decreased productivity and increased sensitivity of stripped trees to drought and heatwaves (Cukor et al., 2019a, b; Vacek et al., 2020). Another important consequence of bark stripping is fungal infection and subsequent wood decay (Vasiliauskas, 1998; Vasiliauskas & Stenlid, 1998; Čermák et al., 2004; Čermák & Strejček, 2007; Butin, 2011; Vasaitis et al., 2012; Rönnberg et al., 2013; Arhipova et al., 2015; Burneviča et al., 2016).

Infection spreads vertically along the tree (Arhipova et al., 2015; Burneviča et al., 2016) and is linearly correlated with wound length, whereas the spread of wound decay beyond the wound margin is limited (Vasiliauskas & Stenlid, 1998; Mäkinen et al., 2007; Arhipova et al., 2015). Decay in the Norway spruce was reported to range from 2.7–62.5 cm·year⁻¹, finally reaching an extent of 1.5–6 m (Čermák et al., 2004; Čermák & Strejček, 2007; Rönnberg et al., 2013; Vacek, et al., 2020) depending on tree age and the age of the wounds (Čermák & Strejček, 2007). Further, decay was reported to increase with site fertility (Vasaitis et al., 2012; Burneviča et al., 2016). Even though wound sizes for different tree species vary a little, pathogenic consequences vary between species, since fungi colonizing wounds are tree species specific (Mäkinen et al., 2007; Metzler et al., 2012) and have different spread rates (Vasiliauskas, 1998; Mäkinen et al., 2007; Metzler et al., 2012).

For example, Mäkinen et al. (2007) isolated different fungi from the Norway spruce (*Picea abies* (L.) Karst.)

and Scots pine (*Pinus sylvestris* L.) and Metzler et al. (2012) from the Norway spruce and silver fir (*Abies alba* Mill.). In the Scots pine, a lower proportion of trees were decayed than in the Norway spruce (Mäkinen et al., 2007). Similarly, infection rate for the Norway spruce with pathogens was 4.6 times higher than for silver fir (Metzler et al., 2012). Fungal infection and limited water uptake further increase stand sensitivity to wind and snow damage (Vasiliauskas, 1998; Čermák et al., 2004; Čermák & Strejček, 2007; Burneviča et al., 2016; Snepsts et al., 2020). Damaged stands had a 1.68 times higher probability for wind damage (Snepsts et al., 2020), and pulling experiments evidenced a lower resistance of bark-stripped trees to pulling force (Krisans et al., 2020). However, contrary to expectations, most trees in the pulling experiment were uprooted, and only one bark-stripped tree broke at the wound (Krisans et al., 2020).

In Austria, bark stripping by red deer prevails, whereas wounds inflicted by other cervids are rare (Völk, 1997). The tree species most affected by bark stripping are the Norway spruce, European ash (*Fraxinus excelsior* L.), sweet chestnut (*Castanea sativa* Mill.), and *Sorbus* spp. (Vospernik, 2006). Of these tree species, bark stripping damage of the Norway spruce is considered most important, because of its high economic importance for Austrian forestry, since it constitutes 60.4% of the standing timber volume (BFW, 2021). While the Austrian National Forest Inventory (BFW, 2021) records the presence/absence of bark stripping wounds, wound size, position, and the spatial distribution of damage within stands is not assessed. In particular, within stand spatial patterns have been little investigated in detail before, although bark stripping damage has been reported to be clustered (Gill, 1992).

Further, bark stripping is more common in areas with higher agriculture (Månsson & Jarnemo, 2013; Sun et al., 2020) and increases with the distance to forest roads (Kiffner et al., 2008). Moreover, a substantial increase in damage is found around diversionary feeding stations, constructed to protect forestry and natural habitats (Putman & Staines, 2004).

Deer animals and bark stripping wounds are a frequent source of debate between wildlife managers and forest managers (Reimoser & Gossow, 1996). On the one hand, bark stripping causes important economic damage and seriously devaluates timber (Čermák et al., 2004; Čermák & Strejček, 2007; Vacek et al., 2020; Candaele et al., 2021), and forest managers have a high interest in controlling red deer populations (Kiffner et al., 2008; Candaele et al., 2021). On the other hand, deer animals are a part of the forest ecosystem and are highly valued for hunting and aesthetic reasons (Ehrhart et al., 2022). An objective assessment of bark stripping damage is the basis to settle these differences. For

damage assessment, between-stand and within-stand variation of bark stripping wounds is important. Wound size is an important factor for the economic evaluation since the decay extent is closely linked to it (Arhipova et al., 2015; Vacek et al., 2020).

1.2 Hypotheses and research questions analysed in this paper

The aim of this study was to analyse wound size, position, and its spatial patterns. Specifically, the following hypotheses were analysed:

- Wound size is larger in summer than in winter.
- Winter bark stripping is more common than summer bark stripping.
- Wounds are larger on larger trees.
- Wounds are located at the uphill side of the trees.
- Wound height is animal specific and is therefore at a constant height above ground.
- Wound sizes are larger on trees close to winter feedings and forest roads.
- Wound sizes are spatially clustered.

2 Methods

2.1 Study area

The study was conducted in Gaal/Austria (Fig 1). Precise stand coordinates are given in Table 1. The study area is an area of a high red deer population density; the average number of hunted animals is 1.21 deer per 100 ha of forestland (Reimoser & Reimoser, 2019). The measurements were collected in nine stands, located on moderately steep slopes (40 to 50%) at an elevation of 1009–1622 m (Table 1). Stands were selected based on a visually estimated damage rate of the stands (three stands with a low, medium, and high bark-peeling rate, respectively). However, the following precise assessment of the

stands rather showed a continuum of bark stripping rates than three distinct classes. Trees grow on Cambisols on silicate bedrock (quartz, granite, and feldspar). Soils are classified as moist or fresh (Kilian et al., 1994; FAO, 2015). The study area is classified as a warm, summer continental climate according to Köppen (Wikipedia, 2022). At the nearest climate station in Seckau (Lat = 47.2°, Lon = 15.1°, 863 m above sea level), an annual mean temperature of 6.6 °C and a mean annual precipitation of 817 mm were recorded from 1981 to 2010. The coldest month is January with a mean temperature of - 3.4 °C, and the warmest month is July with a mean temperature of 16.6 °C. In Seckau, there are 141 frost days and 92 days with snow cover (> 1 cm) of which 24 days have a snow cover of more than 20 cm (ZAMG, 2021). Stands are almost totally composed of Norway spruce with admixtures of European larch (*Larix decidua* Mill.), and broad-leaved trees represent less than 5% of the total basal area, except in stand 8 with a larch proportion of 15%.

2.2 Data collection and design

In a first step, each stand was scanned with a laser scanner (“FARO Focus3D X330”—*Faro Technologies Inc., Lake Mary, FL, USA*). The scans were done in multiscan mode with the resolution parameter set to 1/4, resulting in a resolution of $r = 6.136 \text{ mm}/10 \text{ m}$, and the quality parameter set to 4×, resulting in a measuring time of 8 μs per scan point. Scans were co-registered, and tree coordinates were automatically derived from the point clouds using an algorithm (Ritter et al., 2017; Gollob et al., 2019; Gollob et al., 2020). From the laser scans, detailed digital elevation models (DTM) were obtained for each of the nine stands.

Subsequent field assessment encompassed verification of calculated coordinates and diameter at breast height

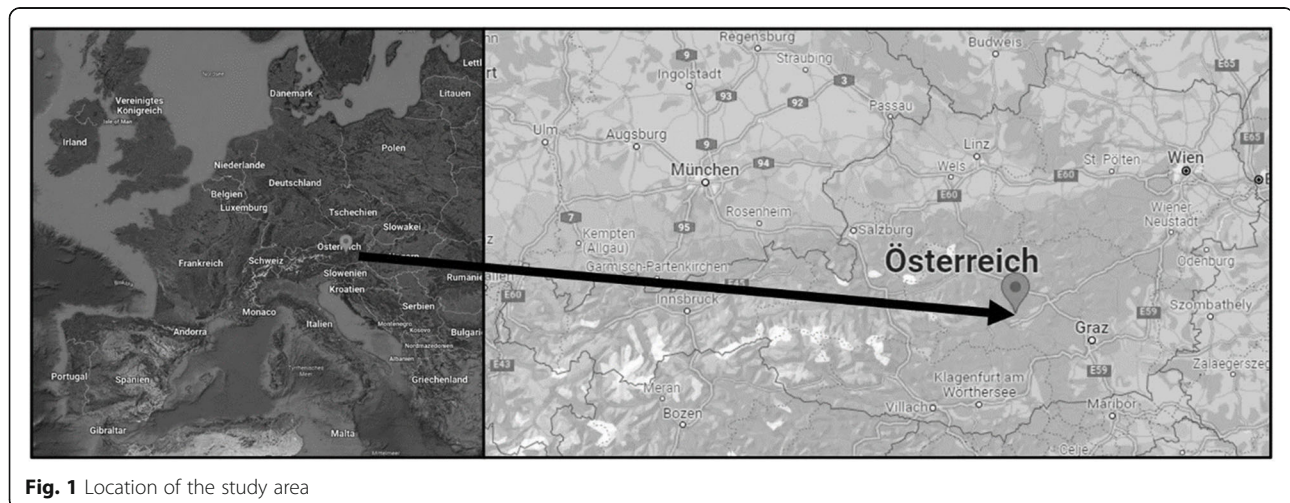


Fig. 1 Location of the study area

Table 1 Location and biometric information of the nine stands

No.	Location	Exposition	E (m)	Area (ha)	n (trees)	N (ha ⁻¹)	BA (m ² × ha ⁻¹)	V (m ³ × ha ⁻¹)	Damage (%)	qmd (cm)	H (m)
1	47° 16' N, 14° 42' E	East	1009	0.63	601	949	64.8	746	60.9	33.3	24.1
2	47° 18' N, 14° 43' E	South	1376	0.29	368	1260	55.2	516	15.8	26.6	18.3
3	47° 21' N, 14° 44' E	South	1508	1.29	923	714	43.5	455	67.8	31.4	18.9
4	47° 19' N, 14° 45' E	East	1578	0.83	882	1067	39.9	337	12.4	24.6	16.6
5	47° 19' N, 14° 46' E	East	1622	1.24	1894	1524	42.3	367	36.4	21.2	16.6
6	47° 17' N, 14° 47' E	West	1130	0.52	600	1144	39.6	434	30.5	23.7	19.5
7	47° 17' N, 14° 48' E	East	1112	1.75	878	502	35.1	398	18.9	33.7	20.2
8	47° 18' N, 14° 49' E	West	1485	1.21	1678	1383	39.6	321	18.7	21.5	15.3
9	47° 20' N, 14° 50' E	West	1438	1.37	1202	880	46.5	420	15.6	29.3	19.0
Total	---	---	---	9.13	9026	---	---	---	---	---	---

Location = Coordinates of the stands; Exposition = Exposition of the stands; E elevation, Area analyzed of the stands, n number of trees in the stands, N stem number per hectare, BA basal area per hectare, V volume per hectare, Damage percentage of damaged trees. qmd quadratic mean diameter; H mean height of the trees

(DBH) and wound characteristics were measured on each tree. In total, 9026 trees with 3832 bark stripping wounds were assessed. For each tree, DBH and tree species were noted, and all wounds were searched for and recorded. Wounds were classified as winter or summer bark stripping damage, and for each damage, the following measurements were taken (Fig. 2), and the following calculations were done:

- Wound length defined as the maximum vertical extent
- Wound width defined as the maximal horizontal extent
- Wound height defined as the distance of the centre of the wound to the ground
- Wound azimuth was measured in degrees
- Wound area was calculated as wound length times wound width (Eq. 1)
- Wound angle was calculated as the difference between the azimuth and the local slope line derived from a 1-m resolution digital elevation model (DTM) from the laser scan (Eq. 2)
- Relative wound width as the quotient of the absolute wound width and the circumference of the tree (Eqs. 3 and 4)

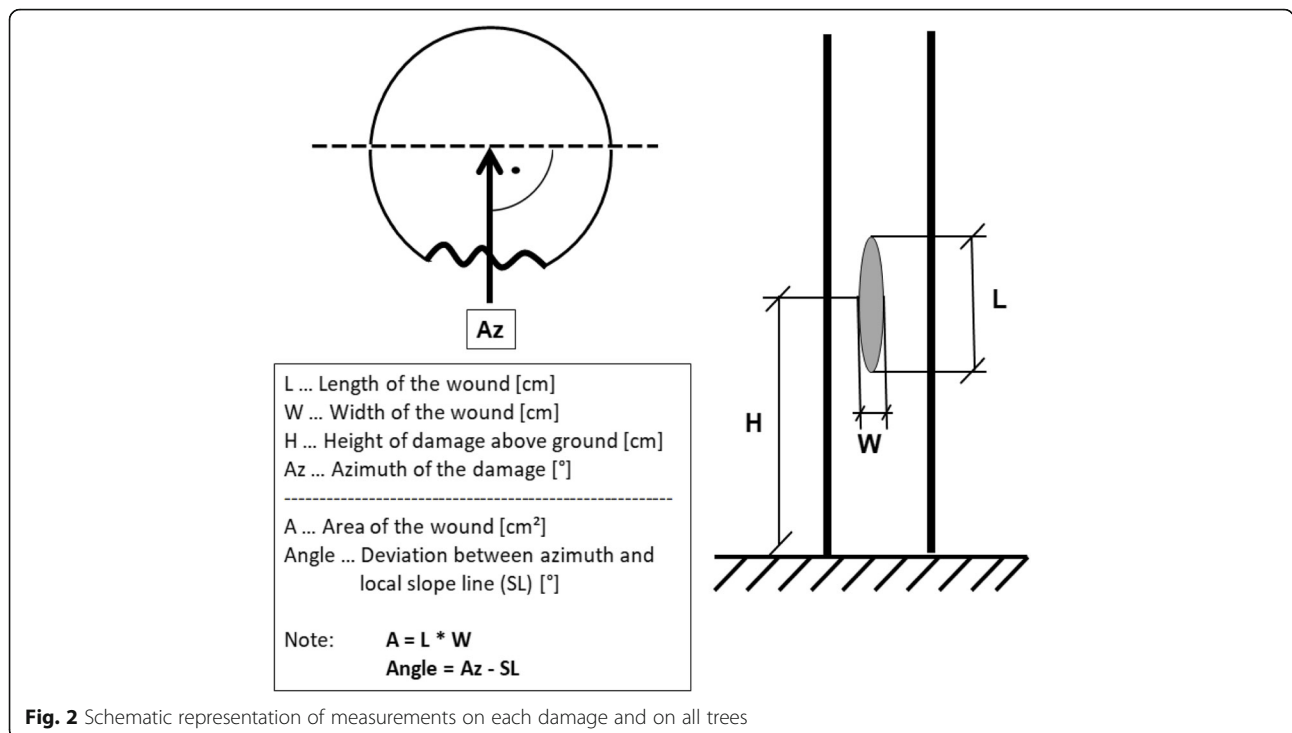


Fig. 2 Schematic representation of measurements on each damage and on all trees

$$Area = Length \times Width \tag{1}$$

$$Angle = Az \times SL \tag{2}$$

$$CF = DBH \times \pi \tag{3}$$

$$Rel.width = \frac{Width}{CF} \tag{4}$$

with Area Calculated area of the bark stripping wound (cm²)

Length Length of the bark stripping wound (cm)

Width Width of the bark stripping wound (cm)

Angle Calculated difference between the wound azimuth and the local slope line (°)

Az Azimuth of the bark stripping wound (°) (Fig. 2)

SL Local slope line (°) calculated from the laser scan data

CF Circumference (cm) of the tree

DBH Diameter at breast height (cm) of the tree

π Mathematical constant

Rel. width Relative width of the wound (-)

2.3 Statistical analysis and modelling of wound sizes with general additive models

Generalized additive models (Hastie & Tibshirani, 1990; Wood, 2017) are flexible models where the dependent variable is modelled by smooth functions of the independent variables. For fitting the models, the r-package mgcv (Wood, 2020) and, for model diagnostics, the r-package mgcViz (Fasiolo et al., 2021) were used. The mgcv-package allows for the inclusion of two-dimensional smoothers, parametric terms, the specification of different distribution families as well as the specification of different link functions.

The generalized additive models (GAM) equation in general is given in Eq. 5:

$$Predicted\ variable = \underbrace{\beta_0}_{Intercept} + \underbrace{\sum_{i=1}^n [\beta_i * x_i]}_{Parametric\ terms} + \underbrace{\sum_{j=1}^n [s(y_j)]}_{Smooth\ terms} \tag{5}$$

with β₀ Intercept

β_i Coefficient for the *i*th parametric term

x_i *i*th parametric term

s(y_j) Smooth function for the *j*th variable (y_j)

In this research, the gamma distribution and the log link function were used to relate the damage length, width, and area and relative wound width (wound width divided by stem circumference) to the predictive variables. Categorical variables such as summer or winter bark peeling and tree species were included as parametric terms. In addition, the nine stands were included as a random effect, but the random effect was not significant.

All variables, except the tree coordinates, were modeled using thin plate regression splines, which are the default smooth function in the mgcv-package with 10 knots. If the default number of knots was appropriate, it was verified with the mgcViz-package (function check), which computes a k-index for each smooth term. A k-index of less than one indicates that the number of knots is too low. The mgcViz-package provides also an automatic model diagnostic plot for each model. This plot contains 4 sub-plots: (i) a quantile–quantile (Q-Q) plot, where the theoretical quantiles are calculated from Monte Carlo simulation and plotted against the observed quantiles, (ii) the histogram of the residuals, (iii) the plot of residuals versus the linear predictor, and (iv) the plot of response versus fitted values (Augustin et al., 2012).

Numerous covariates and covariate combinations were tested for each dependent variable, and the resulting models were ranked according to the adjusted coefficient of determination (adj. r²) and the Akaike information criterion (AIC) (Akaike, 1973). For each dependent variable, the five highest ranked models were considered in detail, and biological plausibility was checked. The highest ranked model for wound height and angle (using also the gamma distribution and the log link function) did not explain more than 3.0% and 10.7% of the total variation, respectively, and therefore, modelling of these characteristics was not pursued. For the other variables (wound length, width, area, and relative width), final model choice was a model formulation that was consistent across all four size variables because the differences in AIC (Akaike, 1973) and adjusted r² between the five best ranked models were minimal.

For the spatial component, we used the soap film smoother (Wood et al., 2008), which is a finite-area smoother using boundary polygons. In our case, spatial wound size distribution was smoothed within each of the nine stands using the stand boundary line as constraint for the smooth.

Finally, the following model was chosen for the four wound size variables (Eq. 6):

$$\left. \begin{matrix} Length \\ Width \\ Area \\ Rel.width \end{matrix} \right\} = \beta_0 + \beta_1 \times w + s(\chi_{Lambert}, y_{Lambert}, bs = 'so') + s(DBH) \tag{6}$$

with Length Length of the bark stripping wound (cm)

Width Width of the bark stripping wound (cm)

Area Calculated area of the wound (cm²)

Rel. width Relative width of the wound (-)

β₀ Intercept

β₁ Coefficient for the parametric term w

w Parametric term; $w = 1$ for winter damage; $w = 0$ for summer damage

$s(x_{Lambert}, y_{Lambert}, bs = 'so')$ Soap film smooth ($bs = 'so'$) for the spatial distribution of wounds using the Lambert coordinates of the trees with wounds

$s(DBH)$ Smoother for DBH (cm). The number of knots (k) was set to $k = 50$ in response to the results of the r-function check

The coefficients (β_0 and β_1) and the smooth functions for the coordinates and the DBH were modeled for length, width, area and relative width separately.

3 Results

3.1 Descriptive statistics and t test

In total, 3832 wounds were measured with an average length of 31.9 cm and an average width of 11.7 cm, resulting in an average wound area of 446.5 cm²; the wounds have an average relative width of 0.177. The average height of the wound centre is 119.4 cm above ground, and wounds were located on the uphill side of the trees with very little deviation from the uphill slope line as indicated by the angle (Table 2). Between stands, variations in length, width, height, area, and angle were minor. In particular, between stand differences in wound height and angle were very small (Table 2).

The difference between the azimuth of damages and the local slope line was tested with a paired Student’s t test. The difference between the two azimuths was not significant (t value = - 0.982; p value 0.326), confirming that damages were located on the uphill side of the trees. Figure 3 shows the histogram of observed angles, peaking at angle = 0.

Winter damage accounted for 79.5% and summer bark stripping damage accounted for 20.5% of all damages observed. Differences in wound height above ground between summer and winter (winter: 119.0 cm; summer:

119.8 cm) were minimal but significant because of the large sample size. Similarly, differences in wound width, length, and area between winter and summer bark peeling damage were significant. Wound width (winter: 11.5 cm; summer: 14.5 cm) differed less than wound length (winter: 26.7 cm; summer: 53.0 cm) or wound area (winter: 360.4 cm², summer: 850.3 cm²). The distribution of wound height above ground, wound width, length, and area by season is shown in the boxplots in Fig. 4, and the relationship between wound length and wound width for both seasons are shown in Fig. 5. For the same wound width, summer bark peeling damage has a longer wound length as is shown by the different regression lines (Fig. 5), explaining 29% and 30% of the variation in wound length.

3.2 Modelling with GAM

A detailed analysis revealed that wound length, width, area, and relative wound width depended on season, Lambert coordinates, and the DBH of the trees; model statistics are given in Table 3. The Q–Q plots created by `gam.check` are given in Fig. 6.

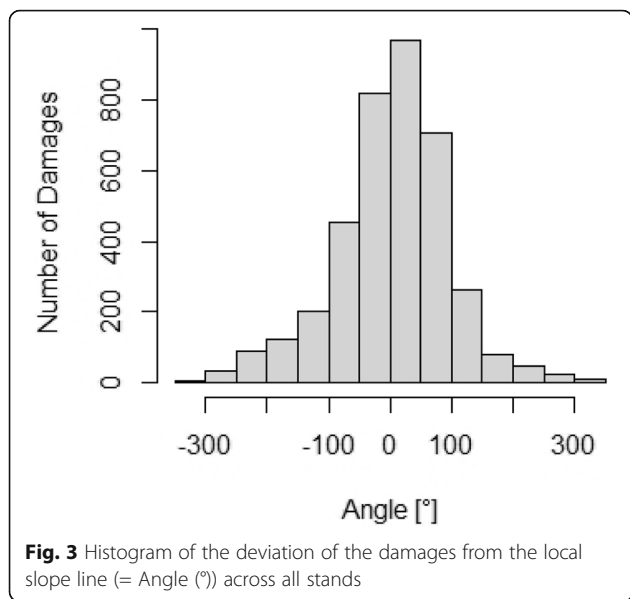
Wound length, width, and area all initially increased with DBH; they had a maximum at a DBH of approximately 35 cm, and then gradually decreased for larger trees. Relative wound width decreased with DBH. Wounds inflicted on trees in summer were considerably larger than wounds formed in winter. In Fig. 7, this information is plotted for stand 1. This relationship was constant across stands; therefore, plots for the other stands are not shown.

Wound length, width, area, and relative wound width varied spatially (Figs. 8, 9, 10, and 11). Spatial patterns for all four variables were similar, but were more pronounced for wound length and area than for wound width and relative wound width. Spatial patterns could

Table 2 Descriptive statistics of bark stripping wounds (mean ± standard deviation)

No.	<i>n</i> (Damage)	Length (cm)	Width (cm)	Height (cm)	Area (cm ²)	Relative width (-)	Angle (°)
1	541	37.1 ± 23.1	14.2 ± 6.8	119.1 ± 20.8	609.6 ± 636.9	0.174 ± 0.093	50.8 ± 79.4
2	62	17.5 ± 10.6	7.4 ± 5.2	119.9 ± 27.6	160.3 ± 257.0	0.110 ± 0.058	- 22.3 ± 54.1
3	1121	33.7 ± 25.0	12.7 ± 5.9	123.2 ± 28.0	505.6 ± 643.3	0.176 ± 0.095	- 26.2 ± 79.7
4	141	23.5 ± 23.5	9.5 ± 4.8	107.5 ± 25.6	289.6 ± 457.7	0.155 ± 0.088	- 7.2 ± 59.8
5	837	33.3 ± 25.2	10.6 ± 5.5	120.6 ± 22.7	431.0 ± 527.9	0.195 ± 0.106	50.8 ± 62.8
6	256	28.5 ± 21.3	11.1 ± 5.5	123.2 ± 27.9	392.8 ± 614.2	0.192 ± 0.106	- 43.7 ± 112.1
7	215	33.6 ± 19.9	11.9 ± 6.3	124.2 ± 31.6	445.6 ± 386.6	0.173 ± 0.108	- 137.2 ± 146.3
8	405	27.5 ± 18.4	10.6 ± 5.4	113.8 ± 29.3	344.6 ± 379.4	0.189 ± 0.090	1.91 ± 81.6
9	254	25.7 ± 14.6	9.5 ± 4.6	106.3 ± 28.7	263.3 ± 244.3	0.121 ± 0.062	- 21.0 ± 95.5
Total	3832	31.9 ± 31.2	11.7 ± 6.0	119.4 ± 26.8	446.5 ± 558.1	0.177 ± 0.098	- 1.9 ± 97.3

n (Damage) = Number of measured damages. Length wound length, Width wound width, Height mad of wound centre above ground, Area wound area, Relative width = Wound width divided by stem circumference; Angle = Deviation of the wound direction from the slope line

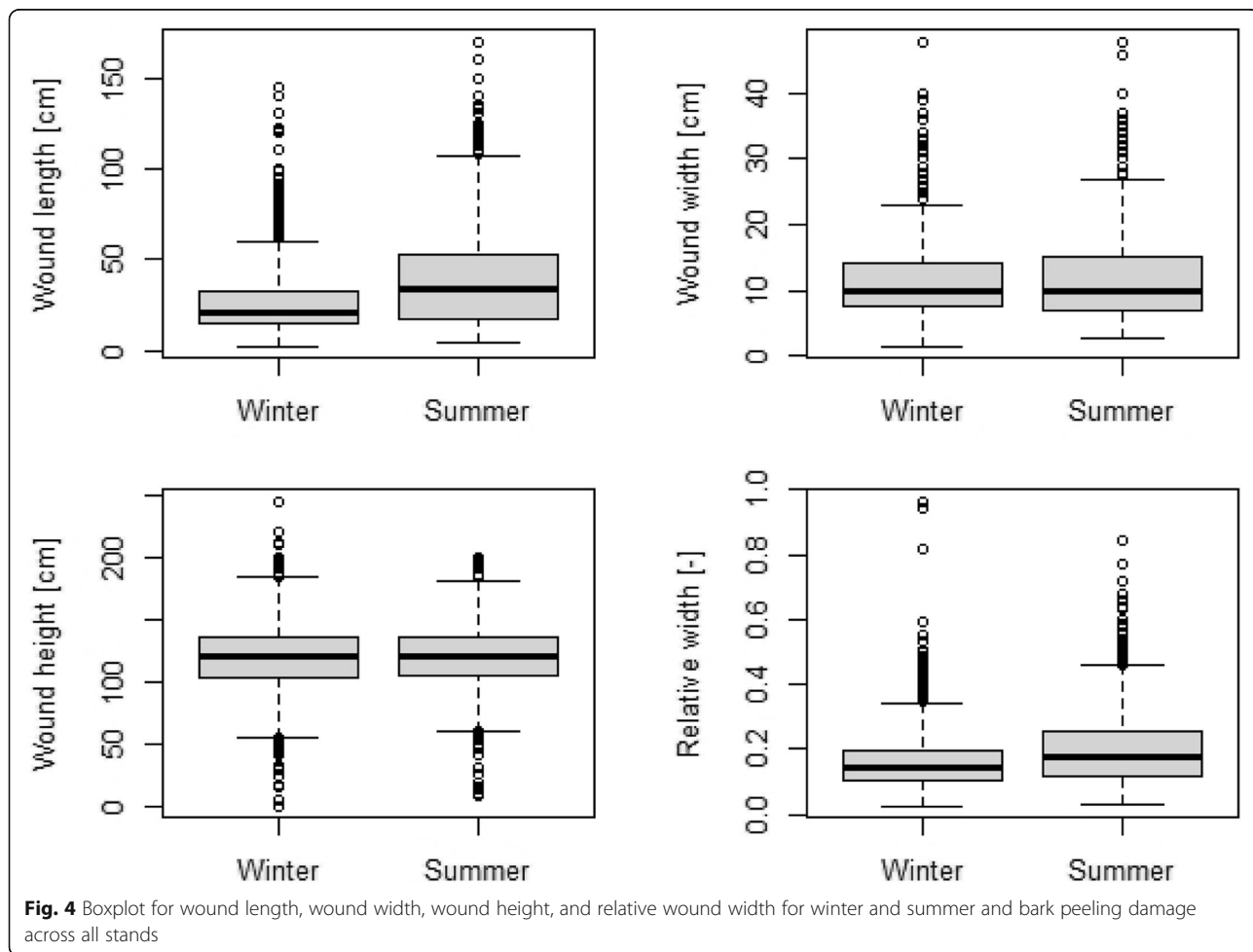


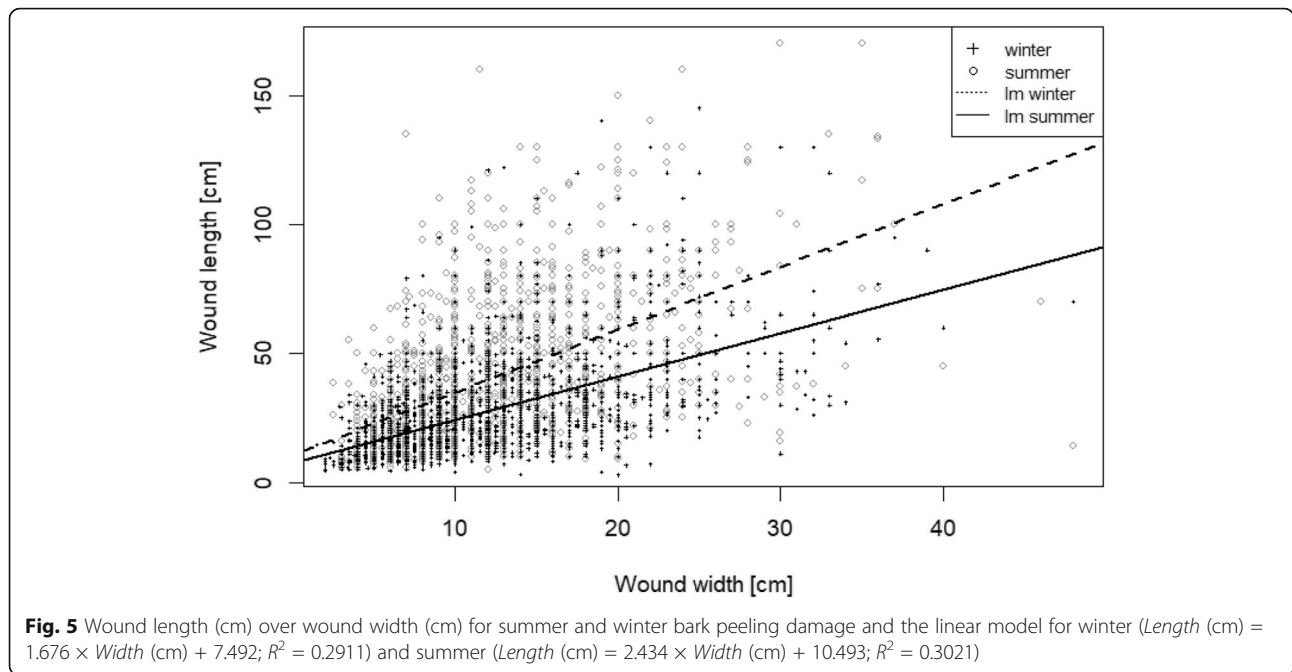
be related to the presence of supplementary feedings in two of the nine stands (stand 2: Feeding in the Southeast; stand 3: Feeding in the Northeast). These 2 stands showed a decreasing gradient in damage size with distance to the supplementary feedings. The other four stands also showed considerable spatial variation of damage, but without any clear explanation for it.

4 Discussion

4.1 Wound position and wound size

In practical forestry, it is common knowledge that in steep terrain, the bark peeling wounds are located on the uphill side of the stem. This side is more accessible for red deer because the local terrain is flatter than on the downhill side, and the animals are able to reach higher parts of the tree with thinner bark, which they prefer. This behaviour was almost invariable in our study: in contrast, on flat terrain, no dependence of wound occurrence on direction was observed (Welch et al., 1988). It remains unclear, at which slope these two contrasting patterns switch. This interesting fact, which is related to animal behaviour, has also important





consequences for the monitoring of bark stripping damages. If the wounds are exclusively located at one side, this has to be accounted for by the sampling design.

Wound height above ground is specific for different cervid species, and in studies where multiple bark stripping cervids are present, it is used to attribute damage to a specific cervid species (Månsson & Jarnemo, 2013). The certain identification of the causing animal species from wound height above ground is, however, difficult (Månsson & Jarnemo, 2013, Fehér et al., 2016). Wound height observed in this study (Table 2) is closely related to reported heights above ground inflicted by red deer from previous studies (Welch et al., 1988; Arhipova et al., 2015; Burneviča et al., 2016).

Studies on bark stripping of the Norway spruce by red deer report a damage width between 6 cm (Welch et al.,

1988) and 10 cm (Burneviča et al., 2016) and a damage length between 12 cm (Welch et al., 1988) and 33 cm (Burneviča et al., 2016) resulting in a wounded area between 200 cm² (Månsson & Jarnemo, 2013) and 589 cm² (Burneviča et al., 2016). In our study, the wound width observed is within the range reported in the literature but rather on the upper side of it (Table 2). Moreover, these wound sizes inflicted by red deer on Norway spruce were also similar to those found on other tree species (Welch et al., 1988; Vasiliauskas & Stenlid 1998; Arhipova et al., 2015), so that wound size is rather animal specific than a tree species characteristic. Similarly, Welch et al. (1988) also found no differences in wound size between tree species.

In our study, wound length and wound width were measured in the field, whereas wound area was

Table 3 Statistical parameters of the models for wound length, width, area, and relative wound width (width divided by stem circumference).

Model	Adj. R ²	AIC	RMSE	Parametric terms		Smooth terms			
				Term	p values	Term	p values	k'	edf
Length	0.255	31,642.73	5.45 cm	Intercept	< 2e-16 ***	Coordinates	< 2e-16 ***	463	41.66
				w	< 2e-16 ***	DBH	6.92e-07 ***	49	3.08
Width	0.159	22,825.74	19.89 cm	Intercept	< 2e-16 ***	Coordinates	< 2e-16 ***	463	36.43
				w	< 2e-16 ***	DBH	< 2e-16 ***	49	5.03
Area	0.190	53,121.72	498.89 cm ²	Intercept	< 2e-16 ***	Coordinates	< 2e-16 ***	463	49.00
				w	< 2e-16 ***	DBH	< 2e-16 ***	45.52	4.33
Relative width	0.249	- 9382.06	0.0841	Intercept	< 2e-16 ***	Coordinates	< 2e-16 ***	463	36.14
				w	< 2e-16 ***	DBH	< 2e-16 ***	49	4.56

Adj. R² adjusted R²; AIC, Akaike information criterion (Akaike, 1973); RMSE, root mean square error; k', maximum possible degrees of freedom for the term; edf, effective degrees of freedom

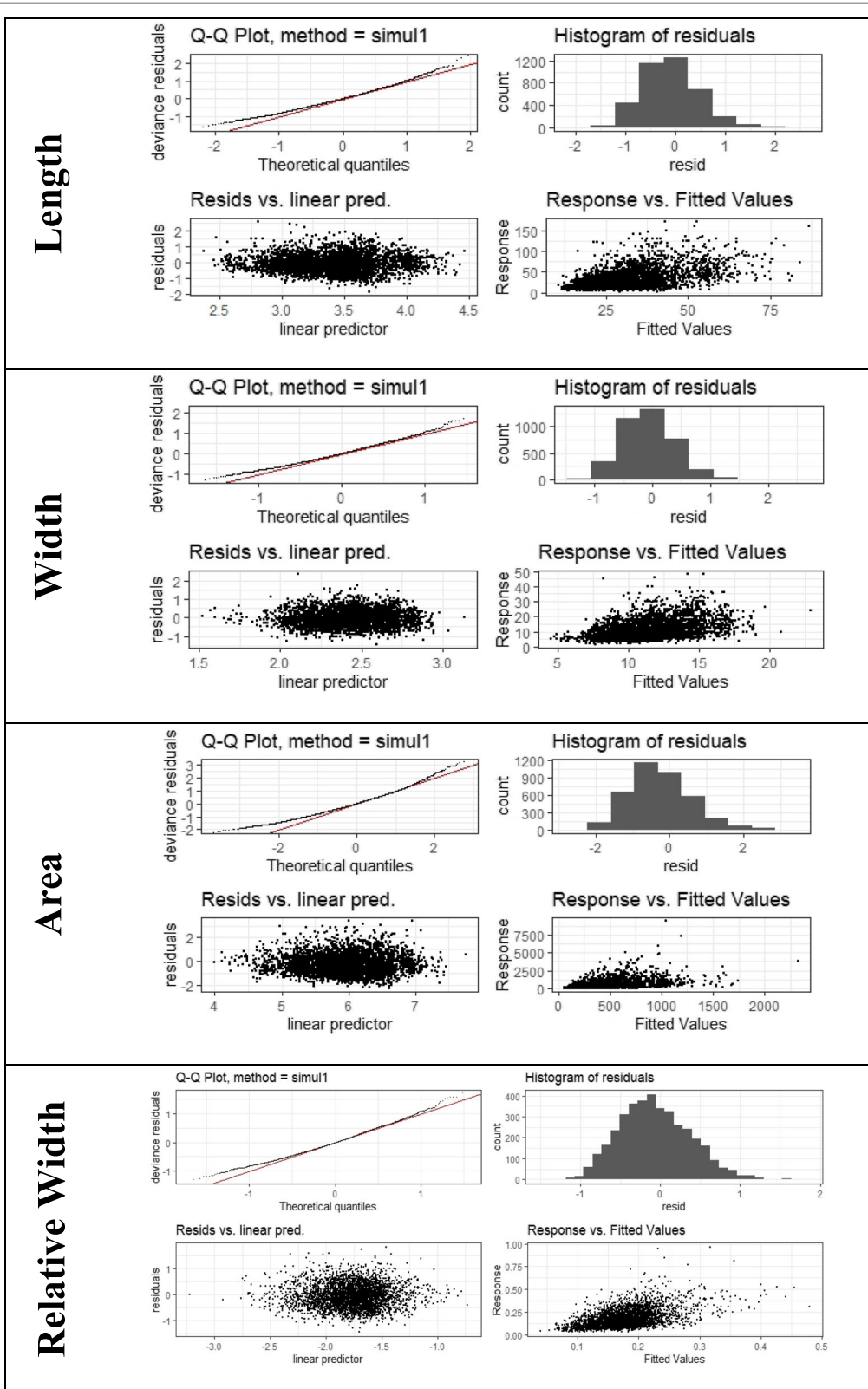
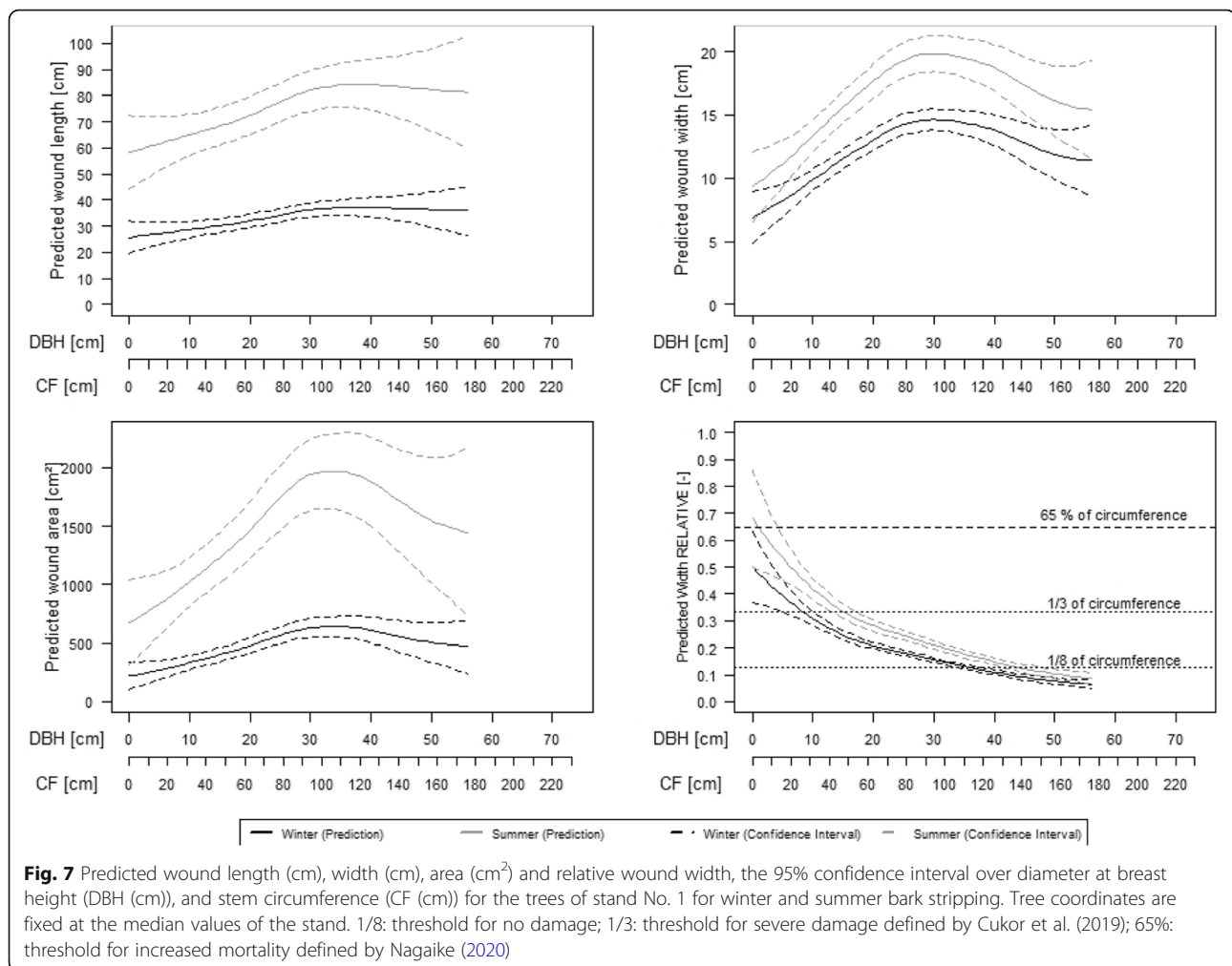


Fig. 6 Residual diagnostic plots for the final models for wound length (cm), width (cm), area (cm²), and relative width (width divided by stem circumference) created by the R-function "gam.check" of the package mgcViz (Augustin et al., 2012)



calculated as rectangular area (wound width × wound length). Wound area was calculated in the same way by Vasiliauskas & Stenlid (1998). In contrast, Arhipova et al. (2015) measured wound size directly in the field by drawing the wound area on a transparent paper and measuring the area in the laboratory with a digital planimeter. This procedure gives more precise area measurements, but was too cost-intensive in this study for the large sample size. Possibly, wound area could be determined from the laser scans, but respective classification algorithms are not yet developed. The wound area calculated in this study, however, overestimates actual wound size.

Studies reporting relative wound size report means of approximately 30% (Cukor et al., 2019a, b; Vacek et al., 2020). Our model shows that percentages of more than 1/3 are mostly observed for smaller trees. A percentage of 65% defined as threshold for increased tree mortality by Nagaïke (2020) is seldom observed in our study and mostly occurs on very small trees. Thus, we do not expect a considerably higher mortality due to bark peeling in our study area, but we expect an increased

vulnerability to drought and wind. An increased vulnerability to drought was reported by Cukor et al. (2019a, b) and Vacek et al. (2020) and is probably due to the wounding of the cambium, and we speculate that this is more closely linked to damage width which differs little between summer and winter wounds. An increased vulnerability to wind was reported by Snepsts et al. (2020) and Krisans et al. (2020) and is very probable in our study area since seven stands are located in areas which are highly prone to wind damage.

Wound size clearly differed between winter and summer bark stripping damage. This is also reported in other studies (Månsson & Jarnemo, 2013; Candaele et al., 2021). In our study, the presence of teeth marks was used to distinguish between winter and summer bark stripping. In winter, the bark is difficult to detach and is gnawed of by red deer leaving teeth marks on the stems. With the rehydration of stems in spring, the bark becomes loosely attached to the tree and can be easily peeled off by red deer resulting in larger wounds. This differentiation between the two types of wounds was in

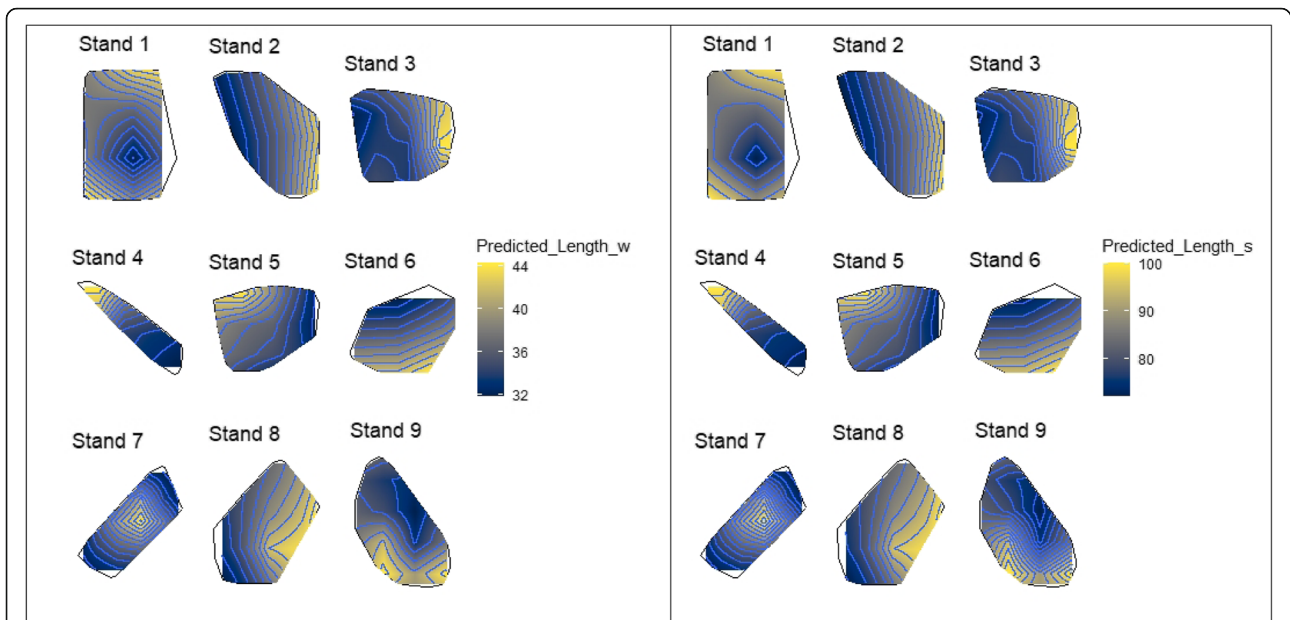


Fig. 8 Spatial distribution of the predicted wound length (cm) for summer and winter bark peeling (left: winter; right: summer) using generalized additive models (GAM) with a soap film smoother. The DBH (cm) is held fixed at the median DBH of each stand

some cases ambiguous in our study, in particular for old wounds, but many wounds could be unambiguously classified. Moreover, assessment of damage type might differ between different field teams; this was however not verified in this study. Further, identification of winter and summer wounds would be more certain, if wounds were assessed yearly, as was done in the study of Candaele et al. (2021).

Interestingly, season of wounding is reported in few wound size studies, possibly because in central Europe winter bark peeling is prevalent (Völk 1997; Månsson and Jarnemo 2013). The percentage of summer bark stripping is 20.5% in our study, which is comparable with other studies (Welch et al., 1988; Månsson and Jarnemo, 2013; Candaele et al., 2021), but percentages may vary regionally. For example, Månsson and Jarnemo

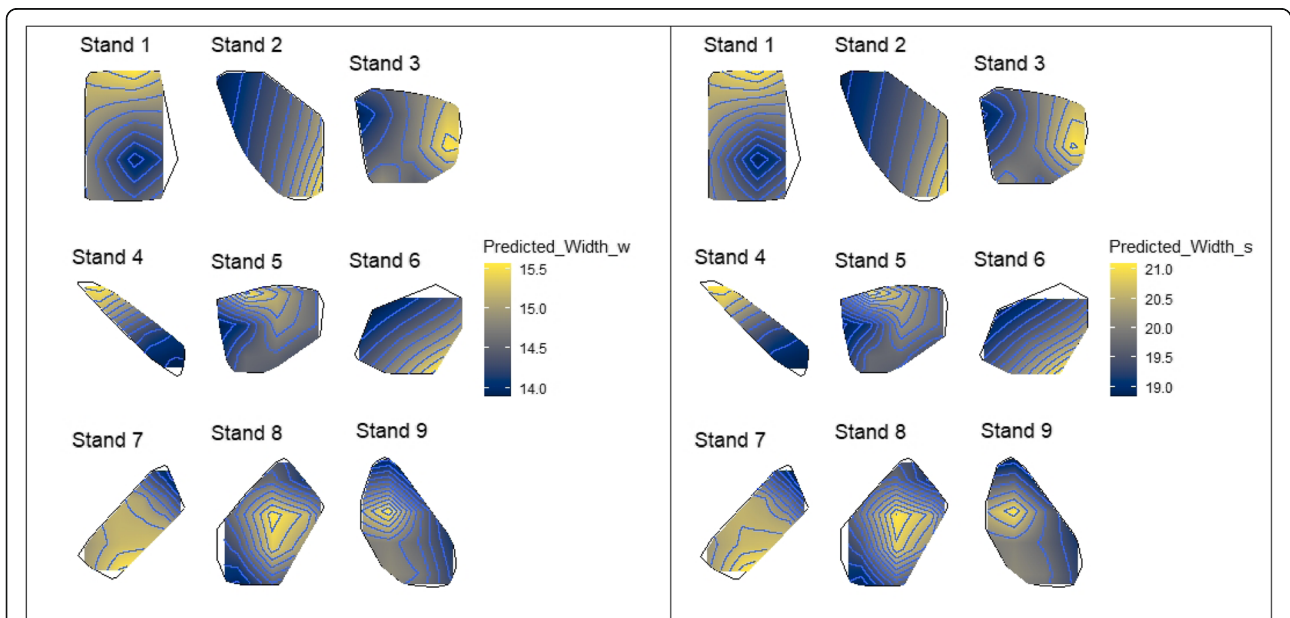


Fig. 9 Spatial distribution of the predicted wound width (cm) for summer and winter bark peeling (left: winter; right: summer) using generalized additive models (GAM) with a soap film smoother. The DBH (cm) is held fixed at the median DBH of each stand

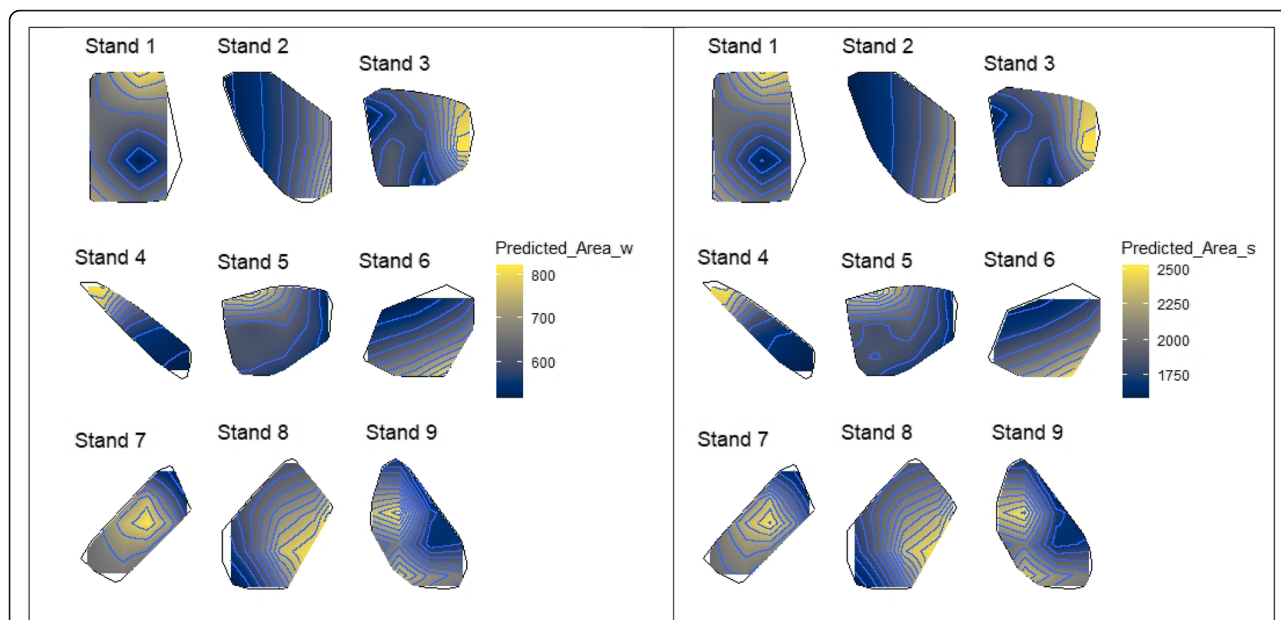


Fig. 10 Spatial distribution of the predicted wound area (cm²) for summer and winter bark peeling (left: winter; right: summer) using generalized additive models (GAM) with a soap film smoother. The DBH (cm) is held fixed at the median DBH of each stand

(2013) reported a summer bark peeling percentage of 26–28% in Southern Sweden and 1–6% in Northern Sweden.

Wounds in general (bark stripping, logging, rockfall, etc.) are entry gates for fungal colonisation (Vasiliauskas, 1998; Vasiliauskas & Stenlid, 1998). Wound infection is linearly related to wound length (Vasiliauskas & Stenlid, 1998; Arhipova et al., 2015), and the decay colon increases with the age of wounds (Čermák & Strejček, 2007). Thus, decay extent in our study will be larger for wounds inflicted in summer. Fungi isolated from the wounds are tree species specific (Vasiliauskas & Stenlid, 1998; Metzler et al., 2012; Arhipova et al., 2015). On the Norway spruce, *Stereum sanguinolentum* (Alb. & Schwein.) Fr. is the most common basidiomycete on infected wounds (Butin, 2011). This fungus is a fast-

spreading species (Čermák & Strejček, 2007), and, therefore, the Norway spruce is more affected than other tree species (Mäkinen et al., 2007; Metzler et al., 2012). Increment losses for individual trees in case of fungal infection are small for harvesting damage (Mäkinen et al., 2007), but higher increment losses are reported for bark stripping damage (Cukor et al., 2019a, b). Nevertheless, the wood devaluation through decay causes much larger economic losses. For instance, Čermák & Strejček (2007) found that the amount of decayed wood accounted for 22–70% (mean 42 %) of the merchantable stem volume.

4.2 Modelling with generalized additive models

Preferences of red deer for particular stands depend on habitat structure, silvicultural systems, and ungulate

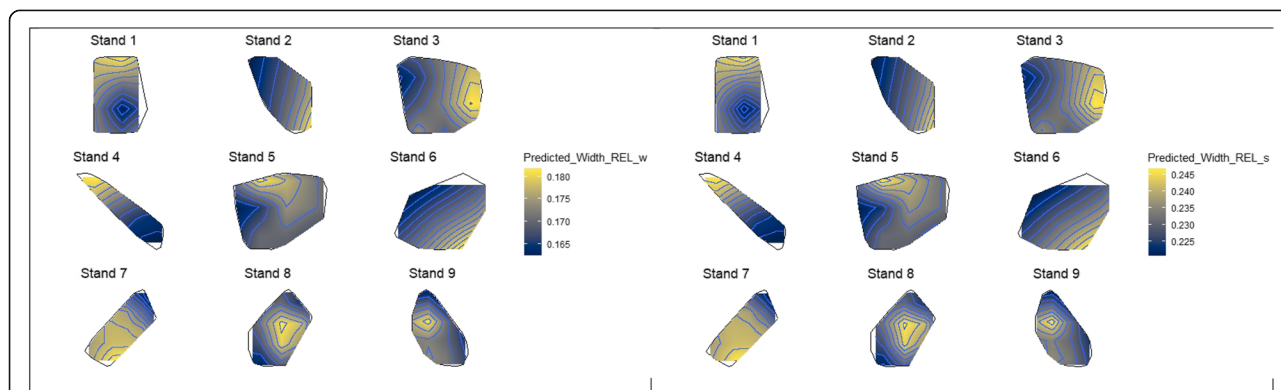


Fig. 11 Spatial distribution of the predicted relative wound width for summer and winter bark peeling (left: winter; right: summer) using generalized additive models (GAM) with a soap film smoother. The DBH (cm) is held fixed at the median DBH of each stand

dynamics. Red deer require not only food but also hiding cover and protection from climate (Reimoser & Gossow, 1996). As a result, large between-stand variations in the presence of deer and bark stripping damage have been reported in numerous studies (Gill, 1992; Vospernik, 2006; Kiffner et al., 2008; Månsson & Jarnemo, 2013). Also, within stands, there are clear dependencies of the occurrence of bark stripping dependent on a number of tree-specific variables (DBH, local density, local slope) (Hahn C, Vospernik S, Gollob C, Ritter T: Bark stripping damage by red deer (*Cervus elaphus* L.): assessing the spatial distribution on the stand level using generalized additive models, submitted). There are considerably less independent variables explaining differences in wound length, width, area, and relative wound width. As discussed above, the season of wounding is a decisive factor. In addition, only DBH and the spatial distribution are explanatory variables for size variables.

For presence/absence of bark peeling of trees, DBH is an important factor, and the presence of wounds often decreases with DBH because small trees have a more digestible bark (Gill, 1992; Kiffner et al., 2008). Similarly, studies on wound size report a smaller DBH of wounded trees than for healthy trees (Cukor et al., 2019a, b; Vacek et al., 2020).

In contrast, wound size itself initially increases with DBH. Obviously, larger wounds can only be inflicted on large-diameter trees. The decrease in older trees (DBH ~ 35 cm) might be due to wound healing and the removal of the most heavily damaged trees during the thinning of the stands. Probably the latter factor is more important since the Norway spruce has a notoriously slow wound healing rate (Vasaitis et al., 2012).

Both presence and absence of bark stripping (Hahn C, Vospernik S, Gollob C, Ritter T: Bark stripping damage by red deer (*Cervus elaphus* L.): assessing the spatial distribution on the stand level using generalized additive models, submitted) and wound size are spatially aggregated. In our study, these patterns can mainly be related to the vicinity of disturbances and forage (feeding sites) and local preferences for hiding cover. Red deer are sensitive animals and avoid disturbances and are usually not found close to forest roads (Kiffner et al., 2008) (Hahn C, Vospernik S, Gollob C, Ritter T: Bark stripping damage by red deer (*Cervus elaphus* L.): assessing the spatial distribution on the stand level using generalized additive models, submitted) or human activities (Kiffner et al., 2008). The spatial patterns revealed in this study for wound size, however, do not show a clear dependence on the proximity to forest roads.

Furthermore, the location of forest stands close to winter feedings has been reported as an important factor for bark peeling damage (Putman and Staines, 2004; Kiffner et al. 2008; Sun et al. 2020) (Hahn C, Vospernik

S, Gollob C, Ritter T: Bark stripping damage by red deer (*Cervus elaphus* L.): assessing the spatial distribution on the stand level using generalized additive models, submitted). The animals aggregate close to the feeding stations at high densities, causing severe damage in the vicinity. Usually, these effects are reported for the presence/absence of bark peeling damage. In our study, a similar effect has been observed for wound size. So not only do the occurrence of wounds increase in the vicinity of feeding stations but also the wound size. This may be due to repeated debarking of the same tree, which has been reported in other studies (Gill, 1992; Arhipova et al., 2015; White, 2019; Nagaike, 2020). In the field assessment, it might not be possible to distinguish this multiple debarking damages, and they may thus be recorded as larger wound size. Because of the high damage rates close to supplementary feedings, it has been much debated in forestry practice and in the scientific literature if supplementary feedings are an appropriate measure to reduce environmental damage (e.g. see Putman & Staines (2004)).

Local preferences of red deer seem to be an important factor in our study, and patterns of wound size clearly differ spatially, with average wound size differences of several centimetres. Such aggregated patterns have been reported for the occurrence of damage (Gill, 1992) and are also found for wound size. It remains however unclear what the causal factors are. Factors that might explain spatial patterns could be hunting regime or population and foraging properties or winter snow cover. The first two factors are however rather homogenous in the investigating stands; for the latter factor, the within-stand variation is not known on a local scale for the studied stands. The multitude of possible influencing factors and their impact has been reviewed by Gill (1992) and more recently by Gerhardt et al. (2013).

5 Conclusion

This study has important implications for silviculture of bark stripping damaged stands and the assessment of bark stripping in forest inventories.

- The high rates of bark stripping in stands and the large wound sizes found in this study in conjunction with results from other studies that report that the spread of rot is linearly related to wound length suggest high economic losses in the investigated stands and in similar stands in Austria. For the pole stands already stripped, heavy thinning interventions and a short rotation of stands might help to reduce economic losses by reducing damage rates by selectively removing the most damaged trees. Thinning might however not be an efficient tool to

reduce damage rates, when damages are clustered, which is shown in this study. Further, it remains unclear what thinning rate to select. Conventional thinning in Austria removes 10–20% of the standing volume, and thinning rates of more than 30% in Norway spruce would result in stand growth reductions. Detailed knowledge of the spatial distribution of damage and damage sizes forms the basis for detailed growth and yield scenario analysis to manage bark-stripped stands; also, information on growth reductions in damaged trees would need to be included.

- To avoid game damage in young stands, reducing the cover of forest stands through increased spacing and admixtures of deciduous species might be an important strategy. An important and probably contributing within-stand factor that is hard to assess is the distribution of within-stand snow cover, which might cause spatial aggregation of red deer in winter.
- The high economic losses through bark stripping and the following infection with wood destroying fungi cause conflicts between forest managers and hunters. An effective and objective damage assessment can therefore provide important information to settle disagreements. Because of the high costs of forest inventories, the design should also be efficient for the detection of bark stripping damages. Our study showed that the damages are not only clustered between stands but also within stands, which needs to be accounted for in forest inventory designs. The knowledge that wounds are mainly found on the uphill side of the stems also needs to be incorporated in forest inventories.

Acknowledgements

We are thankful to the forest company Wasserberg/Stift Heiligenkreuz, and in particular to P. Coelestin Klemens Nebel *OCist.* for the opportunity to make the measurements for our study on their sites and for their support. We thank Ralf Krassnitzer, Franz Gollob, and Philipp Walzl for the careful fieldwork.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability

Not applicable.

Authors' contributions

Conceptualization was done by CH and SV. Methodology was done by CH and SV. Formal analysis was done by CH, SV. Data curation was done by CH and SV. Writing—original draft was done by CH and SV. Writing—review & editing was done by CH and SV. The authors read and approved the final manuscript.

Declarations

Ethics approval and consent to participate

The authors declare that they follow the rules of good scientific practice.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no conflict of interest.

Received: 27 August 2021 Accepted: 14 February 2022

Published online: 24 March 2022

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