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Habitat Preferences of *Boros schneideri* (Coleoptera: Boridae) in the Natural Tree Stands of the Białowieża Forest

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ABSTRACT. We analyzed habitat requirements of *Boros schneideri* (Panzer, 1796) (Coleoptera: Boridae) in the natural forests of the continental biogeographical region, using data collected in the Białowieża Forest. This species has been found on the six host trees, but it preferred dead, standing pine trees, characterized by large diameter, moderately moist and moist phloem but avoided trees in sunny locations. It occurred mostly in mesic and wet coniferous forests. This species demonstrated preferences for old tree stands (over 140-yr old), and its occurrence in younger tree-stand age classes (minimum 31–40-yr old) was not significantly different from random distribution. *B. schneideri* occupied more frequently locations distant from the forest edge, which were less affected by logging. Considering habitat requirements, character of occurrence, and decreasing number of occupied locations in the whole range of distribution, this species can be treated as relict of primeval forests.

Key Words: *Boros schneideri*, saproxylic beetle, habitat requirement, Białowieża Primeval Forest, natural forest

Boridae is a small family of beetles (Coleoptera), represented only by four species worldwide. It belongs to the superfamily Tenebrionoidea and is treated as a monophyletic group. This family consist of three genera: *Lecontia* Champion, 1889 (North America), *Synercticus* Newman, 1842 (Australia, New Guinea), and *Boros* Herbst, 1797 (Eurasia, North America). The last genus is represented by two species—North American *Boros unicolor* Say, 1827 and occurring in Palearctic *Boros schneideri* (Panzer, 1796) (Lawrence and Pollock 1994; Lawrence and Newton 1995; Pollock 2008, 2010).

Morphology of imagines, pupae, and larvae of *B. schneideri* is well known, sufficiently described and illustrated (Saalas 1937, St. George 1940, Leiler 1954, Mamaev et al. 1977, Stebnicka 1991, Kubisz 2004b, Levkaničová 2009, Pollock 2010), but eggs were not described so far.

B. schneideri is widely distributed in north-eastern Europe and Siberia, reaching eastward behind lake Baikal (Buryatia region); it also has been found in Sakhalin, China, and isolated localities in the eastern part of Central Europe (Janovskij 1976, Burakowski et al. 1987). This species was reported from the following European countries and provinces: Germany, Czech Republic, Slovakia, Romania, Ukraine, Poland, Belarus, Lithuania, Latvia, Estonia, Sweden, Finland, Russia (South, Central, and North European Territory), and the Asiatic part of Russia (West and East Siberia, Far East), Japan, China (North-East Territory), and Korea (Pollock 2008, Karalius and Blažytė-Čereškienė 2009, Blažytė-Čereškienė and Karalius 2010). *B. schneideri* became extinct in Western Europe due to excessive logging (Horion 1956; Süda 2003; Kubisz 2004a,b; Karalius and Blažytė-Čereškienė 2009). In all regions is regarded as very rare (Biström and Väisänen 1988; Vilks and Telnov 2003; Kubisz 2004a,b), except for Lithuania, where recently was discovered in many new localities (Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2010, 2012).

Because of rarity and declining number in many European countries, this species draw special attention of European Community and its occurrence determines designation of Natura 2000 areas (Council Directive 92/43/EEC—Annex 2 of the European Union Habitats Directive).

Information on biology and habitat requirements of *B. schneideri* are still insufficient. Most data on this topic were collected in Boreal region, mainly in Lithuania (Baranowski 1977; Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2010, 2012), whereas knowledge from other geographic regions is fragmentary or does not exist at all. Larvae of this species lives under the bark of standing, dead trees, mainly pine *Pinus sylvestris* L. and silver fir *Abies alba* Miller, less often other coniferous and deciduous tree species (Trella 1939; Leiler 1954; Kinelski and Szujecki 1959; Burakowski et al. 1987; Kubisz 2004a,b; Telnov et al. 2006; Karalius and Blažytė-Čereškienė 2009; Blažytė-Čereškienė and Karalius 2010, 2012). According to Kolomic and Bogdanova (1980), imagines of *B. schneideri* are predatory and larvae are sapro-xylophagous. However, Nikitskij et al. (1996) describes this species as sapro-xylo-mycetophagous, with a tendency for necrophagy and predation. Leiler (1954) states that larvae of *B. schneideri* feed on mycelium of *Ophiostoma minus* (Hedgecock) Syd. & P. Syd., whereas Anonim (2011) reports that they are feeding on mycelium of *Aureobasidium* Berkhout 1923 (both fungi from the class Ascomycota). According to information from Slovakia, larvae can also live in bracket fungi from genus *Polyporus* (Basidiomycota; Anonim 2012). The development of larvae takes place under bark, which is slightly detached, phloem is decomposing, and moderately humid. This phase of bark decomposition and under-bark environment is called pyrochroidal (Mamaev et al. 1977). There are some premises indicating that *B. schneideri* is night active. One specimen was captured in the Białowieża Forest using a light. During searching, we did not observe imagines on the surface of trees or in open places, all of them were found under bark, in feeding places. Also another species from Boridae family—Australian *Synercticus heteromerus* Newman—is active at night (Lawrence and Pollock 1994).

The main goal of this study was to identify habitat requirements of this species in the continental part of Europe (Continental region), in natural tree stands of the Białowieża Forest. Detailed studies on habitat selection by *B. schneideri* were conducted in Lithuania, but they were restricted to the managed forests, which differ in species

composition and tree stands structure from the forests of natural origin. Here, we attempt to present primeval, not deformed by human pressure, habitat requirements of this species. The Białowieża Forest, particularly its central part—the Białowieża National Park, is the best preserved forest complex in lowland Europe, in the zone of deciduous and mixed forests (Faliński 2003, Gutowski and Jaroszewicz 2004). We assume that this species has different preferences for host trees in the natural forests of the Continental region than in the northern areas of Europe, e.g., it may occur on more tree species than in boreal forests, where it occupies virtually only pine trees (Blażyte-Čereškienė and Karalius 2010). We also hypothesize that in our study area, *B. schneideri* is more resilient to overshadowing of host trees (higher density of surrounding trees and higher proportion of spruce) than in Lithuania, where it was absent in the localities characterized by 80% of shade and—high share of spruce in the tree stands (Blażyte-Čereškienė and Karalius 2012).

Materials and Methods

Our analyses are based on all available literature on distribution of this species worldwide, in Poland and in the Białowieża Forest, where we performed detailed studies on the ecological requirements of *B. schneideri*.

The Białowieża Forest is a large, compact forest complex located on the Polish-Belarusian border, encompassing an area of about 1,500 km², including 632 km² in Poland. The entire Belarusian part of this forest is declared as a National Park, but on the Polish side, Białowieża National Park protects only 16.6% of an area (~105 km²). Additionally, over 18% of the Polish part (118 km²) is protected as nature reserves, which has been partly excluded from forest management since 2008. The area under strict protection, where any kind of activity leading to ecosystem transformation is prohibited and only limited touristic, educational, and scientific use is allowed, extends to ~57 km² in the Polish part and ~307 km² in the Belarusian part (Okolów et al. 2009). Flora of vascular plants of the Białowieża Forest has 1,071 species; among them, 25 native species of trees and 55 species of shrubs. Dominant species of trees and shrubs (starting from those covering largest area) are *P. sylvestris* L., *Picea abies* (L.) Karst., *Alnus glutinosa* (L.) Gaert., *Quercus robur* L., *Betula pendula* Roth and *Betula pubescens* Ehrhart, *Carpinus betulus* L., *Tilia cordata* Miller, *Fraxinus excelsior* L., *Acer platanoides* L., *Populus tremula* L., *Prunus padus* L., *Corylus avellana* L., and *Salix cinerea* L. Some 171 plant communities of association rank have been identified in the area, including 26 of forest and 4 of scrub (Sokołowski 2004).

The Białowieża Forest is the best preserved natural forest complex in the lowland Europe. This area is universally recognized as a reference site for all observations and studies made in the deciduous and mixed forest of the temperate climatic zone (particularly the strictly protected part of the Białowieża National Park). The important role of the Białowieża Forest should be emphasized in the protection of organisms connected with dead wood (saproxylic)—this area is a Europe wide refuge for many relict species, representative for primeval conditions (Gutowski and Jaroszewicz 2004).

In the Białowieża Forest, many species of insects occur, which are rare and declining in the whole of Europe, including beetles (Coleoptera). In this area, many taxa typical for natural forest habitats survived (Gutowski and Jaroszewicz 2001), which disappeared from many European forests due to human activity (Speight 1989), or their number drastically declined. The Białowieża Forest is an area where the fauna of Coleoptera is fairly well recorded with a total of 3,200 species reported (Gutowski and Jaroszewicz 2001, 2004).

Preliminary investigations of saproxylic beetles in the Białowieża Forest, including *B. schneideri*, started already in 1982, but more detailed and large-scale studies were carried out in years 2008–2012. In the framework of these studies, faunistic data on *B. schneideri* were collected from the entire Polish part of the Białowieża Forest, but in the Belarusian part, only fragmentary data were sampled.

Investigations focused on searching for larvae, pupae, and imagines on potential host trees (dead standing trees, fallen trees and branches, and piles of wood) where the bark was pried to check for preimagines developmental stages or imagines of *B. schneideri*. If presence of this species was confirmed on a given tree, searching was ceased and remaining feeding site was left untouched. We never removed more than one-third of the bark area from a single tree. During investigations, we recorded species and diameter of the host tree, as well as other parameters (like forest type, humidity, and light conditions). Forest type was described during field work and then corrected according to data from Forest management plans prepared for Forestry Districts of Białowieża, Browsk, and Hajnówka (state on 1.01.2002 r.). This source of data was used also to acquire information on the mean age of the dominant tree species, which can be used as a proxy for the age of tree stands and share of *Pic. abies* in a tree stand (%), which provide indirect information about light conditions. We assessed moistness of habitat at the host tree location using three categories: dry, mesic, and wet. The humidity of substrate, in the place where *B. schneideri* was found, was categorized as low, moderate, or high. Light conditions were assessed according to percentage of host tree shadowed by surrounding trees and shrubs, using also three categories—low (below 1/3), moderate (1/3–2/3), and high (above 2/3 of three available for *B. schneideri*).

During our investigations, we found mostly larvae of different size (83.7% of all cases), less often imagines, or both larvae and imagines. The adult forms were found all-year-round, except for June and beginning of July. Feeding places of *B. schneideri* were usually located at the base of a tree, up to several meters high. In the case of trees of smaller diameter, beetles were found only on the length of 2–3 m, but in thicker trees, they occupied the entire trunk, up to the first branches. Considering used methodology (we ceased searching when first specimens were found), it is difficult to estimate actual population size of *B. schneideri* in the Białowieża Forest. Total number of observed or captured imagines was about 100, whereas the number of larvae was several times higher. The field work was continued from the end of winter until late autumn, but only when ambient temperature exceeds +5°C to make it possible for larvae of *B. schneideri* to find secure shelters after the feeding site was exposed. When searching for *B. schneideri*, we also recorded geographic coordinates using GPS (GARMIN GPSmap 60CSx) and occasionally also made photographic documentation. Because of time limitations, we explored only some of potential occurrence sites of this species. In total, we investigated an area of 250 km², checking thousands of trees. We searched in all types of the forest present in the Białowieża Forest, devoting for each forest type the amount of time proportional to the share of given habitat in entire study area.

Statistical Methods. We analyzed habitat requirements of *B. schneideri* on three different level—within entire study area (preferences for the forest type), within tree stands (preferences for the host tree), and in the local scale (preferences for light conditions and humidity of substrate). To characterize effect of variables related to the forest type on *B. schneideri* occurrence, we applied logistic regression model (generalized linear model with multivariate normal random effects and logit link function for the binomial distribution, 0—random locations, 1—site occupied by *B. schneideri*). Following features were included to the model as fixed factors (either continuous or categorical): forest type, mean age of dominant tree species, volume of the tree stand (m³/ha), share of most preferred host tree species (%), share of spruce *Pic. abies* (%), humidity (three categories—dry, mesic, and wet), and distance to the forest edge (m). To adjust for spatial autocorrelation and pseudoreplications, we used a unique spatial address, which was included to the model as random factor. All locations occurring in the same forest compartment (roughly 1 × 1 km) or in adjacent forest compartment were assigned to the same address. Random locations (200 points) were positioned on the map and characterized using data from Forest management plans prepared for Forestry Districts of Białowieża, Browsk, and Hajnówka.

We found *B. schneideri* in 12 different types of the forest, but for the sake of simplicity, we used as predictor in the model only five forest categories, which correspond to following plant associations found in the Białowieża Forest: mesic coniferous forests—*Vaccinio vitis-ideae-Pinetum*, *V. myrtilli-Piceetum*, *Calamagrostio arundinaceae-Piceetum*, *C. arundinaceae-Pinetum*, and *Pino-Quercetum*; wet coniferous forests—*Molinio caeruleae-Pinetum*, *Vaccinio uliginosi-Pinetum*, *Ledo-Sphagnetum magellanici*, and *Quercu-Piceetum typicum*; mesic deciduous forests—*Tilio-Carpinetum typicum*, *Tilio-Carpinetum calamagrostetosum*, *Melitti-Carpinetum*, and *Corylo-Piceetum*; wet deciduous forests—*Tilio-Carpinetum stachyetosum*, *Tilio-Carpinetum circaetosum*, *Tilio-Carpinetum caricetosum*, *Quercu-Piceetum stellarietosum*, *Betulo pubescentis-Piceetum*, and *Sphagno girgensohnii-Piceetum dryopteridetosum*; and alderwoods—*Ribeso nigri-Alnetum*, *Sphagno squarrosi-Alnetum*, *Fraxino-Alnetum*, *Ficario-Ulmetum minoris*, and *Piceo-Alnetum*. The proportion of area occupied by different categories of habitats in the Białowieża Forest was as follows: mesic coniferous forests—18.4%; wet coniferous forests—5.8%; mesic deciduous forests—37.8%; wet deciduous forests—21.7%; and alderwoods—13.6%.

The distance to the forest edge was used as an approximation of human impact on the tree stands, assuming that tree stands located closer to human settlements, and water courses (used in the past for timber transportation) will be more affected than more distant areas.

Additionally, we analyzed preference of *B. schneideri* for the forest category using Resource Selection software with implemented Compositional Analysis method (Aebischer et al. 1993). We compared share of given forest category, where *B. schneideri* was found (used resource) with share of the same forest within entire study area (available resource). The same method was applied to estimate preferences for the host tree, but in this case, we compared share of tree species occupied by *B. schneideri* (used resource) with expected mean share of the same tree species within given forest type (available resource), using data from Sokołowski (2004). To assess if selection of given resource (forest category or species of host tree) was significantly different from random choice, we used Wald statistic. Significance of differences between available and used resources based on 1,000 randomizations and zero values were replaced with small value 0.1.

The effect of shadowing and humidity of substrate on occurrence of *B. schneideri* was analyzed by direct calculation of probability by resampling of locations (applying 1,000 repetitions, Resampling Stats software). This was only very robust estimate, because we assumed that availability of light conditions or humidity for *B. schneideri* was the same in all cases, and we were able to detect only departures from random distribution, which approximate equal proportion of records in each category.

Results

Results of logistic regression revealed that occurrence of *B. schneideri* was significantly affected by forest type, age of tree stand, volume of the tree stand, and distance to the forest edge (Table 1). *B. schneideri* was found mostly in mesic coniferous forest and mesic deciduous

forest, and less frequently in wet coniferous and wet deciduous forests, and only 10 times in alderwoods (Table 2). When comparing data collected for the sites occupied by *B. schneideri* with random locations, we found that coniferous tree stands were significantly more frequently occupied than deciduous forests and alderwoods (Table 1). This observation was also confirmed by analyze of sites occupied by *B. schneideri*, which were not randomly distributed among different forest categories (Wilk's lambda = 0.63; $\chi^2 = 76.57$; $df = 4$, $P < 0.001$). In relation to available habitats, this species preferred coniferous mesic forest over coniferous wet forest ($t = 4.08$, $P < 0.001$), and both coniferous forest categories were preferred over mesic deciduous forest, which was next in ranking of preferred habitats ($t = 4.64$, $P < 0.001$ and $t = 2.10$, $P = 0.04$, for mesic and wet coniferous forest, respectively). There were not significant differences between mesic deciduous forest and alderwood, as well as between wet deciduous forest and alderwood ($t = 153$, $P = 0.14$ and $t = 1.01$, $P = 0.31$, respectively).

B. schneideri was found mostly in the tree stands characterized by high volume. The proportion of occupied trees in different volume classes was the following: $<100 \text{ m}^3/\text{ha}$ —1.2%; 101–200—7.9%; 201–300—19.5%; 301–400—28.7%; 401–500—26.8%; and >500 —15.9%. When compared with random location, *B. schneideri* significantly preferred tree stands with higher volume (Table 1, Fig. 1). We also found that *B. schneideri* occupied sites, which were more distant from the forest edge when compared with random locations (Table 1, Fig. 1). The proportion of spruce in a tree stand had not significant effect on occurrence of *B. schneideri* ($z = -1.60$, $P = 0.11$).

B. schneideri was found in the forests from 31 to 40-yr old (using 10-yr classes) to 281 to 290-yr old. This species occurred significantly more frequently in older tree stands when compared with random locations (Table 1), but relationship between the age of a tree stand and number of occupied sites was not direct. *B. schneideri* occurred less frequently in youngest and oldest tree stands, but it was most common in the tree stands of medium age (multinomial regression, $R^2 = 0.39$; $P = 0.002$; Fig. 2, both linear and square terms of age were significant). Most of sites (27) were found in the tree stands of 151–160-yr old, in the tree stands of 141–150-yr old were 19 sites, 171–180-yr old—17 sites, and in the tree stands of 121–130-yr old—11 sites.

The diameter of a tree in place where beetles were found ranged from 10 to 170 cm (on average 55 cm, $SD = 25.6$ cm). The minimum diameter was recorded for birch (10 cm) and pine (18 cm). Remaining trees had a higher diameter, at least 30–35 cm. Most frequently occupied were dead standing trees—76% of all cases. Only in the case of alder and oak was the proportion of occupied standing dead trees was different, but sample size for those species was small (Table 3). However, in some cases, larvae started to develop in standing trees, which later fell down or had broken. Thus, in fact, preferences for standing trees could be higher than indicated by collected data.

During the study period, we found 183 trees occupied by *B. schneideri*, belonging to six species (from most to least frequently occupied): pine *P. sylvestris* L., oak *Q. robur* L., alder *Al. glutinosa* (L.) Gaertn., spruce *Pic. abies* (L.) Karst., birch *Be. pendula* Roth, and ash *F. excelsior* L. (Table 3). Most frequently occupied tree species was pine (74.7% of all cases). Selection of host tree by *B. schneideri* was significantly different from random (Wilk's lambda = 0.19; $\chi^2 = 272.71$; $df = 4$, $P < 0.001$). In relation to availability of tree species, most preferred one was pine, followed by oak and alder, and finally birch and spruce. Compositional analysis method revealed that difference in preferences of *B. schneideri* for consecutive tree species were significant at $P = 0.001$, except for lack of significant differences between oak and alder ($t = 1.64$, $P = 0.11$).

The selection of trees by *B. schneideri*, which were moderately or high shadowed by surrounding trees was not significantly different from random (resampling method, $P = 0.091$ and $P = 0.223$, respectively), but this species significantly avoided trees characterized by low shading ($P = 0.013$). In this case, larvae of *B. schneideri* were found mainly on the northern side of the tree.

Table 1. Estimates of model parameters (logistic regression) on differences between sites occupied by *B. schneideri* and random locations

Habitat trait	Estimate	SE	z	P
Age	0.014	0.003	5.28	<0.001
Coniferous	1.325	0.263	5.03	<0.001
Volume	0.003	0.001	2.53	0.01
Distance	0.449	0.200	2.25	0.02

Only significant effects are presented. Age, mean age of dominant species; coniferous, proportion of coniferous tree stands; volume, volume of tree stand (m^3/ha); distance, distance of location to the forest edge.

Table 2. Host trees of *B. schneideri* within five forest categories in the Białowieża Forest (number of observations)

Tree species	Forest type					Habitat moistness			
	Mesic coniferous	Wet coniferous	Mesic deciduous	Wet deciduous	Alderwoods	Dry	Mesic	Wet	No data
<i>P. sylvestris</i>	62	17	32	2	1	61	11	2	40
<i>Q. robur</i>	2		9	10	4	13	4	1	7
<i>Pic. abies</i>	2		4	1		1	1		5
<i>Al. glutinosa</i>				4	4	1	3	1	3
<i>Be. pendula</i>	3					1			2
<i>F. excelsior</i>					1		1		—
Total	69	17	45	17	10	77	20	4	57

Habitat moistness was assessed in the place of host tree occurrence, independently of forest type moistness.

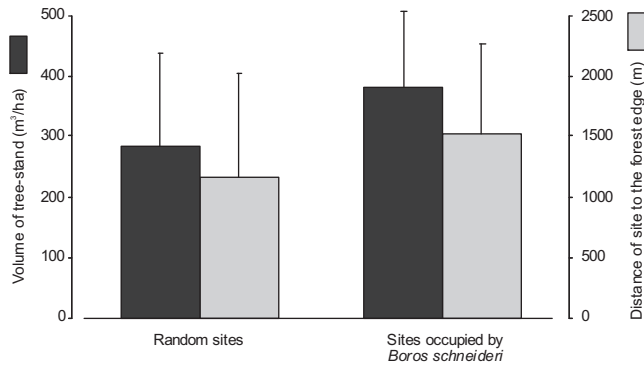


Fig. 1. Volume of tree stand (m^3/ha) and distance to the forest edge of random sites and sites occupied by *B. schneideri* in the Białowieża Forest.

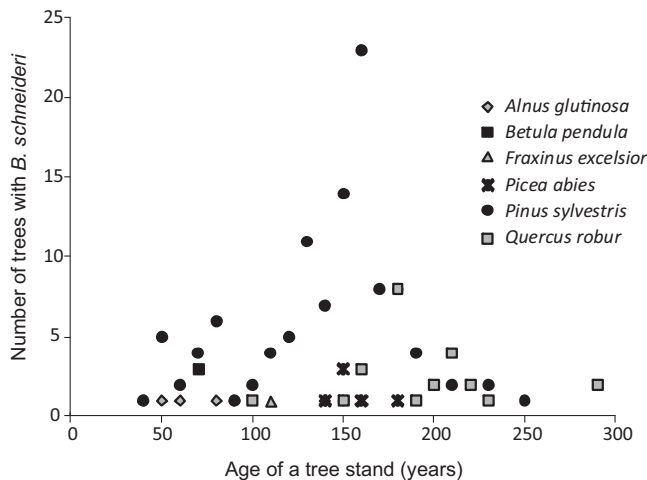


Fig. 2. Relationship between number of trees with *B. schneideri* and an age of a tree stand.

In relation to the substrate humidity (feeding sites of larvae), *B. schneideri* significantly preferred very humid substrate (35 observations, resampling method, $P = 0.001$), but avoided substrate characterized by low humidity (5 observations, resampling method, $P < 0.001$, Table 3). The substrate of moderate humidity was selected by *B. schneideri* randomly (resampling method, $P = 0.224$, Table 3).

Discussion

In the Białowieża Forest, *B. schneideri* was found most frequently coniferous forests, probably due to preference for pine as a host tree. These preferences are more distinct in the boreal zone, where pine is the

only tree, where this species is developing (Blażyte-Čereškienė and Karalius 2010). Second known species from this genus—*B. unicolor*, very rare beetle associated with old growth in North America, has similar preferences for pine (*Pinus* spp.) and other conifers (Majka 2006). Furthermore, *B. schneideri* was found on *Pinus cembra* L. in western Siberia (Krivoluckaja 1965); *Picea jezoensis* (Siebold et Zuccarini) Carrière in eastern Asia (Sakhalin; Tamanuki 1933); *Tilia*, *Salix caprea* L., and *Po. tremula* L. in Russia (Mamaev et al. 1977, Nikitskij et al. 1996); *Larix decidua* Miller and *A. alba* Mill. in southern Poland (Trella 1939, Kinelski and Szujewski 1959, Buchholz et al. 2012); and *Fagus sylvatica* L. in Slovakia (Anonim 2012). Additionally, in the Białowieża Forest, larvae of *B. schneideri* were found on *Q. robur*, *Al. glutinosa*, *Pic. abies*, and *Be. pendula*, but only once under the bark of ash *F. excelsior*. This is a very rare host tree (Mamaev et al. 1977), probably avoided by this species. During our study, we observed mass dying of ash trees, so availability of potential host trees was high, but we found only one occupied tree out of hundreds we examined. In the Białowieża Forest, second most frequently occupied habitat by *B. schneideri* was mesic deciduous forest, where Scots pine also occurs quite often.

According to Mamaev et al. (1977), *B. schneideri* in Russia do not exhibit any preferences for host trees—it can be found “on all widely distributed coniferous tree species and on many species of deciduous trees.” This statement provides partial support for our hypothesis that in moderate climatic conditions, in contrast to boreal zone, this species become less selective. Probably, further north pine tree stands offer much better thermal conditions than spruce or deciduous tree stands. However, in temperate zones, preference for old, standing pine trees are still obvious.

In Lithuania (Blażyte-Čereškienė and Karalius 2012), *B. schneideri* did not exhibit any preferences for position of feeding site against the points of compass, whereas in the Białowieża Forest, this species was found mostly in the northern side of the host trees, but this observation is not confirmed statistically. In our opinion, demands of this species regarding sun exposure are considerably lower in the Continental region (the Białowieża Forest) than in Boreal region (Lithuania). In Lithuania, shade over 80% was not suitable for *B. schneideri* (only 6% of larvae was found in such conditions). Moreover, this species avoided pine tree stands with higher admixture of spruce, demonstrating preferences for sunny exposures (Blażyte-Čereškienė and Karalius 2012). Our study in the natural forests did not confirm these previous observations, because it more frequently occupied overshadowed trees and proportion of spruce in a tree stand, which can be used as approximation for light conditions, and did not affect significantly occurrence of this species. In the Białowieża Forest, we found statistically significant differences between the number of occupied trees in full and moderate shadow and trees exposed to the sun. In the Białowieża Forest, this species occurred also often in the pine-spruce tree stands. Moreover, spruce is a host tree of *B. schneideri* in the Białowieża Forest but also in Finland (Baranowski 1977). The spruce (*Pic. jezoensis*) was also a host tree of this species on Sakhalin (Tamanuki 1933). Probably, there is association between exposure to the sun and humidity, because

Table 3. Host trees and characteristics of breeding material of *B. schneideri* in the Białowieża Forest

Tree species	Number of locations	Tree diameter in the place of BS occurrence (cm)			Position of host tree (number of trees)			Shading of host tree (number of trees)			Humidity of substrate (number of trees)		
		Min.	Max.	Mean (SD)	Laying	Standing	No data	Low	Moderate	High	Low	Moderate	High
<i>P. sylvestris</i>	133	18	120	52.9 (22.5)	9	101	23	23	34	20	5	21	18
<i>Q. robur</i>	26	30	170	74.5 (30.9)	19	3	4	1	4	10		2	11
<i>Al. glutinosa</i>	8	30	80	40.9 (16.1)	5	2	1			6			4
<i>Pic. abies</i>	7	30	90	61.3 (20.1)		7			3	2		1	
<i>Be. pendula</i>	3	10	50	26.7 (17.0)	2	1			1				1
<i>F. excelsior</i>	1	55	55	55.0 (0.00)	1					1			1
No data	5	—	—	—			6						
Total	183	—	—	—	36	114	34	24	42	39	5	24	35

Conditions in the place where *B. schneideri* was found (shading of host tree and humidity of substrate) were estimated by investigator, using three subjective categories (low, moderate, and high).

B. schneideri preferred in the Białowieża Forest more humid substrate. Considering habitat requirements, this species can be treated as inhabitant of the forest interior, at least in temperate climatic zone.

According to Blażyte-Čereškienė and Karalius (2012), probability of occupation of host plant by *B. schneideri* is growing along with increasing diameter and age of a tree, but this species can also occur in the trees of diameter of 10–20 cm (thinnest tree had only 8 cm of diameter), and such trees are most commonly found in managed forests. In natural forests of the Białowieża Forest, occupied trees were much thicker, although there were single cases where *B. schneideri* was found on thin birch (10 cm) and pine (18 cm). Mean diameter of host trees was 53 cm for pine and 74 cm for oak. Also in Finland, where *B. schneideri* was found in the forest of natural character (near Pallosensaara), larvae occurred in pine trees of mean diameter of 40 cm (Baranowski 1977).

It seems that this species prefers, to some extent, trees killed by fire (Hyvärinen 2006, Anonim 2011), but according to Blażyte-Čereškienė and Karalius (2010), most frequently colonize single, dead trees left on clear cuts. In Lithuania, the following forest communities were favored: *Cladonio-Pinetum*, *Vaccinio vitis-idaea-Pinetum*, *V. myrtilli-Pinetum*, *Ledo-Pinetum*, and *Vaccinio uliginosi-Pinetum* (Karalius and Blażyte-Čereškienė 2009; Blażyte-Čereškienė and Karalius 2010, 2012). Our study confirms that this species prefers coniferous tree stands. We cannot say much about intensity of occupation on burned areas, because forest fires in the Białowieża Forest occur only occasionally and are restricted to small areas. However, in the past (until 1874), ground forest fires were more frequent (Niklasson et al. 2010) and shaped habitats, which became more suitable for this species. Fires, which occurred mainly in coniferous tree stands preferred by *B. schneideri*, were of human origin and related to forest bee-keeping. Moreover, fires restricted area covered by Norway spruce and promoted regeneration of Scots pine.

B. schneideri is recognized as relict of primeval forests (Baranowski 1977; Burakowski et al. 1987; Stebnicka 1991; Kubisz 2004a,b). Studies in Lithuania demonstrated that this species occurred significantly more frequently in the central part of large forest complexes than in the forest edge or in small, isolated woods. In those areas, *B. schneideri* preferred forests larger than 200 km², which provided stable life conditions in a long-term perspective (Karalius and Blażyte-Čereškienė 2009). Also, our results confirm preferences of *B. schneideri* for more natural forest, because this species was found more frequently in the locations more distant from the forest edge, which are most probably less affected by logging. On the other hand, Blażyte-Čereškienė and Karalius (2010, 2012) try to undermine an idea that this species is a relict of primeval forests, because, according to their own experiences, *B. schneideri* occurred in a large number of tree stands planted by humans and was found in relatively thin trees (10–20 cm). In our opinion, this species is mainly connected with the forests of natural origin, which guarantee continuity of supply of dead wood. In Poland,

B. schneideri mainly occur in this type of forests (Białowieża Forest—our data, Świętokrzyskie Mountains and Arłamów Forest—Buchholz et al. 2012) where old, standing dead trees are numerous currently and were common in the past. This species disappeared from many localities in Europe due to intensive forest management and a lack of a sufficient amount of dead wood. Occurrence of *B. schneideri* in managed forests in Lithuania indicates that within managed woods exist natural tree stands, and in addition, there are numerous standing, dead pine trees. One can also assume that along with changes of habitat conditions, local populations of *B. schneideri* become adapted to colonization of trees of smaller diameter.

According to available literature, *B. schneideri* occurred in the past more widely in Europe (Lentz 1879, Petri 1912, Łomnicki 1913). This species probably became totally extinct or is found in a limited number of locations and density in many European countries, i.e., in Romania and Germany (Horion 1956, Kubisz 2004b). The main reason for decline of this species were changes in the forest structure (rejuvenation, decrease of tree diameter, and unification of species composition), decrease of forest complex size, but first of all discontinuity of occurrence of natural tree stands. Current forest management in most European countries, particularly in the European Union, should focus on restoration of dead wood supplies in the forest that should promote existence of *B. schneideri*. To save this species, we should provide permanent access to dead trees of large diameter with untouched bark, particularly pine trees. These conditions can be achieved only under strict protection of the tree stands.

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