

| | | | | |
|--|----|---|---------|------|
| POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.) | 55 | 2 | 315–323 | 2007 |
|--|----|---|---------|------|

Regular research paper

Andrzej OLEKSA¹, Werner ULRICH², Robert GAWROŃSKI³

¹ Institute of Biology and Environmental Protection, University of Kazimierz Wielki, Chodkiewicza 30, PL-85-064 Bydgoszcz, Poland, e-mail: olek@ukw.edu.pl

² Department of Animal Ecology, Nicholas Copernicus University, Gagarina 9, PL-87-100 Toruń, Poland, e-mail: ulrichw@uni.torun.pl (*corresponding author*)

³ Ostródzka 4/5, Kasprowicza 8, PL-14-300 Morąg, Poland, e-mail: robgaw@poczta.fm

HOST TREE PREFERENCES OF HERMIT BEETLES (*OSMODERMA EREMITA* SCOP., COLEOPTERA: SCARABAEIDAE) IN A NETWORK OF RURAL AVENUES IN POLAND

ABSTRACT: The occurrence of *Osmoderma eremita* (Scopoli, 1763), an endangered species restricted to hollow trees, was studied in a network of rural avenues in northern Poland. We detected 1002 trees with hollows suitable for hermit beetle development (25% of all trees). Among them, 114 (11%) were occupied by *O. eremita*. The distribution of *O. eremita* was not random with respect to tree species identity. *Tilia cordata* and *Alnus glutinosa* were preferred while *Acer platanoides* and *Carpinus betulus* were avoided. The beetle preferred trees about 450 cm in circumference at 1.3 m height with a tendency towards lower occupancies of the biggest trees having circumferences above 500 cm. *O. eremita* did not show any significant preferences according to hollow entrance area, exposition and road surface type. Contrary to common belief *O. eremita* did not prefer oaks. Our results show that preservation schemes and choices of prime areas for conservation for hermit beetles have to include stands of trees other than oak.

KEY WORDS: Coleoptera, *Osmoderma eremita*, saproxylic beetles, *Tilia cordata*, *Quercus robur*, hollow trees

1. INTRODUCTION

The European hermit beetle *Osmoderma eremita* has, like many other saproxylic

species (Speight 1989), restricted habitat requirements. It was a typical species of old-growth deciduous forests but has declined due to habitat loss and intensive forest management, which reduced the number of trees with hollows necessary for larval development (Speight 1989, Eliasson and Nilsson 2002). Today's middle European forests contain too few hollow trees to sustain viable populations. Therefore the species now depends on refuges outside forests. For example, in Sweden hermit beetles mainly occur in pasture woodlands dominated by oak (Ranius and Jansson 2000). In western France one of the major refuges for *O. eremita* are networks of hedgerows (Vignon and Orabi 2003). Similarly, in northern Poland the beetle has mainly been found in old trees planted along roads in open rural landscapes (Oleksiak *et al.* 2003).

The hermit beetle is regarded as being highly endangered over its entire distributional range (Luce 1996, Schaffrath 2003a, b). It is included in the IUCN Red List of threatened species as facing a high risk of extinction (IUCN 2004) and is protected in the EU countries according to the Bern Convention and as a priority species in Annex II of the Habitat Directive. The presence of

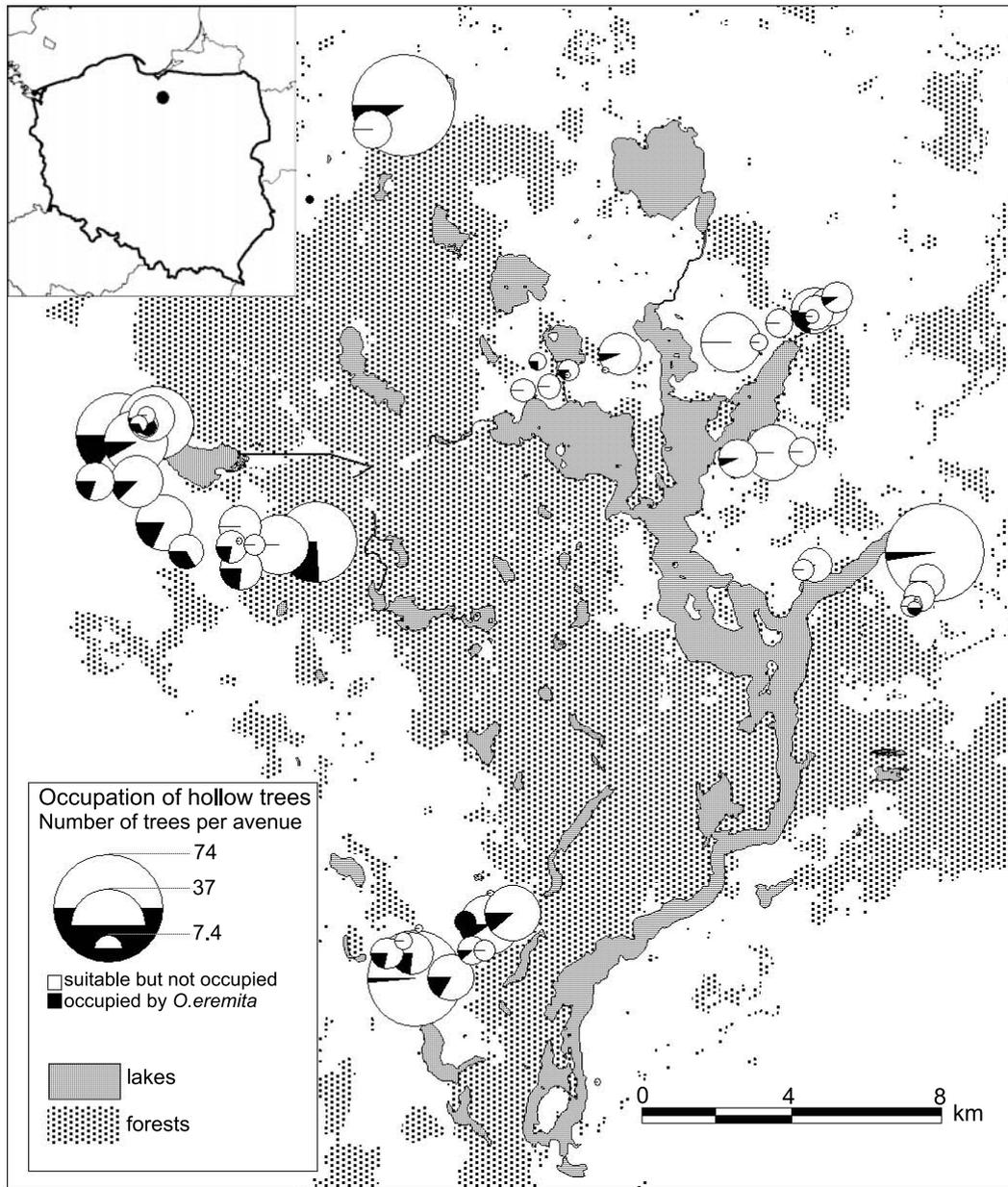


Fig. 1. The study area, number of trees per avenue and % of hollow trees occupied by *Osmoderma eremita*.

O. eremita qualifies for site preservation as a Special Area of Conservation within the “Natura 2000” network. A better knowledge of its habitat requirements and its spatial distribution might therefore be an important element for the regional establishment of prime areas for conservation in many parts of Europe.

However, the habitat requirements and ecological preferences of *O. eremita* are still insufficiently known. *O. eremita* has been

found in many deciduous and exceptionally in coniferous trees (Ranius *et al.* 2005). Many authors claim that *O. eremita* prefers oak trees (Palm 1959; Szwałko 2004). However, this statement is mainly supported by simple host tree counting. Critical studies about beetle occurrences in relation to host tree frequencies are still missing. This lack of knowledge makes any conservation schemes for *O. eremita* premature and might lead to inappropriate choices of prime areas for con-

servation. In this study we focus therefore on the habitat preferences of the hermit beetle and aim to identify tree characteristics and habitat structure to explain regional distribution patterns of *O. eremita*. We deal with a network of rural avenues in Northern Poland because in a previous study Oleksa *et al.* (2003) found that the most important refuges of the beetle in northern Poland are old trees planted along roads in open rural landscapes. Such a regional occurrence pattern of *O. eremita* has previously been studied only for oaks (Ranius and Nilsson 1997, Gerell 2000).

The aim of the present paper is to compare occurrence patterns of *O. eremita* in different tree species at the regional scale and to relate these patterns to a series of tree and environmental characteristics. We will show that *O. eremita* is rather an opportunistic species with respect to host tree identity. This finding might have implications for conservation schemes.

2. MATERIALS AND METHODS

The Iława Lakeland Landscape Park (Fig. 1) is located in northern Poland (53°44'N, 19°35'E; altitude from 90 to 140 m) in the transition zone from a maritime to a continental climate (Gawroński and Oleksa 2006). The mean annual temperature of the region is 7°C (average in July: 17°C; average in January: -2.5°C), the mean precipitation 600 to 650 mm m⁻². The soils are mostly composed of Pleistocene clay and sand deposits (Jutrzenka-Trzebiatowski *et al.* 1997). The study area is a rural landscape rich in old avenues dating back to the early 18th century. For this study we chose 55.5 km of avenues making up over 20% of all old avenues in that area and examined 3932 trees (in July 2003) (Gawroński and Oleksa 2006).

We took samples from all trees with hollows large enough to allow for beetle development and looked for *O. eremita* or its remnants. Larval frass was distinguished from the frass of other saproxylic beetles (especially *Protaetia lugubris* Herbst) according to Pawłowski (1961). We regarded trees as occupied by *O. eremita* if living individuals or remnants were found.

We used the 5 point scale of Pacyniak (1992) to assess tree health 1 – trunk and crown healthy; 2 – hollows present, up to 25% of crown damaged (loss); 3 – 25–50% damaged (loss); 4 – 50–75% damaged (loss); 5 – above 75% damaged (loss) or a dead tree). Trunk circumference was measured at a height of 1.3 m. Avenues were classified according to tree species composition, road surface type (asphalted, dirt, brick paving, and concrete plates). The studied roads were predominately subject to local traffic. The rural roads, including the historical alleys, served predominantly for the transport of agricultural equipment. The roadsides were composed of a mosaic of semi-natural grassland, bushes, and field verges. Bushes were irregularly cut off (once a few years) in order to ensure visibility and thereby to improve traffic safety (Gawroński and Oleksa 2006). We further determined hollow entrance area ($\frac{1}{4} \times \pi \times \text{height of the entrance} \times \text{width of the entrance}$ [m²]) and exposition (8 compass directions: N, NE, E, SE, S, SW, W, NW).

We used the generalized linear model regression of Statistica 7 (Statsoft 2005) with circumference and entrance area as metrically scaled variables and health state and exposition as categorized variables to relate presence / absence data to the variables measured.

Preferences of *O. eremita* with respect to tree species, circumference and health state were further compared with a random sample model. Hermit beetle occurrences were randomly drawn from the overall pool of hollow trees and the resulting frequencies per variables (species identity, circumference and health state) were compared with the observed ones. Expected frequencies and standard deviations were generated from 5000 random samples each using the program *Sample* (Ulrich 2003, Ulrich and Ollik 2005). The frequency distribution of these random samples was in all cases approximately normally distributed. Hence we used the common Z-transformation [$Z = (x - \mu) / \sigma$] to infer the probability levels for the observed values from the standard normal distribution.

To visualize occupancies of *O. eremita* in relation to trunk width and to make the

frequencies of occupancy less dependent on width class choice we used kernel density estimates $h(f,t)$ of the occupancies instead of frequencies per trunk width class and plotted h against trunk width. This allows for a less subjective comparison of overall trunk width with trunk widths of occupied trees. Kernel density estimates were computed with EasyReg (Bierens 2004) using a normal density function and a bandwidth of one sample standard deviation around the sample mean (Bierens 2004).

3. RESULTS

The avenues examined were dominated by the small-leaved lime *Tilia cordata*, which made up 52% of all trees examined. Ash (*Fraxinus excelsior*) accounted for 11%, Norway maple (*Acer platanoides*) for 10%, and the pedunculate oak *Quercus robur* for 9%. All other species accounted for only 17% of the total. We detected 1002 trees (25%) with hollows suitable for hermit beetle development (Table 1). Among them, 114 (11%) were occupied by *O. eremita*. 91% of these records regarded *Tilia cordata*.

However, the distribution of *O. eremita* was not random with respect to tree species identity (Tables 1, 2). In *Tilia cordata* and *Alnus glutinosa*, occurrence frequencies were significantly higher than predicted from a random sample model in which 114 occurrences were taken at random out of the total number of trees with hollows ($P < 0.0001$ for lime and $P < 0.001$ for alder). On the other hand, *Acer platanoides* was not inhabited although the random sample model predicted occurrences ($P < 0.0001$) (Table 2). The occupancy of oak did not deviate from the expectation (Table 2).

Osmoderma colonised only trees thicker than 210 cm circumference (Fig. 2) and preferred those above 450 cm circumference. Inhabited trees were in the mean thicker than potentially suitable trees (those with hollows) ($P(U) < 0.0001$).

Trees of health class 1 do not have (by definition) hollows and were therefore not colonised by *O. eremita*. Colonised trees had a slightly but significantly ($P(t) < 0.00001$) worse health state (mean 2.8) than the potentially suitable (mean 2.4) (Table 2). Trees above health class 3 were more often colo-

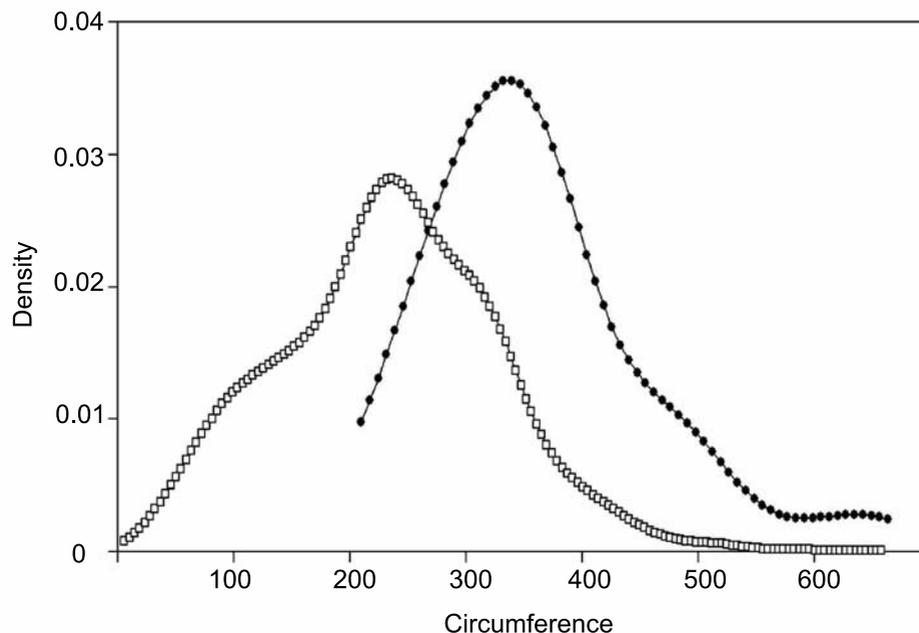


Fig. 2. Occupancy of trees (kernel density frequencies) by *Osmoderma eremita* in relation to circumference (cm). White squares: unoccupied trees, black circles: trees with the beetle.

Table 1. Frequency of tree species in the avenues studied and occupancy of hollow trees by *O. eremita*.

| Tree species | Occa- sions | % of all trees | Number of hollow trees | % of all hollow trees | Number of trees with <i>O. eremita</i> | % of all trees with <i>O. eremita</i> | % of hollow trees* with <i>O. eremita</i> |
|-------------------------------|----------------|-------------------|---------------------------|-----------------------------|--|---|---|
| <i>Tilia cordata</i> | 2052 | 52 | 706 | 70 | 104 | 91 | 15 |
| <i>Fraxinus excelsior</i> | 445 | 11 | 34 | 3 | 2 | 2 | 6 |
| <i>Acer platanoides</i> | 410 | 10 | 143 | 14 | 0 | 0 | 0 |
| <i>Quercus robur</i> | 369 | 9 | 21 | 2 | 2 | 2 | 10 |
| <i>Betula pendula</i> | 105 | 3 | 6 | 1 | 0 | 0 | 0 |
| <i>Carpinus betulus</i> | 78 | 2 | 36 | 4 | 1 | 1 | 3 |
| <i>Salix alba</i> | 77 | 2 | 21 | 2 | 1 | 1 | 5 |
| <i>Alnus glutinosa</i> | 56 | 1 | 4 | <1 | 3 | 3 | 75 |
| <i>Pyrus communis</i> | 56 | 1 | 0 | 0 | – | – | – |
| <i>Aesculus hippocastanum</i> | 51 | 1 | 17 | 2 | 1 | 1 | 6 |
| <i>Acer pseudoplatanus</i> | 34 | 1 | 1 | <1 | 0 | 0 | 0 |
| <i>Ulmus glabra</i> | 32 | 1 | 2 | <1 | 0 | 0 | 0 |
| <i>Populus tremula</i> | 29 | 1 | 0 | 0 | – | – | – |
| <i>Crataegus</i> sp. | 24 | 1 | 1 | <1 | 0 | 0 | 0 |
| <i>Populus nigra</i> | 24 | 1 | 1 | <1 | 0 | 0 | 0 |
| <i>Malus domestica</i> | 23 | 1 | 3 | <1 | 0 | 0 | 0 |
| <i>Acer saccharinum</i> | 15 | <1 | 1 | <1 | 0 | 0 | 0 |
| <i>Pinus sylvestris</i> | 12 | <1 | 1 | <1 | 0 | 0 | 0 |
| <i>Picea abies</i> | 11 | <1 | 0 | 0 | – | – | – |
| <i>Salix caprea</i> | 9 | <1 | 4 | <1 | 0 | 0 | 0 |
| <i>Fagus sylvatica</i> | 6 | <1 | 0 | 0 | – | – | – |
| <i>Robinia pseudoacacia</i> | 5 | <1 | 0 | 0 | – | – | – |
| <i>Sorbus aucuparia</i> | 4 | <1 | 0 | 0 | – | – | – |
| <i>Acer campestre</i> | 1 | <1 | 0 | 0 | – | – | – |
| <i>Larix decidua</i> | 1 | <1 | 0 | 0 | – | – | – |
| <i>Prunus avium</i> | 1 | <1 | 0 | 0 | – | – | – |
| <i>Prunus domestica</i> | 1 | <1 | 0 | 0 | – | – | – |
| <i>Prunus padus</i> | 1 | <1 | 0 | 0 | – | – | – |
| Total | 3932 | 100 | 1002 | 100 | 114 | 100 | – |

* % of all hollow trees of a given species inhabited by *O. eremita*.

Table 2. Differences between observed and expected occupancies of trees. Expected occupancies were obtained by a random sampling of 114 trees (the actual number of *O. eremita* found) out of the total of 1002 hollow trees. Means and standard deviations of the expectation were estimated from 5000 replicates. Only tree species with significant deviations and oak are shown.

| Tree species | Number of hollow trees | Trees with <i>Osmo-derma eremita</i> | Expected number of occupied trees | SD of expected value | Z | P |
|-------------------------|------------------------|--------------------------------------|-----------------------------------|----------------------|-------|---------|
| <i>Tilia cordata</i> | 706 | 104 | 81.02 | 4.96 | 4.63 | <0.0001 |
| <i>Alnus glutinosa</i> | 4 | 3 | 0.47 | 0.67 | 3.81 | 0.0003 |
| <i>Carpinus betulus</i> | 36 | 1 | 4.21 | 1.88 | -2.19 | 0.04 |
| <i>Acer platanoides</i> | 143 | 0 | 16.42 | 3.91 | -4.20 | <0.0001 |
| <i>Quercus robur</i> | 21 | 2 | 2.30 | 1.57 | -1.47 | > 0.05 |

Table 3. Differences between observed and expected occupancies of trees by *O. eremita* according to tree health class (from healthy (1) to heavily damaged (5)). Calculation of expectations as in Table 3.

| Tree health class | Trees with <i>Osmo-derma eremita</i> | Expected number of occupied trees | SD of expected value | Z | P |
|-------------------|--------------------------------------|-----------------------------------|----------------------|-------|----------|
| 1 | 0 | 38.29 | 5.50 | -6.97 | <0.00001 |
| 2 | 60 | 59.61 | 5.58 | -0.11 | 0.40 |
| 3 | 32 | 10.57 | 3.13 | 6.84 | <0.00001 |
| 4 | 9 | 2.06 | 1.43 | 4.86 | <0.00001 |
| 5 | 13 | 2.48 | 1.44 | 7.30 | <0.00001 |
| Total | 114 | | | | |

nised than expected from a random sample model (Table 3).

O. eremita did not show any significant preferences according to hollow entrance area, exposition and road surface type. Frequencies of inhabited trees did not differ from those expected from a random sample (data not shown). To eliminate the possible effect of health state and circumference we used a generalized linear model regression with health state, circumference, entrance area, and exposition as predictors of beetle occurrence. This analysis did not point to entrance area (χ^2 of simple effect <0.01; $P = 0.98$) and exposition (χ^2 of simple effect = 5.01; $P = 0.29$) as significant predictor variables of beetle occurrence (data not shown). Instead, circumference turned out to be the only significant predictor of beetle occurrence (χ^2 of simple effect = 6.60; $P = 0.01$).

4. DISCUSSION

Ranius and Nilsson (1997) have argued that hermit beetles do not have very strong microhabitat preferences but are associated with certain rot stages. *O. eremita* should therefore colonise all suitable trees according to their availability. Ranius *et al.* (2005) pointed to oak as the most often colonised tree in almost all European countries. This would be another argument in favour of a better protection of sites rich in old oaks. Our results, however, do not confirm this view. Oaks were not more frequently colonised than expected from the regional frequency of oaks. These contrasting results can be explained by the fact that many previous counts of *O. eremita* were selectively directed to stands rich in old oaks and did not take host tree frequencies into account.

However, it should be mentioned that beetle occurrence per tree seems to vary widely throughout Europe. Ranius and Nilsson (1997) found *O. eremita* in 32% to 62% of Swedish oaks, whereas our survey gave only a frequency of 10%. This variability might be explained either by regional differences in beetle behaviour or by some positive functional response. In the latter case the beetle would preferentially deposit eggs in the most frequent host tree. Further regional surveys in other countries with different tree composition are necessary to answer this question.

The preference for *Tilia cordata* and *Alnus glutinosa* might be a result of the larger amount of rotten wood in limes and alders compared to other trees. Both species have rather soft wood that is susceptible to decay. Defence mechanisms in lime are relatively weak and the tree is prone to fungal infection (Baum and Schwarze 2002). However, it is difficult to measure these variables precisely and to interpret differences in occupancy of trees with hollows by *O. eremita* with regard to quantity and quality of rotten wood.

O. eremita and many other saproxylic species favour trees with thicker trunks (Table 3, Ranius and Jansson 2000, Grove 2002). This preference is probably caused by the more stable microclimate within the hollows of thicker trees (Sedgeley 2001). However, we observed a slight tendency towards lower occupancies of the biggest trees having circumferences above 500 cm. Ranius and Nilsson (1997) described a similar effect. These findings contradict literature claims that *O. eremita* prefers very thick trees (Martin 1993). It might be that the cavities in very thick trees (especially in *Tilia cordata*) are too wide to allow for a stable microclimate necessary for larval development.

The hermit beetle is rather thermophilic and is associated with warmer stands (Ranius and Nilsson 1997). We expected therefore that trees planted along asphalted roads should be preferred because the black surface warms up more strongly. However, we did not find any preferences for the material of the road surface. Further, our results did not reveal a preference for hollows with entrances directed to south or west as Ranius and Nilsson (1997) found in oak stands in southern Sweden.

The present results show that *O. eremita* occupies anthropogenic habitats if suitable trees are present and does not require old-growth forests to survive. On the contrary, forests with a dense canopy seem to be avoided (Oleksa unpublished). These findings suggest that avenues with old trees might play a crucial role in the preservation of this species. Further studies are needed to investigate the occurrence of *Osmoderma* in different types of habitats. Without comparative inventories in semi-natural and natural forests we are not able to judge whether the species is connected with anthropogenic habitats or whether such environments play only a secondary role.

The protection of *O. eremita* requires the preservation of sites with a network of suitable trees in space and time. Its low dispersal ability seems to be one of the causes for its sensitivity to tree management and vulnerability to habitat fragmentation (Ranius and Hed in 2001). Any preservation strategy must take long-term processes of cavity creation and disappearance into account. The creation of a new tree cavity can take several tens to hundreds of years in trees with harder wood, like oak or beech. In trees with softer wood, like lime or willow, hollow creation is much faster. The age of a lime tree can be roughly estimated as $\text{age} = 0.5 \text{ circumference}$ ($R^2 = 0.84$; using data of 24 trees provided by Pacyniak 1992). The age of the youngest occupied lime tree in the investigated area should therefore be about 100 years (circumference 210 cm). The thinnest occupied lime we found (unpubl. data) was only 150 cm equivalent to an age of about 70 years. Only a few oaks and beeches younger than 150 years develop large hollows (Nilsson *et al.* 2001).

Avenues with trees that are old enough to harbour saproxylic organisms are quite frequent elements of landscape in some parts of Poland, especially in East Prussia. However, such trees have so far not been investigated on a large scale. Thus, at least in some parts of Poland, *O. eremita* might not be as rare as suggested by the available data (Oleksa *et al.* 2003, Szwajko 2004). This should also hold for other European countries (cf. Antonsson *et al.* 2003).

O. eremita might serve as an umbrella species (Ranius *et al.* 2005). The presence

of *O. eremita* indicates high species richness a many threatened invertebrate species associated with old trees (Ranius 2002a, b). Thus, the preservation of the hermit beetle is of importance for the survival of other species too. The preservation and restoration of the habitats of this species means, therefore, the maintenance of a larger number of other species that depend on the same type of habitat.

Previous studies (Vignon and Orabi 2003) suggested that *O. eremita* might be suited as an indicator of the continuity of networks of hollow trees in space and time. Avenues form linear structures in landscapes that enable the dispersal of saproxylic organisms even if they have a limited dispersal potential. The maintenance of the spatial and temporal continuity of avenues might be a key factor in the preservation of the hermit beetle as well as other saproxylic beetles.

ACKNOWLEDGMENTS We thank Thomas Ranius for critical and valuable suggestions on earlier versions of the manuscript. Miss Hazel Pearson kindly improved our English. This work was in part supported by the Iława Lakeland Landscape Park. We wish to thank all employees of the Park who helped us during the field work.

5. REFERENCES

- Antonsson K., Hedin J., Jansson N., Nilsson S.G., Ranius, T. 2003 – Läderbaggens (*Osmoderma eremita*) förekomst i Sverige [Occurrence of the hermit beetle (*Osmoderma eremita*) in Sweden] – Entomol. Tidskr. 124: 225–239. (in Swedish)
- Baum S., Schwarze F.W.M.R. 2002 – Large-leaved lime (*Tilia platyphyllos*) has a low ability to compartmentalize decay fungi via reaction zone formation – New Phytologist 154: 481–490.
- Bierens H.J. 2004 – EasyReg international. User guide – <http://grizzly.la.psu.edu/~hbierens/EASYREG.HTM>
- Eliasson P., Nilsson S.G. 2002 – ‘You should hate young oaks and young nobleman’. The environmental history of oaks in eighteenth- and nineteenth-century Sweden – Entomol. Tidskr. 121: 225–239.
- Gawroński R., Oleksa A. 2006 – Wstępna waloryzacja alei śródpolnych Parku Krajobrazowego Pojezierza Iławskiego na podstawie chrząszczy saproksylicznych [Preliminary valorisation of rural avenues of the Iława Lakeland Landscape Park based on saproxylic beetles] – Parki Narodowe i Rezerваты Przyrody. 25(1): 85–107. (in Polish)
- Gerell R. 2000 – Allernas betydelse för rödlis-tade vedlevande skalbaggar [The importance of avenues for threatened saproxylic beetles] – Entomol. Tidskr. 121: 59–66. (in Swedish)
- Grove S.J. 2002 – Saproxylic insect ecology and the sustainable management of forests – Ann. Rev. Ecol. and Syst. 33: 1–23.
- Hedin J., Ranius T. 2002 – Using radio telemetry to study dispersal of the beetle *Osmoderma eremita* living in hollow trees – Comp. Electr. Agriculture 35: 171–180.
- IUCN 2004 – IUCN Red List of Threatened Species – www.redli.
- Jutrzenka-Trzebiatowski A., Hołdyński Cz., Polakowski B. 1997 – Roślinność rzeczywista Parku Krajobrazowego Pojezierza Iławskiego [Actual vegetation of the Iława Lakeland Landscape Park] – Wydaw. ART, Olsztyn. (in Polish)
- Luce, J.-M. 1996 – *Osmoderma eremita* (Scopoli, 1763). (In: Background information on invertebrates of the Habitats Directive and the Bern Convention, Part I: Crustacea, Coleoptera and Lepidoptera, Eds: van Helsdingen, P.J., Willemsse, L., Speight, M.C.D.) – Council of Europe, Strasbourg, pp. 65–69.
- Martin O. 1993 – Fredede insekter i Danmark. Del 2: Biller knyttet til skov [Threatened Insects of Denmark. Part 2: Beetles connected with forests] – Entomol. Meddel. 57: 63–76.
- Nilsson S.G., Hedin J., Niklasson M. 2001 – Biodiversity and its assessment in boreal and nemoral forests – Scand. J. Forest Res. Suppl. 3: 10–26.
- Oleksa A., Szwajko P., Gawroński R. 2003 – Pachnica *Osmoderma eremita* (Scopoli, 1763) (*Coleoptera: Scarabaeoidea*) w Polsce – występowanie, zagrożenia i ochrona [The hermit beetle *Osmoderma eremita* (Scopoli, 1763) (*Coleoptera: Scarabaeoidea*) in Poland – occurrence, threats and protection] – Roczn. Nauk. Pol. Tow. Ochr. Przyr. “Salamandra” 7: 101–123. (in Polish)
- Pacyniak C. 1992 – Najstarsze drzewa w Polsce [The oldest trees in Poland] – Wydawnictwo PTTK „Kraj”, Warszawa. (in Polish)
- Palm T. 1959 – Die Holz- und Rindenkäfer der süd- und mittelschwedischen Laubäume [Wood and bark boring beetles of the south- and middle Swedish broadleaved trees] – Opuscula Entomol. Suppl. XVI. (in German)
- Pawłowski J. 1961 – Próchnojady blaszkorożne w biocenozie leśnej Polski [Lamellicorn cario-

- phages in forest biocenoses of Poland] – *Ekologia polska* s. A, 9(21): 355–437. (in Polish)
- Ranius T., Hedin J. 2001 – The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows – *Oecologia* 126: 363–370.
- Ranius T., Jansson N. 2000 – The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with hollow oaks – *Biol. Conserv.* 95: 85–94.
- Ranius T., Nilsson S.G. 1997 – Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees – *J. Insect Conserv.* 1: 193–204.
- Ranius T. 2002a – *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows – *Biodiv. Conserv.* 11: 931–941.
- Ranius T. 2002b – Population ecology and conservation of beetles and pseudoscorpions living in hollow oaks in Sweden – *Anim. Biodiv. Conserv.* 25: 53–68.
- Ranius T., Jansson N. 2002 – A comparison of three methods to survey saproxylic beetles in hollow oaks – *Biodiv. Conserv.* 11: 1759–1771.
- Ranius T., Aguado L.O., Antonsson K., Audisio P., Ballerio A., Carpaneto G.M., Chobot K., Gjurašin B., Hansen O., Huijbregts H., Lakatos F., Martin O., Neculiseanu Z., Nikitsky N.B., Paill W., Pirnat A., Rizun V., Ruicănescu A., Stegner J., Süda I., Szałko P., Tamutis V., Telnov D., Tsinkevich V., Versteirt V., Vignon V., Vögeli M., Zach P. 2005 – *Osmoderma eremita* (Coleoptera: Scarabaeidae: Cetoniinae) in Europe – *Anim. Biodiv. Conserv.* 28: 1–44.
- Schaffrath U. 2003a – Zu Lebensweise, Verbreitung und Gefährdung von *Osmoderma eremita* (Scopoli, 1763) (Coleoptera; Scarabaeoidea, Cetoniidae, Trichiinae) [Biology, distribution and threat of *Osmoderma eremita* (Scopoli, 1763) (Coleoptera; Scarabaeoidea, Cetoniidae, Trichiinae)], Teil 1 – *Philippia* 10: 157–248. (in German)
- Schaffrath U. 2003b – Zu Lebensweise, Verbreitung und Gefährdung von *Osmoderma eremita* (Scopoli, 1763) (Coleoptera; Scarabaeoidea, Cetoniidae, Trichiinae) [Biology, distribution and threat of *Osmoderma eremita* (Scopoli, 1763) (Coleoptera; Scarabaeoidea, Cetoniidae, Trichiinae)], Teil 2 – *Philippia* 10: 249–336. (in German)
- Sedgeley J.A. 2001 – Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand – *J. Appl. Ecol.* 38: 425–438.
- Speight M.C.D. 1989 – Saproxylic invertebrates and their conservation – Council of Europe, Strasbourg.
- StatSoft Inc. 2005 – STATISTICA (data analysis software system), version 7.1 – www.statsoft.com.
- Szałko P. 2004 – *Osmoderma eremita* (Scopoli, 1763), Pachnica (Coleoptera, Scarabaeidae). (In: Polska czerwona księga zwierząt, Eds: Głowaciński Z., Nowacki J.), [*Osmoderma eremita* (Scopoli, 1763), The hermit beetle (Coleoptera, Scarabaeidae). (In: Polish Red Data Book of Animals, Eds: Głowaciński Z., Nowacki J.)] – IOP Kraków. (in Polish)
- Ulrich W. 2003 – Sample – a FORTRAN program for taking series of random samples – www.uni.torun.pl/~ulrichw
- Ulrich W., Ollik M. 2005 – Limits to the estimation of species richness: The use of relative abundance distributions – *Div. and Distr.* 11: 265–273.
- Vignon V., Orabi P. 2003 – Exploring the hedgerows network in the west of France for the conservation of saproxylic beetles (*Osmoderma eremita*, *Gnorimus variabilis*, *Lucanus cervus*, *Cerambyx cerdo*) – Proceedings of 2nd pan-European Conference on Saproxylic Beetles. People's Trust for Endangered Species.

(Received after revising August 2006)