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Vertical stratification and microhabitat selection by the Great Capricorn Beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks

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Abstract. The great capricorn beetle or Cerambyx longicorn (*Cerambyx cerdo*, Linnaeus, 1758) is an internationally protected umbrella species representing the highly diverse and endangered fauna associated with senescent oaks. For the conservation and monitoring of populations of *C. cerdo* it is important to have a good knowledge of its microhabitat requirements. We investigated determinants and patterns of *C. cerdo* distribution within individual old, open-grown oaks. Trees inhabited by this species were climbed, and the number of exit holes and environmental variables recorded at two sites in the Czech Republic. Distribution of exit holes in relation to height above the ground, trunk shading by branches, orientation in terms of the four cardinal directions, diameter, surface and volume of inhabited tree parts were investigated. This study revealed that the number of exit holes in the trunks of large open-grown oaks was positively associated with the diameter of the trunk and openness and negatively with height above the ground, and the effects of diameter and openness changed with height. The number of exit holes in the surface of a trunk was also associated with the cardinal orientation of the surface. Approximately half of both *C. cerdo* populations studied developed less than 4 m and approximately a third less than 2 m above the ground. This indicates that most *C. cerdo* develop near the ground. Active management that prevents canopy closure is thus crucial for the survival of *C. cerdo* and searching for exit holes is an effective method of detecting sites inhabited by this species.

INTRODUCTION

Organisms associated with old trees and dead wood are among the most diverse and endangered elements of European biodiversity (Berg et al., 1994; Davies et al., 2008). Many highly endangered species are associated with senescent, open-grown trees of large diameter, especially oaks (e.g. Ranius & Jansson, 2000; Ranius, 2002; Buse et al., 2008a; Skarpaas et al., 2011). Such trees used to be common and an indispensable element in European landscapes in the past, e.g., open pasture woodlands and coppices with standards. Modern intensification of land use, however, has resulted in the loss of such trees from the landscape due to increased canopy closure in commercial as well as protected woodlands and removal of old trees from farmed areas (e.g. Warren & Key, 1991; Rackham, 1998; Vera, 2000).

The great capricorn beetle (*Cerambyx cerdo*, Linnaeus, 1758) is one of the largest longhorn beetles living in Europe. It acts as an ecosystem engineer (Buse et al., 2008b) and, together with the stag beetle (*Lucanus cervus* Linnaeus, 1758) serve for the general public and legislature as umbrella species representing a diverse and highly endangered fauna associated with old oaks (Buse et al., 2008a; Ducasse & Brustel, 2008). Apart from being protected and/or red-listed in many European countries (Jäch, 1994; Geiser, 1998; Witkowski et al., 2003; Farkač et al., 2005; Jurc et al., 2008), *C. cerdo* is explicitly protected under the EU Habitats Directive (Council of the European Communities, 1992), classified as globally vulnerable according to the IUCN Red List of Threatened Species (IUCN, 2007) and is nearly a threatened species in Europe (Nieto & Alexander, 2010). *C. cerdo* occurs in most of Europe, the whole Mediterranean region and the Caucasus (Bílý & Mehl, 1989; Sláma, 1998; Sama, 2002). It is common in the south but rare and rapidly declining in the northern part of its range (e.g. Sláma, 1998; Ehnström & Axelsson, 2002; Starzyk, 2004; Jurc et al., 2008; Ellwanger, 2009). It is extinct in the United Kingdom (Alexander, 2002).

Larvae of *C. cerdo* develop mainly in the trunks, but also branches and roots of oaks (*Quercus* spp.); other species of trees are occasionally used, including e.g. chestnut (*Castanea sativa*), and probably also elm (*Ulmus* spp.) and common walnut (*Juglans regia*) (Sláma, 1998). Larval development takes three or more years (Sama, 2002). Adults are 24 to 53 mm long and active from May to August, peaking in June and early July, when the beetles are most active at dusk feeding on the sap of old trees (Heyrovský, 1955; Sláma, 1998). Occupied trees can be identified by typical oval exit holes up to 20 mm wide on the trunk or thick branches; typical signs of recent activity include wood meal and fresh exit holes the interior walls of which are a red colour (Buse et al., 2007). This beetle prefers old, sun exposed trees (Sláma, 1998; Buse et al., 2007). Tree vitality, age, thickness of bark, trunk diameter, distance to the next colonized tree and trunk insolation increase the probability of the occurrence of *C. cerdo* (Buse et al., 2007).

Whereas the determinants of the distribution of *C. cerdo* in a landscape and among trees are described (Buse et al., 2007; 2008b) little is known about the factors affecting its distribution within individual trees. Such information is, however, crucial for the conservation of this species and for monitoring its populations. If the beetle prefers tree tops, it is likely to survive in closed canopy oak stands, often undetected. If, on the other hand, the majority of a population inhabits the lower parts of trunks, the presence of *C. cerdo* would be easy to detect and inhabited sites would need to be actively managed. We therefore investigated the distribution of *C. cerdo* exit holes in old open-grown oaks in relation to: (i) Height above the ground, (ii) shading, (iii) cardinal orientation and (iv) diameter of the parts of the trunk inhabited.

METHODS

Study sites

This study was conducted in southern and central Bohemia (western part of the Czech Republic) in parkland-like woodlands with old, open-grown oaks. Two sites were surveyed, Hluboka nad Vltavou and the Lanska Game Reserve. The Hluboka site is located in south-western Czech Republic, 115 km S of Prague (49°2´N, 14°26´E, 380 m a.s.l.) in the Budejovicka Basin, near the river Vltava. The bedrock consists of sandstone, puddingstone and clay-stone. Mean annual temperature is 7.1°C and mean annual rainfall nearly 659 mm. The study took place in system of alleys of trees and wooded meadows (recently converted into a golf-course) with open-grown oaks of up to 200 years old (max DBH ~160 centimetres) (Hauck & Cizek, 2006). The locality is protected as a Site of Community Importance (total area: 67.2 ha), with *C. cerdo* as one of its target species. It hosts numerous saproxylic species associated with old oaks. The second site, the Lanska Game Reserve, is located 40 km W of Prague (50°5´N, 13°55´E; 300–461 m a.s.l.) in the Krivoklatsko Protected Landscape Area and UNESCO Biosphere Reserve. This is an upland area with deep valleys with bedrock consisting of slate mainly covered by cambisol and partly by gley. Mean annual temperature is 8.2°C and mean annual rainfall nearly 590 mm. The game reserve (total area 3,000 ha) mostly consists of beech and oak-hornbeam forests, patches of planted conifers and several meadows and pastures with scattered old oaks (*Quercus robur*). The site is a local saproxylic biodiversity hot-spot (Horák & Rébl, 2012).

Sampling design

Trees with *C. cerdo* exit holes and currently inhabited by the species (i.e. with larval frass on the bark and/or at the base of the tree) were surveyed. For safety reasons and also to avoid the effect of larval activity on the environmental conditions biasing the results, the trees climbed were relatively healthy (most of the tree alive, tree top not completely dead) and probably not inhabited by *C. cerdo* for longer than one or two decades (Kletečka & Klečka, 2003). Each tree surveyed was divided into 2 meter long vertical sections (0–2 m above the ground, 2–4 m, 4–6 m, 6–8 m ... up to 14 m). Each vertical section was divided into four trunk segments according to their orientation (North, East, South or West). Trees were climbed using the two-rope climbing technique. Environmental variables and number of *C. cerdo* exit holes were recorded for each segment of trunk. Exit holes were counted; height of each tree, and diameter in the middle of each 2 m vertical section were measured. Estimates of the outer surface and volume of wood in each segment of trunk segment were based on its diameter. Orientation (cardinal direction of the segment) was identified using magnetic compass (North, East, South, West).

Variables

Eight explanatory variables were used: (i) Height – mean vertical height in meters of a 2 m long section of trunk from the ground, ranging from 1 to 13 m (1 – sections 0–2 m above the ground, 3 – 2–4 m, 5 – 4–6 m etc.). Continuous. (ii) Openness – shading of each segment by the branches or crowns of surrounding trees or shrubs on a scale of 1–5 (1 – fully shaded; 2 – mostly shaded, 3 – half shaded, 4 – mostly exposed, 5 – fully exposed). Continuous. (iii) Diameter – diameter in centimetres at the middle of each vertical section of trunk. Continuous, in centimetres. (iv) Surface area – surface of each segment of trunk in square centimetres. Continuous. (v) Volume of wood – volume of each segment of trunk in cubic centimetres. Continuous. (vi) Orientation – cardinal direction of each segment of trunk (North, East, South or West). Categorical: (vii) Tree – serial number of the tree and (viii) Site – location of study area (Lanska obora or Hluboka nad Vltavou).

The response variables were the number and density of *C. cerdo* exit holes in each segment of trunk. The density was the number of exit holes divided by the area of each segment of trunk (in m^2, analysis 2, see below), or volume (in m^3, analysis 3, see below) of each trunk segment. All response variables were continuous.

Analyses

Three analyses were carried out using R 2.7.2 (Maindonald & Braun, 2003), in which the association between the number of exit holes and their density per m^2 and per m^3, and environmental variables was investigated using multiple LME (Linear mixed-effect models) (Crawley, 2007; Zurr et al., 2009). In the first analysis, the number of *C. cerdo* exit holes on each segment of trunk was the response variable. The height, diameter, openness and orientation of each segment of trunk were fixed effect variables and the tree a random effect variable. Surface area ($r_s = 1$) and volume of wood ($r_s = 1$) were not included in the final model because of their strong multicollinearity with diameter (tested using Spearman rank correlation). The final model investigated the association between the number of exit holes and the height, diameter, openness, orientation and interactions of height and diameter, and height and openness. In the second analysis, the density of exit holes per m^2 was the response variable. This was done in order to correct for differences in sampling effort, i.e. the lower segments of trunks have the largest diameter and greatest surface areas. The height, openness and orientation were fixed effect variables and the tree a random effect variable. In the third analysis, the density of exit holes per m^3 was the response variable. The height, openness and orientation were fixed effect variables the tree a random effect variable. In all analyses, the response variable was Poisson distributed as it was transformed using a ln(number of exit holes + 1) transformation in order to achieve the normal distribution required by LME. The best models and order of variables were chosen using AIC (Akaike's Information Criterion, Akaike, 1974). Models were fitted using the ML method (maximum likelihood). The relationships among variables were investigated in order to identify strong correlations between pre-

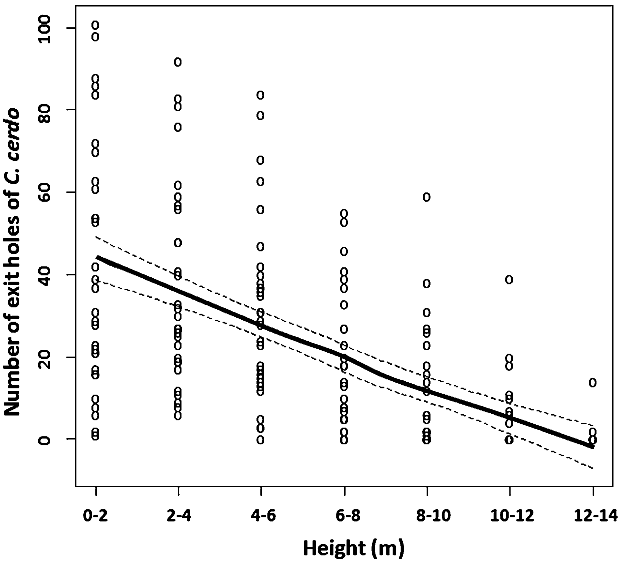

Fig. 1. Vertical stratification of the exit holes of the great capricorn beetle (*Cerambyx cerdo*) on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic (both sites combined). Depicted as number of *C. cerdo* exit holes in 2 m long sections of trunk at particular heights.

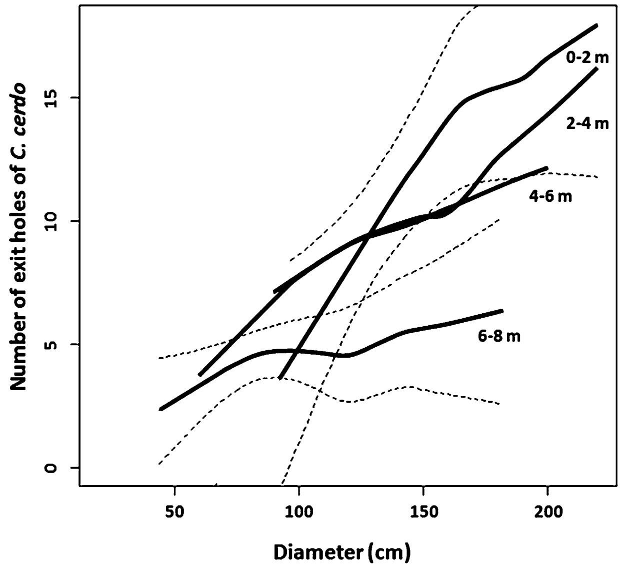

Fig. 2. The effect of trunk diameter on relationship between the number of exit holes of the great capricorn beetle (*Cerambyx cerdo*) at particular heights on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic (both sites combined). Solid lines show the relation between trunk diameter and number of exit holes in 2 m long section of trunk at a particular height; dashed lines show 95% CI for the 0–2 m and 6–8 m heights.

dictors. The final models were fitted using the REML method (restricted maximum likelihood). All the vertical trunk segments measured were included in the analyses.

The association between the number of exit holes and site was tested using LME. The response variable was transformed using a ln(number of exit holes + 1) transformation. The site was the fixed effect variable and tree a random effect variable. The association between height of tree and tree diameter (at a height of 1 m) and site was investigated using ANOVA.

Charts showing the relationships between the number of exit holes of *C. cerdo* and given variables (Figs 1–3) were created using LOESS (locally weighted scatter plot smoothing) function in the R 2.7.2.

RESULTS

In total, 30 oaks were climbed (22 in the Lanska Game Reserve and eight at Hluboka nad Vltavou), data on 169 vertical trunk sections and 676 trunk segments were collected and 4259 exit holes of *C. cerdo* were recorded. Mean height and diameter (at 1 m above the ground) with standard deviation (*SD*) of trees were 10.5 m (± 2.1) and 127 cm (± 10.9), respectively, at the Hluboka site, and 11.5 m (± 2.5) and 142 cm (± 36.1) at the Lány site. Site had no effect on number of exit holes ($F_{1, 28}$ = 0.80; P > 0.05), tree diameter ($F_{1, 28}$ = 1.41; P > 0.05) or tree height ($F_{1, 28}$ = 1.14; P > 0.05). All the trees were taller than 6 m; number of tree sections investigated at a given height, and vertical distribution of exit holes is given for both sites separately and combined (see Table 1). Mean number of exit holes at a given height was calculated as the number of all exit-holes in all the sections at a given height/number of tree sections investigated at that height (Table 1). Density of exit holes at different heights was the number of exit holes in a given 2 m long trunk section divided by the area of bark on that section (Table 1). Numbers of exit holes were similar on East (Mean 27.7; SD ± 26.6) and North (26.9; ± 28.3) facing segments, and also on South (43.1; ± 36.8) and West facing segments (44.3; ± 37.7).

Table 1. Vertical distribution of the exit holes of the great capricorn beetle (*Cerambyx cerdo*) on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic. (a – both sites combined, b – Hluboka, c – Lanska). * number of all exit-holes at a given height/number of trees; ** number of exit-holes per m^2 of bark surface at a given height/number of trees.

Meters above the ground	Number of trees (**a**; b; c)	Total (relative) number of exit holes recorded (**a**; b; c)	Mean number* (relative), median and SD of number of exit holes (a)	Mean density**, median and SD of density of exit holes (a)
0–2	**30**; 8; 22	**1253 (29.4%)**; 386 (28.3%); 867 (29.9%)	41.8 (27.9%); 34; 29.4	4.7; 3.8; 3.1
2–4	**30**; 8; 22	**1114 (26.2%)**; 349 (25.6%); 765 (26.4%)	37.1 (24.8%); 28,5; 22.1	4.8; 3.9; 3.1
4–6	**30**; 8; 22	**944 (22.1%)**; 296 (21.7%); 648 (22.4%)	31.5 (21%); 30; 20.3	4.7; 4.2; 3.3
6–8	**29**; 8; 21	**526 (12.4%)**; 140 (10.3%); 386 (13.3%)	18.1 (12.1%); 14; 15.9	3.4; 2.5; 3.1
8–10	**24**; 6; 18	**291 (6,8%)**; 118 (8.7%); 173 (6%)	12.1 (8.1%); 5.5; 11.7	2.9; 1.2; 4.2
10–12	**17**; 3; 14	**115 (2,7%)**; 59 (4.3%); 56 (1.9%)	6.8 (4.5%) 0; 6.8	2.4; 0; 4.4
12–14	**9**; 1; 8	**16 (0.4%)**; 14 (1%). 2 (0.1%)	2.1 (1.4%); 0; 0.7	1.1; 0; 3.2

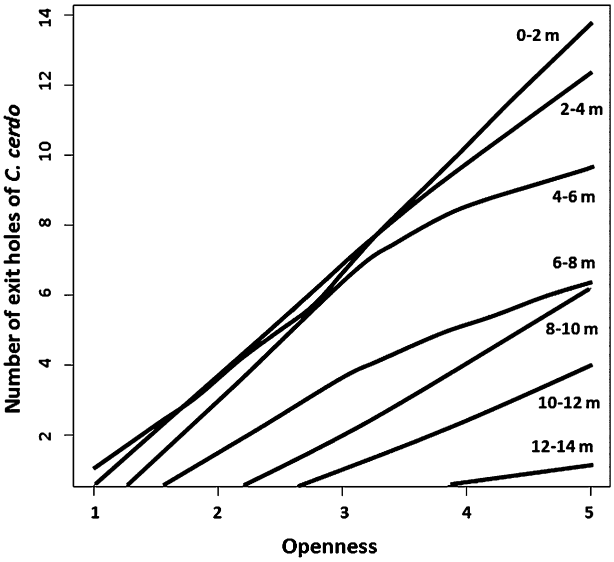

Fig. 3. Effect of openness on the number of exit holes of the great capricorn beetle (*Cerambyx cerdo*) changes with height on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic (both sites combined). This is depicted in terms of the number of exit holes in 2 m long segments of trunk and openness of the environment. 1 – fully shaded; 2 – mostly shaded, 3 – half shaded, 4 – mostly exposed, 5 – fully exposed.

In the first analysis with the number of exit holes as a response variable, the Linear mixed-effect model (LME) (Table 2) revealed that the number of exit holes in a trunk segment was negatively affected by the height of the segment from the ground (Fig. 1), and positively affected by its diameter (Fig. 2) and openness (Fig. 3). The effect of orientation was significant; the effect of diameter and openness on number of exit holes changed with height (Figs 2, 3). In the second and third analyses, the Linear mixed-effect model (LME) (Table 2) revealed that the number of exit holes per m^2 and per m^3 were negatively affected by the height above the ground and positively by openness; the effect of orientation was significant (Table 2).

DISCUSSION

This study revealed that the larvae of *Cerambyx cerdo* occur mainly in sun-exposed parts of large diameter of large, open-grown oaks, especially those near the ground and facing west or south. Previous studies of the habitat preferences of *C. cerdo* at the landscape and between-tree levels indicate that its distribution is affected by tree vitality, age, bark thickness, trunk diameter, insolation and habitat openness (Buse et al., 2007). Similar variables thus influence *C. cerdo* distribution within individual trees and at larger scales.

TABLE 2. Environmental characteristics affecting the distribution of exit holes of the great capricorn beetle (*Cerambyx cerdo*) on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic. Model 1 predicts the association between the number of exit holes and the environmental variables and some of their interactions (Linear mixed-effect model). Model 2 predicts the association between the density of exit holes per m^2 of bark surface and the environmental variables. Model 3 predicts the association between the density of exit holes per m^3 of wood and the environmental variables (Linear mixed-effect model). The final models include all the variables and interactions cited below (Model 1 null deviance = 0.602, residual deviance = 1.007; Model 2 null deviance = 0.524, residual deviance = 0.691; Model 3 null deviance = 0.854, residual deviance = 1.132).

	Regression coefficient *b*	SE	*d.f.*	*F*	*P*
Model 1					
Intercept	–0.902	0.500	1, 638	156.022	< 0.0001
Height	–0.027	0.044	1, 638	276.715	< 0.0001
Diameter	0.380	0.004	1, 638	14.929	< 0.0001
Openness	0.552	0.075	1, 638	114.699	0.0001
Orientation	–	–	3, 638	7.647	< 0.0001
North	0.064	0.085	–	–	–
South	0.248	0.085	–	–	–
West	0.353	0.085	–	–	–
Height : Diameter	0.001	0.001	1, 638	10.092	0.0016
Height : Openness	–0.024	0.010	1, 638	6.485	0.0111
Model 2					
Intercept	0.151	0.180	1, 641	128.939	< 0.0001
Height	–0.072	0.008	1, 641	128.300	< 0.0001
Openness	0.347	0.032	1, 641	122.944	< 0.0001
Orientation	–	–	3, 641	6.284	< 0.0001
North	0.057	0.076	–	–	–
South	0.205	0.076	–	–	–
West	0.293	0.076	–	–	–
Model 3					
Intercept	0.021	0.293	1, 641	138.477	< 0.0001
Height	–0.082	0.013	1, 641	74.835	< 0.0001
Openness	0.594	0.053	1, 641	133.606	< 0.0001
Orientation	–	–	3, 641	4.411	0.004
North	0.079	0.124	–	–	–
South	0.250	0.123	–	–	–
West	0.410	0.123	–	–	–

Trunk diameter is generally recognised as a key determinant of saproxylic beetle diversity (Ranius & Jansson, 2000; Ranius, 2002; Buse et al., 2008b; Foit, 2010) and an important factor affecting the presence of *C. cerdo* at both sites studied (Hauck & Cizek, 2006; Sreiber, 2010). Large trees are old and less vigorous, and offer a wide variety of longer lasting and a greater volume of dead wood microhabitats (Warren & Key, 1991; Irmler et al., 1996; Siitonen et al., 2000; Lindhe & Lindelöw, 2004; Radu, 2006) and thus better conditions for the development of *C. cerdo* larvae.

Effect of solar radiation

Both openness and orientation affect the amount of solar radiation reaching the trunk. The higher number of exit holes on those parts of trunks facing south and west could thus be explained by their higher heat intake. This accords with the fact that *C. cerdo* is a thermophilous species in Central Europe (Buse et al., 2007). Preference of xylophagous and saproxylic insects for sun-exposed wood is common and is discussed elsewhere (Ranius & Jansson, 2000; Kappes & Topp, 2004; Moretti et al., 2004; Lindhe et al., 2005; Vodka et al., 2009; Horak et al., 2011).

The change in effect of openness (i.e. solar radiation) with height does not mean that this beetle exhibited a lower light requirement higher up the trunks of the trees. It is an artifact of this beetle's preference for those parts of the trunk and branches with the greatest diameters. Since the branches and stems near the tops of trees are mostly thin, the numbers of exit holes high in a tree are generally low (see above). In addition, oak branches and stems are rarely fully shaded near tree tops (mostly they were half or not shaded in this study) and, therefore, the openness gradient is shorter.

There is an interesting pattern in the distribution of exit holes in those parts of the trunk facing the four cardinal directions. Numbers of exit holes on the west and south facing sides were similar, although the south facing side receives more heat than the west side (Allen et al., 2006, Zeleny & Chytry, 2007). Also, the numbers of exit holes were similar on the north and the east facing sides, although the latter receive more heat (cf. Zeleny & Chytry, 2007). This may be explained by the fact that the peak activity of *C. cerdo* adults occurs late in the evening in June (Bílý & Mehl, 1989). At this time, the west oriented part of trunks are the warmest as they accumulate heat during most of the afternoon, when even north facing parts are exposed to solar radiation (Allen et al., 2006). Thus *C. cerdo* females might oviposit on those parts of the trunk that are warmest when they are active rather than those parts that receive the highest heat intake during the whole day, which would most benefit the larvae (Sláma, 1998). On the other hand, larvae often migrate under the bark and/or in the inner parts of the trunk for distances of up to several decimetres. Thus an exit hole indicates where pupation rather than ovipositon occurred. The observed pattern is probably a result of the preferences of both ovipositing females and larvae.

Activity of *C. cerdo* larvae often results in the gradual death of the whole or parts of inhabited trees. It is true that larval activity in causing the death of nearby branches is likely to increase the amount of solar radiation reaching the trunk. The observed relation between the number of exit holes and openness thus could be due to larval activity. The effect of the orientation towards cardinal directions and habitat openness at a larger scale (Buse et al., 2007), however, show that the amount of solar radiation affects the distribution of *C. cerdo* exit holes.

Vertical stratification

The number and density of *C. cerdo* exit holes decreased with height. At both study sites, about half of the population developed in those parts of trunks between 0–4 m above the ground and approximately a third in those parts less than 2 m above the ground. This is an important result, indicating that the bulk of the *C. cerdo* population develops near the ground. This is useful information when monitoring and estimating the size of *C. cerdo* populations inhabiting open-grown old oaks.

Lower parts of trunks are of larger diameter with a greater area of bark and a greater volume wood than the upper parts. This, however, does not fully explain the vertical stratification of exit holes, as exit-hole density decreased with height even when bark area and wood volume were accounted for in the analyses. Thus this beetle prefers the lower parts of trunks for reasons other than the resources available to the larvae. Despite the preference for the lower parts of trunks, *C. cerdo* diameter requirements seemed to decrease with height, as indicated by the effect of the interaction. Previous inventories of trees inhabited by this beetle demonstrate that at both the sites studied *C. cerdo* nearly never inhabits trees with DBH <80 cm (Hauck & Cizek, 2006; Sreiber, 2010). We recorded exit holes also on much thinner parts of the trunk high above ground. This agrees with the fact that its larvae feed in the wood of weakened trees (see above) and thus often develop in oaks of much smaller diameters at sites where tree growth is slower.

C. cerdo preference for lower, insolated parts of tree trunks may explain the decrease in the abundance of this species during the last century (Sláma, 1998; Buse et al., 2007, 2008b). Transition of forest pastures, coppices and coppices with standards into high, closed-canopy forests (Warren & Key, 1991; Rackham, 1998; Vera, 2000) affected this beetle in two ways. Firstly, it decreased habitat quality by shading the bases of suitable trees. Secondly it led to gradual disappearance of the habitat, i.e. open-grown oaks that are most likely to reach the trunk diameters required by this species.

C. cerdo prefer the trunks of large, open-grown oaks, especially the sun-exposed parts of the west and south facing sides of the lower parts of the trunks. Our results also suggest that the bulk of the *C. cerdo* populations develop near the ground. Searching for exit holes is thus an effective method of detecting sites inhabited by this species and active management preventing canopy closure is thus crucial for the survival of *C. cerdo*.

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