

Factors determining the occurrence of Flat Bugs (*Aradidae*) in beech dominated forests

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Abstract

The habitat requirements of most Aradidae and the decisive factors that influence their occurrence are still poorly understood. To reduce this lack of knowledge a standardised survey of Aradidae in two large beech forest areas of Bavaria (northern Steigerwald and High Spessart) was conducted. The following hypotheses were tested: 1) With increasing 'habitat tradition' (temporal continuity), population densities of Aradidae increase, 2) Increasing dead wood supply supports higher abundance of Aradidae, 3) There are key structures for particular species with respect to type of dead wood, diameter and exposure to sunlight, and 4) The occurrence of particular fungi species determines the occurrence of Aradidae. In our study, Aradidae were sampled in point sample plots by flight-interception traps and time-standardised hand collection. To analyse specific habitat requirements additional sampling was performed to increase the sample size. Four species of Aradidae were observed in the two forest areas: Aneurus avenius, Aradus betulae, A. conspicuus and A. depressus. The results demonstrate that all species have different and specific habitat requirements. Especially for A. betulae 'habitat tradition' of standing dead wood of large dimensions infested by Fomes fomentarius seems to be crucial. Hence, A. betulae was only observed in the Spessart and only at the sites with 'habitat tradition'.

Keywords: *Aradidae*, habitat tradition, dead wood amount, habitat requirements, beech forests

Zusammenfassung

Die Habitatansprüche der meisten *Aradidae* sowie die entscheidenden Faktoren die ihr Auftreten bedingen werden immer noch wenig verstanden. Um diese Wissenslücke zu verringern wurde eine standardisierte Aufnahme der *Aradidae* in zwei großen Buchenwaldgebieten Bayerns (nördlicher Steiger-

wald, Hochspessart) durchgeführt. Dabei wurden folgende Hypothesen getestet: 1) Die Populationsdichten der *Aradidae* steigen mit zunehmender Totholztradition, 2) erhöhte Verfügbarkeit an Totholz fördert eine höhere Abundanz der *Aradidae*, 3) es gibt Schlüsselstrukturen für bestimmte Arten in Bezug auf Totholztyp, -durchmesser und Sonnen-Exposition und 4) das Auftreten bestimmter Pilzarten bestimmt das Vorkommen der *Aradidae*. Zu diesem Zweck wurden *Aradidae* im Probekreisen mit Hilfe von Luftteklektoren und zeitnormierte Handaufsammlungen erfasst. Zur Analyse von spezifischen Habitatansprüchen wurden zusätzliche Fänge durchgeführt um die Stichprobengröße zu erhöhen. Vier Arten der *Aradidae* wurden in den beiden Gebieten festgestellt: *Aneurus avenius*, *Aradus betulae*, *A. conspicuus* und *A. depressus*. Die Ergebnisse zeigen, dass alle Arten unterschiedliche und spezifische Habitatansprüche haben. Besonders für *A. betulae* scheint die Totholztradition, von starkem, von *Fomes fomentarius* besiedeltem, stehendem Totholz, eine entscheidende Rolle zu spielen. Folglich wurde sie Art nur am Totholz-traditionsreicheren Waldstandort, dem Spessart, gefunden.

Schlüsselbegriffe: *Aradidae*, Totholztradition, Totholzmenge, Habitatansprüche, Buchenwälder

Introduction

Flat bugs (*Aradidae*) are a very old family among the *Heteroptera*. The oldest records are from Burmese amber (around 100 million years BP; HEISS & GRIMALDI 2001, 2002). Records in Baltic amber were dated to 40-50 million years BP (HEISS 1997, 1998, 2002). Despite their great phylogenetic age and resulting scientific interest, the ecology of *Aradidae* is poorly understood. Current knowledge is based largely on individual observations and rearings (FÖRSTER 1953, GYLLENSVÄRD 1958), as well as a few review articles including general information on the ecology of particular species (e.g. WAGNER 1966, TAMANINI 1981, LIS 1990, STEHLIK & HEISS 2001). It is known that most species are linked to dead wood structures, where they feed on wood decaying fungi. With their extremely long rostrum, which is curled in the head capsule when not in use, they pierce deeply into dead wood structures to broach cryptic fungal hyphae (WEBER 1930).

The decisive factors for the occurrence of *Aradidae* have not previously been studied in detail. With reference to saproxylic beetles and land snails MÜLLER (2005a) and MÜLLER et al. (2005a) demonstrated their dependency on the amount of dead wood by means of cutpoint analyses. 'Habitat tradition' (temporal continuity in supply of old growth dead wood and forest structures, according to MÜLLER et al. 2005b) is known to be another crucial factor for the occurrence of saproxylic beetles (MÜLLER 2005b, MÜLLER et al.

2005b). Hence, forest management clearly affects the occurrence of species linked to dead wood structures. The higher number of flat bug records in the eastern part of Europe, where larger continuous “untouched” forests still exist, indicates that similar factors might be of significance in this taxa. HALIÖVAARA & VÄISÄNEN (1983), for example, assume that most *Aradidae* species declined as a result of human activity in Finland. In many cases the occurrence of particular fungi species might be crucial, as was demonstrated by JONSELL et al. (2005), exemplified by studying *Aradus corticalis* and *Fomitopsis pinicola* on spruce high stumps in Sweden. Comparable studies on other species are still not available.

In Germany most flat bug species are rarely recorded. Hence, 68% of all *Aradidae* occurring in Germany are listed in the Red List (GÜNTHER et al. 1998, HOFFMANN & MELBER 2003), in Bavaria even 87% (ACHTZIGER et al. 2003). The protection of these species is only possible, if the decisive factors determining their occurrence are known. The aim of the present study is to broaden our knowledge of the crucial factors governing the occurrence of *Aradidae* in beech dominated forests. We tested the following hypotheses:

1. With increasing ‘habitat tradition’, population densities of *Aradidae* increase.
2. Increasing dead wood supply leads to a greater abundance of *Aradidae*.
3. There are key structures for particular species with respect to type of dead wood, diameter and exposure to the sun.
4. The occurrence of particular fungi species determines the occurrence of *Aradidae*.

To test these hypotheses *Aradidae* were collected in beech dominated closed forest areas of the northern Steigerwald and the High Spessart using flight interception traps and hand collection in the years 2005 and 2006.

Material and Methods

Study sites

The study was conducted in two large beech dominated forest areas in Northern Bavaria, Germany; the ‘Steigerwald’ and the ‘Spessart’ (Fig. 1). Because the surveys at the two sites were part of two different large scale projects (Steigerwald, see MÜLLER 2005a; Spessart, see BÜBLER et al. 2007), an identical approach was not possible. As far as possible the design of the second study was adapted to that of the first. This enabled a comparison between the two sites.

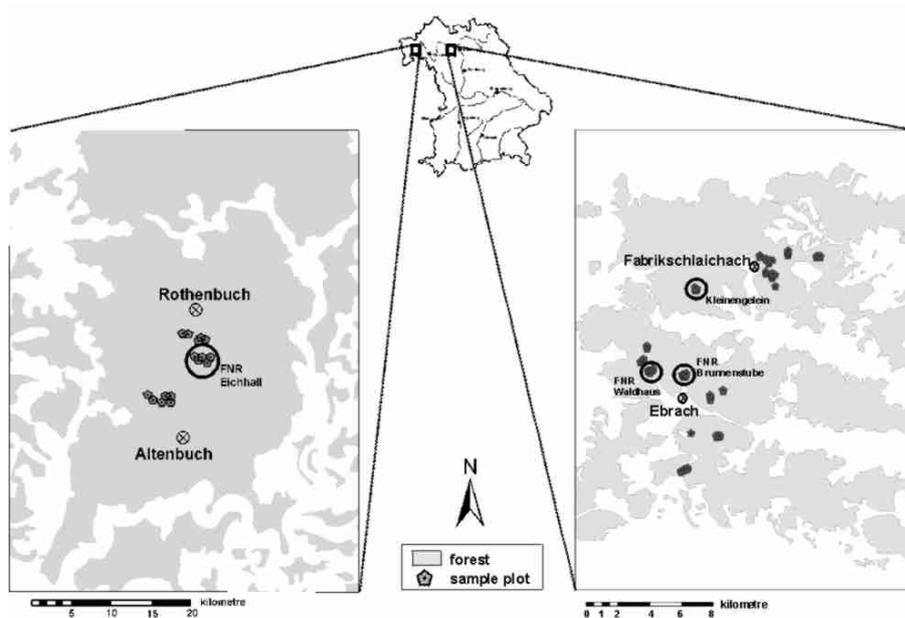


Fig. 1: Study sites and plots in the two forest areas “High Spessart” (left) and “Northern Steigerwald” (right). Different sites and Forest Nature reserves are marked (Spessart: Altenbuch=SP-A, Rothenbuch=SP-B, FNR Eichhall=SP-C; Steigerwald: Fabrikschlaichach=ST-A, Ebrach=ST-B, FNR Waldhaus / FNR Brunnenstube / Kleinengelein=ST-C).

Geologically, both regions are part of the “Franconia Escarpment Landscape” (GERSTBERGER 2001). The forest growth zone of the Steigerwald is ‘Franconian Keuper and Alb Foreland’, the Growth district ‘Steigerwald’. The study sites in the Spessart are located in the forest growth zone ‘Spessart-Odenwald’, within the growth district ‘Brownstone-Spessart’, in the growth sub-district ‘High Spessart’. The map of potential natural forest vegetation of Bavaria includes the Steigerwald in the category ‘colline and submontane beech and oak-hornbeam forests’ (*G a l i o - C a r p i n e t u m*) and the High Spessart in the ‘colline and high montane beech forests’ (*L u z u l o - F a g e t u m*)’ (WALENTOWSKI et al. 2001, WALENTOWSKI et al. 2006).

The study area Steigerwald is part of the warm-temperate climate within the transition area between maritime and continental climate. The climate in the Spessart is stated to be temperate-oceanic (BAYFORKLIM 1996). Average annual temperature varies between 7-8°C in both forest areas. Average annual precipitation is 850mm in the Steigerwald (LISCHEID 2001) and 900-1,000mm in the Spessart.

The northern Steigerwald comprises a forest area of 22,500ha. Altitude of study plots ranges between 325 and 520m a.s.l. (see MÜLLER 2005a). With 200,000ha the Spessart is one of the largest deciduous forests in Germany. The 'High Spessart', particularly the 'Heisterblock' including 240-415 year old oaks (*Quercus petraea*) and up to 180 year old beeches (*Fagus sylvatica*) can be referred to as one of the oldest forests in Central Europe outside the Alps (BUßLER & LOY 2004). The long tradition of old trees and dead wood structures within a relatively large area make these forests highly valuable for the conservation of the naturally evolved biodiversity of Central European forests. This has already been impressively demonstrated for saproxylic beetles (e.g. BUßLER & LOY 2004). Altitude of study plots ranges between 310 and 450m a.s.l. For details of stands studied in the High Spessart see BUßLER et al. (2007).

Sampling design and data analysis

The *Aradidae* were sampled by flight-interception traps (FIT; Steigerwald: March-October 2004, Spessart: May-October 2006) as well as by hand collecting (Steigerwald: 16.-25. May 2005; Spessart: 15.-19. May 2006) within 69 (Steigerwald) and 45 (Spessart) point sample plots (18m radius) (table 1). Flight interception traps were installed in the centre of each plot and emptied monthly. Hand collecting was standardised to 45min sampling in each plot. The data collected in these point sample plots were used for further statistical analyses with respect to the four hypotheses.

Tab. 1: Summary of sampled stand and tree categories. FIT=Flight interception trap (WINTER et al. 1999)

forest age [years]	Steigerwald			Spessart		
	ST-A 100- 200	ST-B 100- 200	ST-C up to 350	SP-A 100- 200	SP-B 100- 200	SP-C up to 420
Mean dead wood volume of deciduous trees [m ³ /ha]	22	34	>150	14	27	68
Number of point sample plots	24	24	21	15	15	15
Number of FITs near ground	24	24	21	15	15	15
Oak crown (FIT)	9	9	9	/	/	/
Beech crown healthy (FIT)	12	12	12	/	/	/
Beech crown 'die-back' (FIT)	12	12	12	/	/	/
Beech trees with rot holes (FIT)	6	2	9	/	/	/

ST-A: managed forest site Fabrikschleichach; ST-B: managed forest site Ebrach; ST-C: Forest Nature Reserves Waldhaus, Brunnenstube, Kleinengelein (designation as a FNR planned). SP-A: managed forest site Altenbuch; SP-B: managed forest site Rothenbuch, SP-C: Forest Nature Reserve Eichhall.

'Habitat tradition' is defined as temporal continuity in the occurrence of dead wood structures of various decomposition stages necessary for the colonisation by particular fungi species that are used as food resources by *Aradidae*. The effects of 'habitat tradition' (hypothesis 1) were studied in two approaches:

1. Comparison of two areas of different continuity in dead wood structures and old trees (Spessart>Steigerwald). We predicted that abundance of *Aradidae* is higher in the forest area with longer habitat tradition (Spessart) compared with a forest area with shorter habitat tradition (Steigerwald). The hypothesis of independence between the two forest areas was tested with the "independent two-sample location test" based on distribution of permutations (HOLLANDER & WOLFE 1999). The calculation was performed using the add-on package "coin" (HOTHORN et al. 2007) for the R.2.4.1 system for statistical computing (IHAKA & GENTLEMAN 1996).
2. Within these two areas three categories of different intensities of forestry operations and therefore different habitat tradition were classified:

a) Steigerwald

Category ST-A: 100-200 year old managed forest stands at site Fabrikschleichach. This site can be characterised by intensive yield management and silviculture over many decades, aimed at production of high quality timber. Only for a short, recent period has more importance been attached to dead wood and habitat trees.

Category ST-B: 100-200 year old managed forest stands at site Ebrach. At this site a long tradition of forest management orientated towards nature conservation exists. Dead wood and habitat trees are highly valued.

Category ST-C: Three totally protected Forest Nature Reserves (FNR) with up to 350 year old beech trees; FNR Waldhaus, FNR Brunnenstube and Kleinengelein (planned to be designated as FNR). In the FNRs all kinds of forest management have ceased; the protection of natural forest processes is of the greatest importance.

b) Spessart (for details concerning SP-A and SP-B see BUßLER et al. 2007)

Category SP-A: 100-200 year old managed forest stands at site Altenbuch. This site is characterised by intensive yield management and attention given to growth of high quality wood over many decades.

Category SP-B: 100-200 year old managed forest stands at site Rothenbuch. At this site the 'Rothenbuch concept of habitat trees and dead wood' was implemented more than 15 years ago (BUßLER et al. 2007).

Following this concept, habitat trees are specifically protected and accumulation of dead wood is encouraged.

Category SP-C: A totally protected Forest Nature Reserve (FNR) of 67ha with up to 420 year old trees; FNR Eichhall. All forest management has ceased; the protection of forest processes is of the greatest importance.

We predicted that abundance of *Aradidae* increases from category A to C at both sites. The hypothesis of independence between the three categories of different management intensity and the dependent variable "number of sampled *Aradidae*" was tested with the "linear-by-linear association test of resampling-based multiple testing" (AGRESTI 2002). The calculation was performed using the add-on package "coin" (HOTHORN et al. 2007) for the R.2.4.1 system for statistical computing (IHAKA & GENTLEMAN 1996).

The greater the amount of dead wood, the higher is the chance for *Aradidae* to find suitable structures (decomposition stage, fungi as food resources). For analysing the dependence of *Aradidae* on dead wood supply (hypothesis 2) two different approaches were used:

- 1) Dead wood structures of different categories were measured (solid volume per hectare) in each of 69 point sample plots (Steigerwald) and 30 point sample plots (Spessart SP-A, SP-B; in NWR Eichhall no inventory was undertaken because of a lack of manpower). The following dead wood categories were defined: standing dead wood (>12cm diameter), lying dead wood (>12cm diameter), dead wood <12cm diameter, stumps (height <1m).
- 2) During the survey of *Aradidae* in each point sample plot an inventory of the number of dead wood structures classified as standing and lying dead wood and different diameter classes (>25cm, <25cm, <10cm, <5cm) was performed. Additionally the number of stumps (<1m height) was counted.

In both approaches a multiple correlation analysis of the abundance of *Aradidae* (separated by species) and the amount and number of dead wood structures (separated by different categories) was performed. Therefore a Spearman correlation test, adjusted by Bonferroni-Holm, was calculated using the add-on package "coin" (HOTHORN et al. 2006, 2007) within the R2.4.1. system for statistical computing (IHAKA & GENTLEMAN 1996).

For analysing key structures for *Aradidae* (hypothesis 3) a descriptive analysis was performed: The analysis was focused on three parameters:

- a) type of dead wood (lying / standing stems, dead branches on living trees, dead branches situated in the lower vegetation, stumps < 1m high).

- b) diameter of dead wood structures, and
- c) exposure to sunlight (shaded, semi-shaded, sunny).

To achieve a higher sample size, additional sampling outside the point sample plots at sites SP-B and SP-C was performed in the Spessart (4.5.2006, 3./4.7.2006).

Additionally, we tested if *Aradidae* also occur in higher forest strata when suitable resources are available, based on sampling by crown flight-interception traps in the Steigerwald during 2004. For this purpose flight-interception traps were installed on healthy and unhealthy ('die-back') beech trees (*Fagus sylvatica*) at heights of 1-28m and in crowns of healthy oaks (*Quercus petraea*) at heights of 13-24m.

To analyse the dependence of *Aradidae* on the occurrence of particular fungi species (hypothesis 4), two different approaches were used:

- 1) A statistical approach: A fungi inventory was performed in all 69 point sample plots in the Steigerwald in four surveys (20.04.-01.05., 18.07.-29.07., 24.09.-30.09., 14.10.-23.10.) during 2004 and in 30 plots in the Spessart (SP-A, SP-B) in four surveys (21.-22.04., 05.-07.07., 21-23.09., 08.-10.11.) during 2006. Statistical analysis was performed by a Spearman correlation test, adjusted by Bonferroni-Holm, as described above. In the analyses for the Steigerwald all observed fungi species that are described as possible host species in literature and species that were found on bark samples (see point 2) were included; *Trametes versicolor*, *T. hirsuta*, *T. gibbosa*, *Bjerkandera adusta*, *Polyporus* sp., *Fomes fomentarius*, *Fomitopsis pinicola*, *Hypoxylon fragiforme*, *Diatrype disciformis*, *Diatrype stigma*, *Schizophyllum commune*, *Ganoderma applanatum*, *Eutypella quaternata*. In the Spessart only part of these species was surveyed quantitatively and therefore only these were included in that analysis: *T. versicolor*, *T. hirsuta*, *T. gibbosa*, *B. adusta*, *F. fomentarius*, *G. applanatum*.
- 2) A descriptive approach: All bark parts where *Aradidae* were found were analysed for fungi.

The determination of *Aradidae* was done by the first author (M.G.) based on the publications of WAGNER (1966), KANYUKOVA (1984) and VÁSÁRHELYI (1985). Surveys and determination of fungi were carried out by the co-authors (Steigerwald H. E.; Spessart: M. B.). Fungi were determined in the laboratory using genus-specific special literature (DENNIS 1968, BARNETT & HUNTER 1972, BREITENBACH & KRÄNZLIN 1984–2005, ELLIS & ELLIS 1985, PETRINI & MÜLLER 1986, HJORTSTAM et al. 1987-1988, KRIEGLSTEINER 2000-2003). Voucher specimens of all species (*Aradidae*, Fungi) are in the collection of the first author.

Results

In the Steigerwald a total of 197 specimens of three flat bug species were collected: *Aneurus avenius* (148 specimens on 33 dead wood structures, 1 in flight interception trap), *Aradus conspicuus* (44 specimens on 22 dead wood structures, 3 in flight interception traps) and *Aradus depressus* (1 in flight interception trap). In the Spessart a total of 251 specimens of four species were observed: *A. avenius*, *Aradus betulae*, *A. conspicuus* and *A. depressus* (see Fig. 2). Because of aggregations on optimal habitat trees, *A. betulae* was the most abundant species (151 specimens on 14 habitat trees), followed by *A. conspicuus* (88 specimens on 59 dead wood structures), *A. avenius* (11 specimens on 10 dead wood structures), and *A. depressus* (2 specimens, 1 landed on a red tee-shirt during the survey, 1 on dead wood structure). All species and specimens that were sampled in the point sample plots are shown in Table 2. Sample sizes resulting from hand collecting in point sample plots (192 specimens of two species (*A. avenius*, *A. conspicuus*) in the Steigerwald and 90 specimens of three species (*A. avenius*, *A. conspicuus*, *A. betulae*) in the Spessart) were much higher than those from trap-sampling (Steigerwald: 3 specimens/2 species, Spessart: 2 specimens/1 species). All specimens collected in traps were found between April and June, with the exception of one *A. avenius*, sampled in July in the crown of a beech.

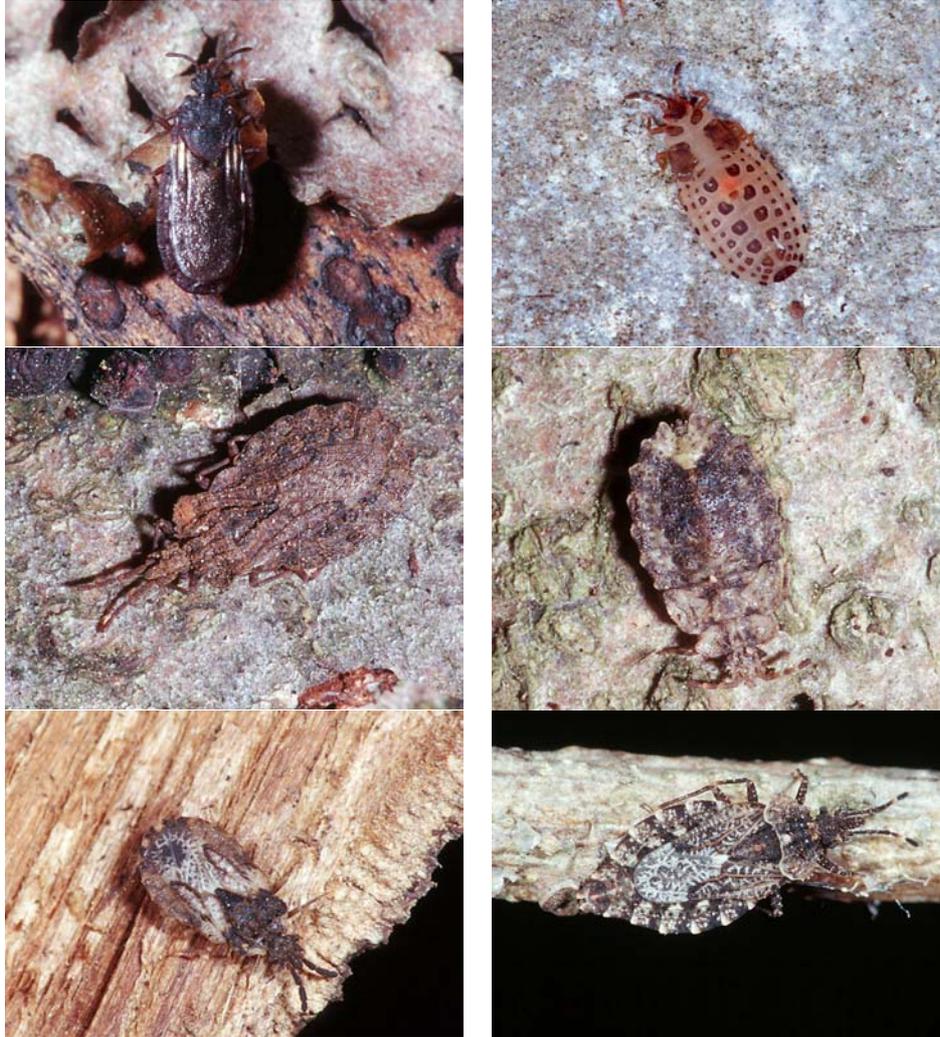


Fig. 2: The four observed species of Aradidae: a) *Aneurus avenius*, b) *A. avenius* juv., c) *Aradus conspicuus*, d) *A. conspicuus* juv., e) *Aradus depressus*, f) *Aradus betulae*. (Photos: M. GOßNER)

Dependence on 'habitat tradition'

An overview of sampling results from point sample plots is given in Table 2.

Tab. 2: Records of *Aradidae* in relation to management intensity. Number of point sample plots and total number of sampled specimens in these plots is given. In brackets: number of specimens sampled by flight interception traps.

	Steigerwald			total ST	Spessart			total SP
	ST-A	ST-B	ST-C		SP-A	SP-B	SP-C	
Number of point sample plots	24	24	21	69	15	15	15	45
<i>Aneurus avenius</i> (DUFOUR, 1833)	51	42	55	148	4	2	0	6
<i>Aradus betulae</i> (LINNAEUS, 1758)	0	0	0	0	0	37	11	48
<i>Aradus conspicuus</i> (HERRICH-SCHAEFFER, 1835)	9	29 (2)	8	46 (2)	25	6	5 (2)	36
<i>Aradus depressus</i> (FABRICIUS, 1794)		1 (1)		1 (1)	0	0	0	0
total	60	72 (3)	63	195 (3)	29	45	16 (2)	90 (2)

Total number of sampled *Aradidae* was significantly higher in the Steigerwald compared to the Spessart (location test: $Z=2.48$; $p<0.02$). This results solely from the high abundance of *A. avenius* at this site ($Z=4.63$; $p<0.0001$). No significant difference in abundance between sites was observed for *A. conspicuus*. *A. betulae* was exclusively found in the Spessart, the comparison with the Steigerwald was significant ($Z=2.16$; $p<0.04$). Apart from the greater abundance of *A. avenius*, the conspicuously larger number of individuals per dead wood structure in the Steigerwald compared to the Spessart was remarkable (location test; $Z=2.55$; $p<0.02$). The average number of *A. conspicuus* per dead wood structure, however, was significantly higher in the Spessart ($Z=1.79$, $p<0.04$). No increase in flat bug abundance with increasing 'habitat tradition' (categories ST-A \rightarrow ST-C) was observed in the Steigerwald, either for total number of *Aradidae* or for the two most abundant species (linear by linear association test: $p>0.10$). In the Spessart, the number of captured species even decreased significantly with increasing 'habitat tradition' ($Z=2.276$, $p<0.03$). This could be traced back to the abundant and steady occurrence of *A. conspicuus* in SP-A (Fig. 3). In contrast, *A. betulae* was exclusively observed in stands of higher 'habitat tradition' (SP-B and SP-C) (Tab.2).

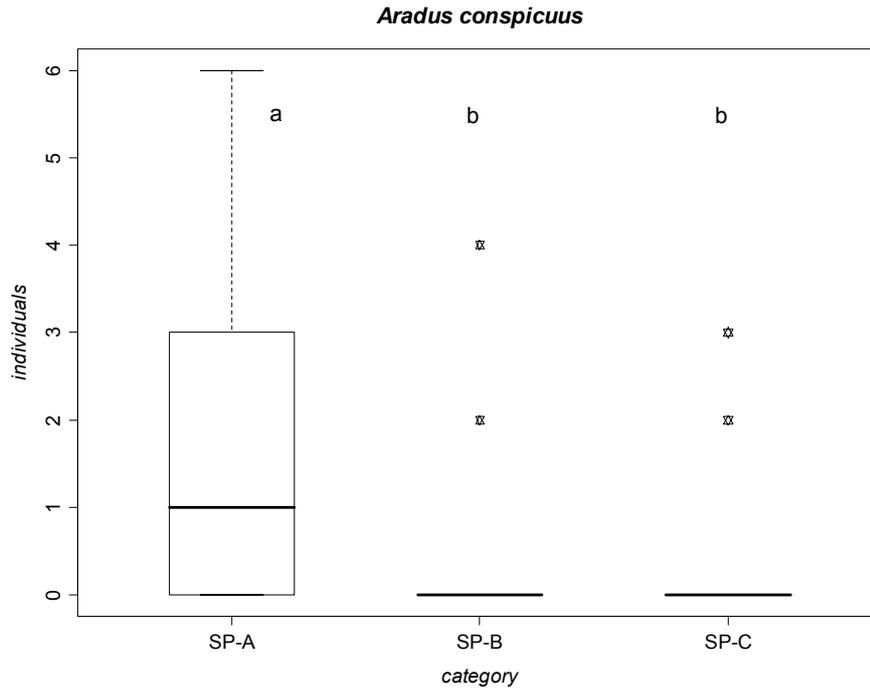


Fig. 3: Average number (median) of *Aradus conspicuus* sampled in plots of different 'habitat tradition' (SP-A<SP-B<SP-C) in the forest area Spessart (n=15 point sampling plots in each category). In SP-A *A. conspicuus* was observed in 8 plots, in SP-B and SP-C in 2 plots. Letters indicate significant differences.

Dependence on dead wood amount and dead wood parameters

No correlation was found between deadwood amount (m³/ha) in the point sample plots and the abundance of *Aradidae*, either for the Steigerwald or for the Spessart (Spearman correlation analysis, adjusted by Bonferroni-Holm: $p > 0.10$). In Spessart, however, a positive correlation between the number of standing dead wood structures <5cm and the abundance of *A. avenius* (estimated correlation coefficient: 0.407, $p = 0.050$) was observed. Moreover the number of sampled *A. conspicuus* was positively correlated with the number of stumps (<1m height) in the point sample plot (estimated correlation coefficient: 0.387, $p = 0.078$).

More than 97% of all investigated dead wood structures originated from *F. sylvatica*, the proportion of other tree species (*Carpinus*, *Quercus*, *Alnus*, *Ulmus*, *Picea*, *Larix*, *Pinus*) was <1%. Hence, almost all records of *Aradidae*

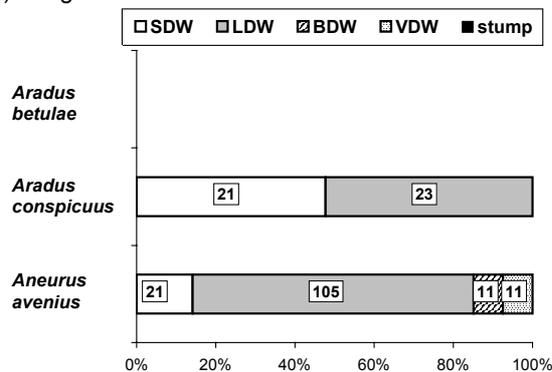
were from *F. sylvatica*. Only two samples with a total of five *A. avenius* were obtained from *Carpinus betulus* in the Steigerwald. One female of *A. conspicuus* was found under the bark of a recently deceased standing oak tree of >1m diameter in the FNR Eichhall.

Almost all specimens were found under the bark of dead branches or stems, and once under the bark of the root plate of a fallen tree in the FNR Eichhall. In 97% of all observations the bark had already become detached from the dead wood. In two cases (*A. conspicuus*) the dead wood was very fresh and the bark was therefore difficult to remove from the wood (degree of decay 1, according to ALBRECHT 1991). In three samples (4 specimens) of *A. conspicuus* an incipient decomposition of the wood body was observed. In the remaining records of *A. avenius* and *A. conspicuus* the stage of decay of the wood was not recorded (but probably this was degree of decay 2). Specimens of *A. betulae* were observed within a wide spectrum of decomposition stages, from dying but still foliated beech trees to dead, standing trunks at an advanced stage of decomposition where only small areas with bark remained.

Type of dead wood

A. avenius primarily occurred in dead branches lying on the forest floor, but also in dead young beech trees of small diameter, in dead branches suspended in the lower vegetation (on shrubs etc.), and dead branches on living trees (Fig. 4). In contrast, *A. conspicuus* was observed in standing and lying dead wood in similar proportions (Fig. 4). Especially in the intensively managed forest stands in the Spessart (SP-A) this species was observed frequently in beech stumps of 30-50cm height, covered by moss.

a) Steigerwald



b) Spessart

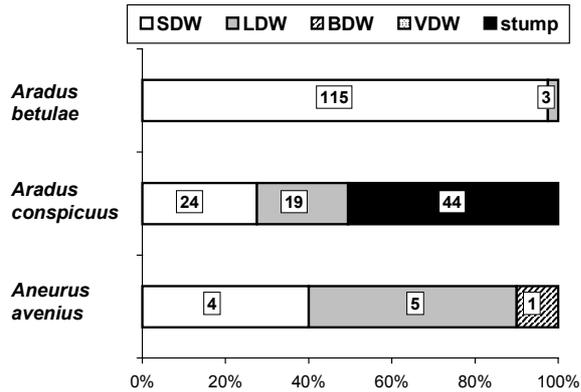


Fig. 4: Number and percentage of Aradidae, sampled in different types of dead wood: SDW=standing dead wood, LDW=lying dead wood, BDW: dead branches on living trees, VDW: dead branches suspended in the lower vegetation, stump=stumps <1m height.

95% of all records of *A. avenius* and 87% of *A. conspicuus* were observed in branches and stems without contact to the ground. Two specimens were sampled by flight interception traps at heights out of the reach of a researcher. One specimen of *A. conspicuus* was found in a trap that was installed 4 meters in front of a rot hole, one specimen of *A. avenius* on a beech tree with crown die-back at a height of 14 meters.

Diameter of dead wood

The distribution of diameter classes of dead wood and therefore the potential structural availability for Aradidae was comparable at both sites (Fig. 5). Aradidae were found in a total of 4.4% (Steigerwald) and 3.4% (Spessart) of all investigated dead wood structures. *A. avenius* primarily colonised thin dead wood structures of maximum 10cm diameter, exhibiting a peak at 2cm. In contrast, *A. conspicuus* occurred in thicker dead branches and stems (Fig. 6). With 10cm, the peak was conspicuously lower in the Steigerwald compared to the Spessart (60cm). This was mainly because a high number of beech stumps were colonised by *A. conspicuus* in SP-A. *A. betulae* was observed almost exclusively in dead wood structures with diameter >60cm.

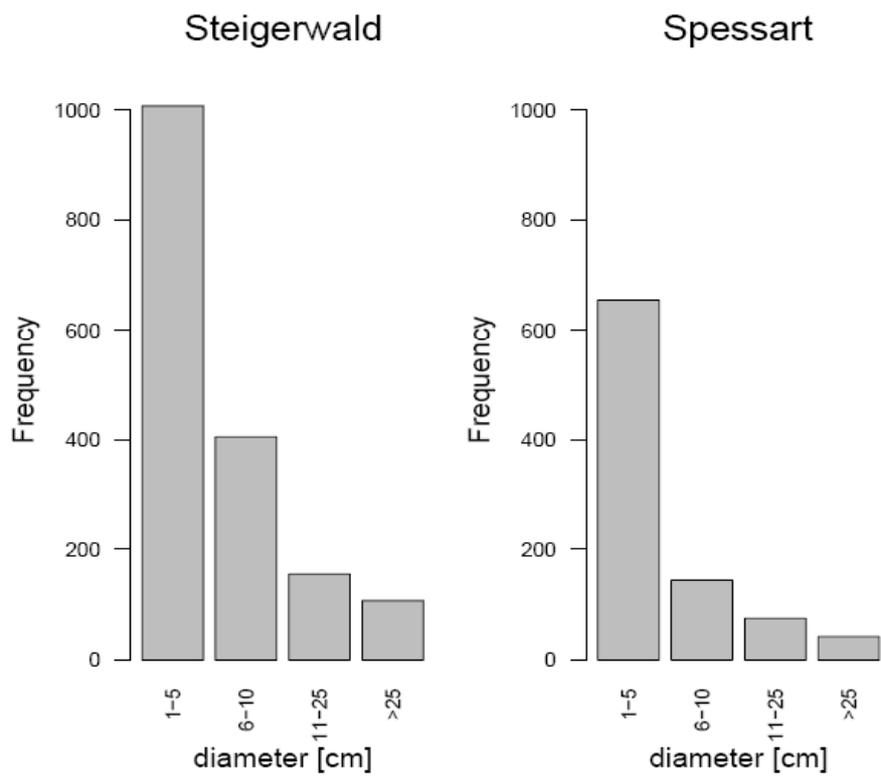


Fig. 5: Distribution of diameter classes of dead wood in the Steigerwald and in the Spessart.

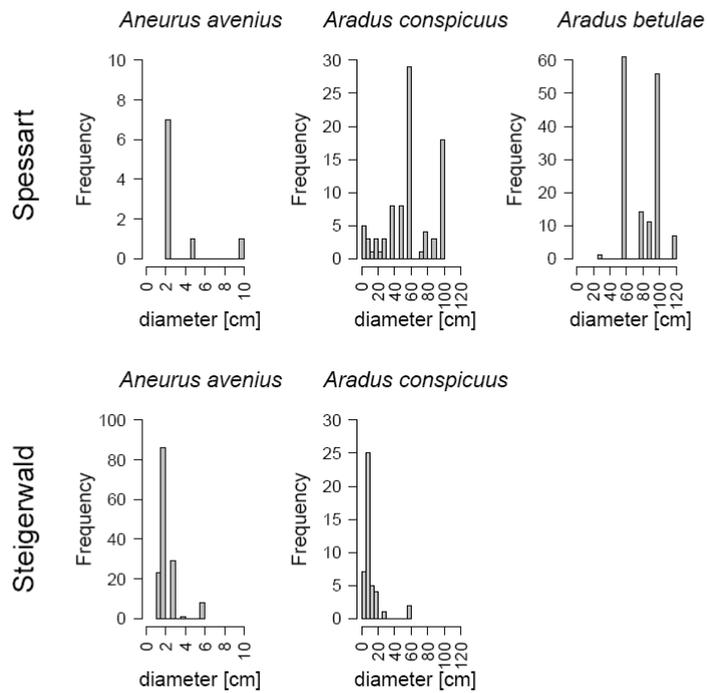
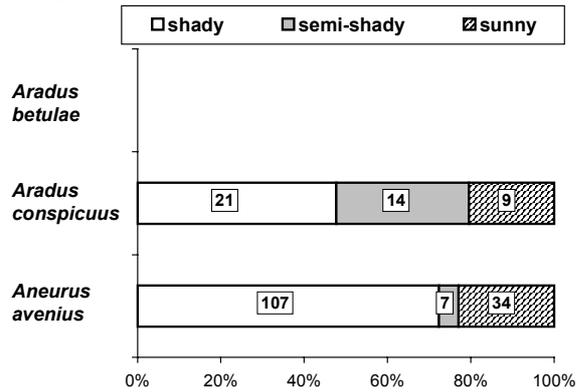


Fig. 6: Histograms, showing the frequencies of *Aneurus avenius*, *Aradus conspicuus* and *Aradus betulae*, found in dead wood structures of different diameter. Note that scales differ between figures.

Exposure to sunlight

The majority of *A. avenius* was sampled in shady places (Fig. 7). *A. conspicuus* occurred more often in more open forest areas and *A. betulae* was observed exclusively in semi-shady and sunny places.

a) Steigerwald



b) Spessart

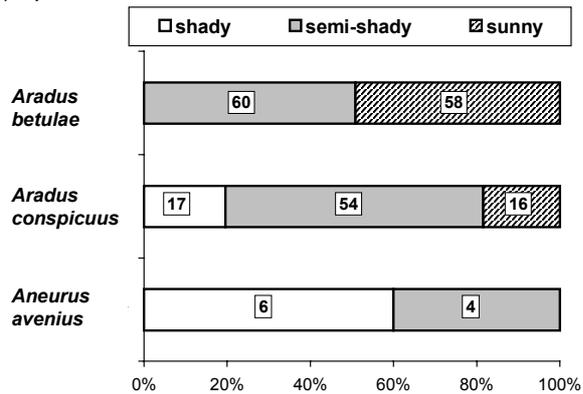


Fig. 7: Number and percentage of *Aradidae*, sampled in dead wood exposed to different levels of sunlight.

Dependence on fungi

A correlation analysis between the number of sampled *A. conspicuus* und *A. avenius* and the occurrence of fungi species in the point sample plots revealed no significant differences in results, neither for the Steigerwald nor for the Spessart ($p > 0.10$).

Fungi species were found in 80% (Steigerwald) and 89% (Spessart) of all bark samples associated with *A. conspicuus* (Steigerwald). For *A. avenius* corresponding figures were 24% (Steigerwald) and 33% (Spessart), and in *A. betulae* 100% (Spessart). Table 3 shows recorded fungi species. In some cases two fungi species were observed in one bark sample. For *A.*

conspicuus in the studied stands, *Hypoxylon fragiforme* seems to be important in the Steigerwald and *Bjerkandera adusta* in the Spessart. However, *A. conspicuus* was observed while feeding only on *B. adusta*. Most records of *A. avenius* were from bark samples containing *Xylariaceae* (*Sphaeriales*) (above all *Hypoxylon fragiforme*) and Fungi Imperfecti (*Coelomycetes*) (above all *Asterosporium asterospermum*). *A. betulae* occurred almost exclusively on dead standing trunks of beech colonised by *Fomes fomentarius*.

Tab. 3: Number and frequency (in brackets) of *Aradus conspicuus* and *Aneurus avenius* found in bark samples together with fungi species. In some cases a second fungus species was observed (Fungus 2).

<i>Aneurus avenius</i> Fungus 1	Fungus 2	Steigerwald (det. H. Engel)	Spessart (det M. Blaschke)
Xylariaceae (Sphaeriales)			
<i>Hypoxylon fragiforme</i>	/	4 (2)	
<i>Hypoxylon fragiforme</i>	Fungi Imperfecti (Hyphomycetes)	4 (1)	
	<i>Cryptocoryneum condensatum</i>		
<i>Hypoxylon ferrugineum</i>	/	1 (1)	
Diatrypaceae, Sphaeriales (Diatrypales)			
<i>Diatrype disciformis</i>	/	3 (1)	
<i>Diatrype stigma</i>	/		1 (1)
Fungi Imperfecti (Coelomycetes)			
<i>Asterosporium asterospermum</i>	/	10 (4)	
Fungi Imperfecti (Hyphomycetes)			
<i>Cryptocoryneum condensatum</i>	<i>Digitodesmium elegans</i>	3 (1)	
(anamorphic fungi)			
<i>Polymorphum rugosem</i>	/	1 (1)	
Schizophyllaceae (Aphyllorphales)			
<i>Schizophyllum commune</i>	/		1 (1)
<i>Schizophyllum commune</i>	<i>Nectria</i> sp. (Nectriaceae)	1 (1)	
Nectriaceae, Hypocreales			
<i>Nectria coccinea</i>	/	1 (1)	
Ascodichaenaceae (Rhytismatales)			
<i>Ascodichaena rugosa</i>	/		1 (1)
Pyronomycetes (Ascomycetes)			
	/	2 (1)	

Aradus conspicuus			
Fungus 1	Fungus 2	Steigerwald	Spessart
Xylariaceae (Sphaeriales)			
<i>Hypoxylon fragiforme</i>	/	26 (6)	
Coriolaceae (Polyporales)			
<i>Bjerkandera adusta</i>	/	1 (1)	51 (19)
<i>Trametes gibbosa</i>	/		4 (3)
<i>Trametes versicolor</i>	/		7 (3)
<i>Trametes hirsuta</i>	/		1 (1)
<i>Trametes hirsuta</i>	Pyronomycetes (Ascomycetes)	2 (2)	
<i>Trametes hirsuta</i>	Schizophyllaceae (Aphylophorales)		2 (1)
	<i>Schizophyllum commune</i>		
<i>Trametes sp.</i>	/		
<i>Fomes fomentarius</i>	/		11 (2)
Coriolaceae (Polyporales)			
	/	2 (1)	
Diatrypaceae (Diatrypales)			
<i>Eutypella quaternata</i>	Corticaceae (Aphylophorales)		
	<i>Schizopora paradoxa</i>	1 (1)	
Fungi Imperfecti (Coelomycetes)			
<i>Asterosporium asterospermum</i>	/	1 (1)	
<i>Asterosporium asterospermum</i>	Fungi Imperfecti (Hyphomycetes)	1 (1)	
	<i>Digitodesmium elegans</i>		1 (1)
Nectriaceae (Hypocreales)			
<i>Nectria coccinea cf.</i>	/		3 (1)
Tricholomataceae (Agaricales)			
<i>Armillaria sp.</i>	/		1 (1)
Coriolaceae (Polyporales)			
<i>Antrodia hoehnelii</i>	/		
Pyronomycetes (Ascomycetes)	/	1 (1)	
Aradus betulae			
Fungus 1	Fungus 2	Steigerwald	Spessart
Coriolaceae (Polyporales)			
<i>Fomes fomentarius</i>	/		116 (16)
<i>Trametes sp.</i>	/		1 (1)
Ganodermataceae (Polyporales)			
<i>Ganoderma applanatum</i>	/		1 (1)

Discussion

In Bavaria 11 species of Aradidae are known to occur in dead wood of *Fagus sylvatica* (HEISS 1972, STEHLIK & HEISS 2001, HOFFMANN & MELBER 2003). Of these, only four species were observed in the present study in the closed forest areas of the Steigerwald and the Spessart: *A. avenius*, *A. betulae*, *A. conspicuus* and *A. depressus*. There are several possible reasons for the absence of the other species. Species such as *Aneurus laevis*, *Aradus crenaticollis* and *A. versicolor* have not been found in Bavaria since 1950. Although *A. laevis* and *A. versicolor* have been observed in the Spessart (STADLER 1928, SINGER 1952), they might be very rare in this region, occurring only locally. Moreover, *A. laevis* and *A. versicolor* seem to prefer warmer climates (SINGER 1952, SCHNEID 1954, STEHLIK & HEISS 2001). In the Spessart they have been observed at lower altitudes only (SINGER 1952). *A. betulinus*, *A. obtectus* and *A. corticalis* mainly colonise conifer dead wood (HEISS 1972, STEHLIK & HEISS 2001) and have only seldom been recorded in dead wood of *Fagus sylvatica* (SINGER 1952, STEHLIK & HEISS 2001). Another reason why *A. betulinus*, *A. obtectus* and also *A. dissimilis* were not found in the present study might be their preference for higher altitudes (HEISS 1972).

A. depressus is usually the most abundant species on deciduous trees. At both study sites it was found only as single specimens. Possibly this species is more abundant in more open forest areas in mixed deciduous stands. In stands of coppice with standards containing *Quercus*, *Populus*, *Tilia*, *Carpinus* etc. in the southern Steigerwald this species was frequently recorded (in 24% of all traps, GOßNER, unpubl. data). All species sampled apart from *A. depressus* are listed as “threat suspected but status unknown” in the Red List of endangered species of Bavaria (ACHTZIGER et al. 2003). *A. betulae* is even categorized as “very endangered or endangered” for Germany (GÜNTHER et al. 1998).

Generally, flight interception-traps are not a suitable method for collecting *Aradidae*. As demonstrated above, only a few specimens were caught using this method. Our results support the idea that these species fly only during the mating season (April-June). Flight activity undertaken during searches for suitable dead wood structures for their brood, is too low to allow the *Aradidae* fauna of a particular habitat to be sampled representatively based on individuals caught in flight. Hence, reliable data on *Aradidae* can only be obtained by hand-collecting.

Dependence on ‘habitat tradition’

Species composition in the present study differed significantly between the Steigerwald and the Spessart. For example *A. betulae* occurred exclusively in the Spessart and *A. avenius* was more abundant in the Steigerwald.

Differences in climate between the Steigerwald and the Spessart are not thought to be crucial in explaining the differences between these forest areas. Both species have a broad amplitude in their climatic requirements (HEISS 1972, STEHLIK & HEISS 2001). Also, availability of suitable habitats seems not to be limited in either forest area. Most probably, shorter habitat tradition and therefore discontinuity in the availability of suitable breeding substrate is the reason for the absence of *A. betulae* in the Steigerwald compared to the Spessart. With a few exceptions all specimens of this species recorded for Bavaria are from the Alps (Upper Bavaria), especially from old forest sites such as the Forest Nature Reserve Friedergries (pers. observation). SCHUSTER (1987, 1993, 2001, 2005) mentions some records of *A. betulae* from different sites in Upper Bavaria (Walchensee, Sylvensteinsee, Reit im Winkl). Outside the Alps previous records are from dealpine relict occurrences (Chiemseemoor, SCHUSTER 2001; Kendlmühlfilzen, BRÄU pers. comm.), the Bavarian Forest (SCHUSTER 2001) and the Spessart (SINGER 1952). The Spessart can be referred to as one of the oldest forests of Central Europe outside the Alps (BUßLER & LOY 2004). In the Steigerwald habitat tradition was probably interrupted in the past and since that time recolonisation by *A. betulae* has not taken place. The importance of habitat tradition for *A. betulae* is confirmed by the fact that within the Spessart it was only observed at sites with long habitat tradition (Rothenbuch) and not in the intensively managed forest area of Altenbuch. MORDEL (2001) also suggested that *A. betulae* is restricted in Germany to a few ancient woodland sites such as pasture woodlands, or nearly virgin forest relict sites. In Finland, however, HELIÖVAARA & VÄISÄNEN (1983) did not find a noticeable decrease of *A. betulae* caused by human activity. Probably habitat tradition was not interrupted in this region.

For *A. avenius*, *A. conspicuus* and *A. depressus* habitat tradition seems not to be an important factor in the forest areas studied. This agrees with previous findings. These species are recorded from a wide range of sites scattered throughout Bavaria (BRÄU pers. comm.). However, the absence from some regions might be the result of very intensive land-use in the past. One example is the region of Middle Swabia. This area is naturally stocked with beech forests, but today it is dominated by spruce forests as a result of strong human impact over centuries. In a comprehensive five-year study (see GOßNER 2004, GOßNER et al. 2006), including a beech forest nature reserve of 11.5ha (Krebswiese-Langerjergen) and an oak forest nature reserve of 7.1ha (Seeben), only *A. depressus* was found, and this only at the site with a higher proportion and diversity of deciduous trees. From the whole administrative district of Swabia only three records of *A. conspicuus* are known (SCHUSTER 2001, 2005). Hence, interruption of 'habitat tradition' might have a negative impact on the distribution of this species, too. In contrast to *A. betulae*, however, *A. conspicuus* might be able to colonise alternative structures in intensively managed forest stands. For example, in

the Spessart at site Altenbuch *A. conspicuus* was found frequently in beech stumps <50cm height. In more natural habitats they mainly occur in standing and lying dead wood structures. Therefore in forest areas where it has survived human impact, it also colonises intensively managed stands where these contain suitable habitats.

Dependence on dead wood amount, dead wood parameters and fungi

In contrast to studies on other saproxylic species groups (MÜLLER 2005a, MÜLLER et al. 2005a) no strong correlation between dead wood amount and the occurrence of *Aradidae* was observed in the present study. However this result might be biased by the overall low densities of *Aradidae* in beech forests. Two correlations between deadwood structures and the occurrence of *Aradidae* species in the Spessart (standing dead wood <5cm for *A. avenius*, number of stumps <1m height for *A. conspicuus*) indicate that dead wood amount of suitable quality might also be an important factor for *Aradidae*. Nevertheless, such a correlation has not yet been statistically verified.

The determination of preferred fungi species was difficult. *Aradidae* often suck on cryptic hyphae where no fruit bodies are noticeable. Therefore the fungus in the bark sample sometimes might not be a source of nutrition for the flat bug species. Only in some cases were *Aradidae* observed while sucking on fungus fruit bodies. No statistical correlation between the occurrence of a particular fungus species and the abundance of *Aradidae* in the point sample plots could be found. This might be an effect of temporary availability of suitable developmental stage of decay (expressed in the mechanical properties of the microhabitat) and of fungi at a suitable developmental stage for feeding. Dependent on locality and exposure to sunlight, fungi might dry out. Hence, even if preferences exist for a particular fungus species, *Aradidae* rely on the possibility of switching to other fungi at a suitable stage of development for their brood (HEISS pers. comm.). Nevertheless, results of the present study demonstrated that *A. avenius*, *A. betulae* and *A. conspicuus* have different habitat requirements and allowed the definition of these preferences.

A. avenius is known to occur under the thin, loose bark of logs and branches of various deciduous tree species (*Fagus*, *Quercus*, *Carpinus*, *Tilia*, *Betula*, *Alnus*) and rarely also on *Larix* (HEISS 1972, STEHLIK & HEISS 2001). Moreover, SCHUSTER (1987, 1990, 1993, 2001, 2005) found it in dead wood of *Salix* and in one case of *Picea*. The occurrence on *Fagus* and *Carpinus* could be confirmed in the present study. Our study clearly indicates the preference of *A. avenius* for branches of small diameter. Besides branches lying on the ground (SINGER 1952, STEHLIK & HEISS 2001), *A. avenius* also colonised dead branches on living trees, dead branches suspended in lower

vegetation and thin, dead young beeches. This species is often found in shady places within dense regeneration of beech several meters high which includes a high proportion of dead wood. A significant correlation was found in the Spessart between the abundance of *A. avenius* and the number of young dead beech trees in the point sample plots. The capture of one specimen in a flight-interception trap at a height of 14 meters indicates that dead branches in the higher canopy might be also used as a habitat by this species. In a study in the Hienheimer Forst in lower Bavaria *A. avenius* was also found in the crowns of beech (28.5m) and oak (24m) (SCHUBERT 1998, GOßNER 2006). Preferred fungus species are difficult to define for this bug species. Our results indicate the importance of species of the genera *Hypoxylon* (*Sphaeriales*) and *Diatrype* (*Diatrypales*) and *Asterosporium asterospermum* (Fungi Imperfecti (*Coelomycetes*)). In previous publications no particular fungus food resource is mentioned (e.g. STEHLIK & HEISS 2001). In other regions we found *A. avenius* together with *Diatrype bullata* (*Diatrypales*) on *Alnus* (Isar floodplain near Sylvenstein Reservoir), *Nectria ditissima* (*Hypocreales*) on *Carpinus betulus* (NSG Kl. Schenkenwald, Baden-Württemberg), and *Stereum hirsutum* (*Russulales*) on *Quercus* (afforestation areas, Aschaffenburg) (leg. GOßNER, det. BLASCHKE; unpubl. data). Possibly a wide range of fungi species is used by *A. avenius*.

A. betulae was nearly exclusively observed in standing dead wood of large dimensions in semi-shady to sunny sites. This agrees with the data given by KORINEK (1935) and GYLLENSVÄRD (1958). They pointed out that *A. betulae* avoids dense forests. *A. betulae* was strongly associated with *Fomes fomentarius* in the present study (Fig. 7b). Hence, tinder fungus seems to be the key species for *A. betulae* in the beech forest of the High Spessart, although this species has been also observed feeding on other fungi such as *Piptoporus betulinus*, *Fomitopsis pinicola* (KORINEK 1935, HELIÖVAARA & VÄISÄNEN 1983), *Leptoporus* sp. (TAMANINI 1981) and *Trametes* sp. (TAMANINI 1961). The occurrence on other fungi and tree species (*Betula*, *Ulmus*, *Acer*, *Alnus*, *Salix*, *Populus*, *Quercus*, *Tilia*, *Abies*, *Pinus*) might be at least partly an example of regional differentiation. While in Finland (HELIÖVAARA & VÄISÄNEN 1983) and Poland (LIS 1990) *A. betulae* occurs mainly on *Betula* infested by *P. betulinus*, in Slovakia (STEHLIK & HEISS 2001), North Tyrol (HEISS 1972) and Bavaria (SCHUSTER 1987, 1993, 2005, present study) *F. sylvatica* infested by *F. fomentarius* seems to be the preferred habitat of *A. betulae*. It was observed in the present study that single individuals of *A. betulae* can even be observed on *Fomes* infested living trees (Fig. 7a) and reach highest abundance on dead, standing trunks with fruit bodies of *F. fomentarius* at sunny sites (Fig. 8b). There, many groups of *A. betulae* can be observed on the bark (Fig. 6) and on fungal fruit bodies (Fig. 7b). Single specimens are found until the fruit bodies are rotten and no bark is left on the trunks. This habit indicates a strong conservatism in this species, with a low dispersion willingness until the suitability of the

colonised structure is strongly reduced. This behaviour might be one reason for its status as an endangered species.



Fig.7: Habitats for *Aradidae*: a) beech stumps colonised by *Bjerkandera adusta* provide a suitable habitat for *Aradus conspicuus* in intensively managed stands in the High Spessart. b) dead, standing trunks of beech colonised by *Fomes fomentarius* are the habitat for *Aradus betulae* in stands with habitat tradition in the High Spessart. (Photos: M. GOßNER)



Fig.8: Still foliated trees infested by *Fomes fomentarius* (a) are already colonised by single *Aradus betulae*. High populations occur on old, dead, standing trunks with fruit bodies of *F. fomentarius* at sunny sites (b). When all fruit bodies are rotten, no specimens can be found any more. (Photos: M. GOßNER)



Fig. 9: Many groups of adults and larvae of *A. betulae* can be observed on the bark of large, dead, standing trunks infested by *Fomes fomentarius* in stands with 'habitat tradition' in the High Spessart. (Photo: M. GOßNER)

A. conspicuus prefers larger dead wood structures, irrespective of the type (lying/standing), in places ranging widely from shaded to sunny. Its requirements for heat and sun seem to be somewhere between those of *A. avenius* and *A. betulae*. This confirms the results of the experimental study of *A. conspicuus* and *A. betulae* in the laboratory by GYLLENSVÄRD (1958) in Sweden. Beech stumps (30-50cm height) left after felling in the stands were found to be suitable habitats in intensively forested areas in the Spessart in the present study (Fig. 7a). It is unclear, however, if these stumps can serve as suitable surrogate habitats if no primary structures are left in the surrounding forest. Such stumps can serve as habitats for a few years, giving food for several generations and then cease to be suitable. Consequently, these insects either die or find a new suitable microhabitat by migration in the following spring. *A. conspicuus* is regarded as a typical inhabitant of beech forests. In the catalogue of natural habitats of the Habitats directive in Brandenburg, *A. conspicuus* is mentioned as a species characterising two beech forest types, *Asperulo-Fagetum* and *Cephalanthero-Fagion* (BEUTLER & BEUTLER 2002). All records of *A. conspicuus* in Bavaria are from *F. sylvatica* (SCHUSTER 1993, 2001, 2005). According to HEISS (1972), LIS (1990) and STEHLIK & HEISS (2001) *A. conspicuus* exhibits a preference for beech, but occurs also on other deciduous tree species (*Populus*, *Quercus*, *Acer*) and occasionally also on conifers. MÖLLER (2005) describes *Bjerkandera adusta* as the key fungus for the occurrence of *A. conspicuus*. This could be confirmed by our study in the Spessart. SCHUSTER (2001) also found *A. conspicuus* on *B. adusta* in the Bernried Park (Upper Bavaria). However, regional differentiation might

occur. In the Steigerwald *A. conspicuus* was primarily found together with *Hypoxylon fragiforme* and only once with *B. adusta*. In other regions other fungi species of the *Polyporales* are mentioned (*Polyporus*, *Leptoporus*, *Fomes*, *Trametes* sp.; TAMANINI 1981, STEHLIK & HEISS 2001). Some records from these genera were also made in the present study.

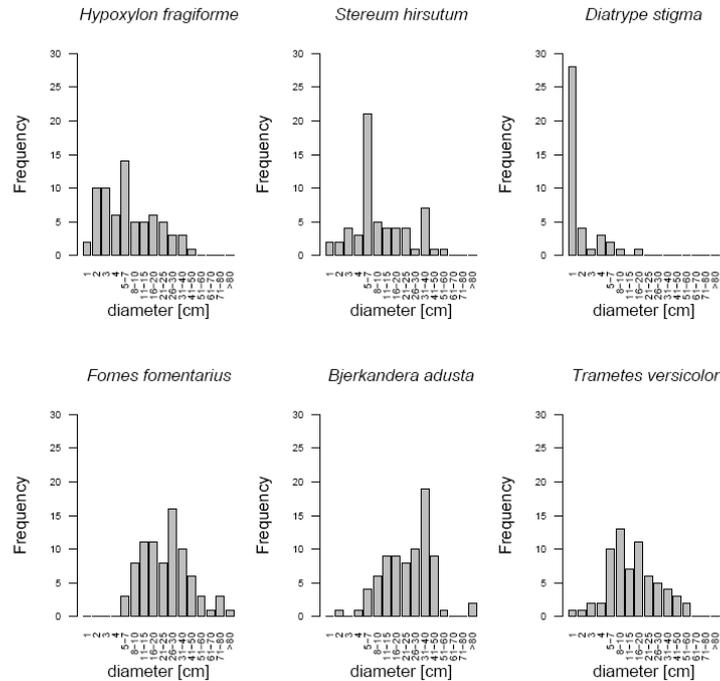


Fig. 10: Barplots, showing the frequencies of fungi species that are potential food resources for *Aradidae*, found in dead wood structures of different diameter in Forest Nature Reserves in Bavaria (adapted from BLASCHKE et al. 2003).

The preference of *Aradidae* for specific dead wood parameters can primarily be explained by the preference of particular fungi for these structures. This is illustrated by the occurrence of fungi species on dead wood structures of different diameter in Bavarian Forest Nature Reserves (Fig. 10). *Hypoxylon fragiforme*, *Stereum hirsutum* and *Diatrype stigma* as potential food resource for *A. avenius* prefer small diameter classes while *Fomes fomentarius* as potential food resource for *A. betulae* and *Bjerkandera adusta* and *Trametes*

versicolor for *A. conspicuus* prefer larger diameter classes. This fits quite well with the observed preference of *Aradidae* species (Fig. 6).

Conclusions

It can be concluded that:

- 1) Flight-interception traps are not a suitable method for assessing the population of *Aradidae*. An accurate inventory can be made only by hand-collecting.
- 2) All species of *Aradidae* found use fungal hyphae as the nutrition source. Hence all other factors are secondary and the occurrence of fungi at a suitable developmental stage is an essential precondition for the occurrence of *Aradidae*.
- 3) Because fungi species that are reported as important to *Aradidae* species are widely distributed, the protection of suitable dead wood structures seems to be critical. Most of the endangered *Aradidae* are dependent on dead wood of large dimensions, especially dead, standing trunks (e.g. *A. betulae*). The massive decrease and fragmentation of relatively undisturbed forests are responsible for their endangerment. Hence, protection of these structures on a landscape scale is necessary to establish habitat connection.
- 4) At least for some *Aradidae* species like *A. betulae* 'habitat tradition' seems to be a decisive factor for their occurrence. Because the Spessart is one of the last refuges for *A. betulae* in Bavaria outside the Alps, there is a specific argument for the protection of the old growth forest remains in the Spessart. The establishment of the 'Rothenbuch concept for habitat trees and dead wood' has to be seen as an important step towards the protection of *A. betulae*.
- 5) There is still a lack in knowledge about the specific habitat requirements of flat bugs, especially food preferences. Future studies should concentrate on surveying *Aradidae* found sucking on fungi, combined with an accurate determination of fungi species.

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