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The use of water-filled tree holes by vertebrates in temperate forests

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Water-filled tree holes (WHs), commonly referred to as dendrotelmata, develop when water accumulates in cavities related to tree architecture or in rotten parts of the tree. These structures can occur in forest ecosystems and may represent essential microhabitats in the life cycle of various animal species. WHs form temporary microhabitats during wet periods and sometimes sustain water throughout dry seasons. Research on the use of WHs by organisms mainly focuses on invertebrates developing in these while vertebrates are rarely mentioned. A literature search on the use of WHs by vertebrates revealed that attention has been given only to vertebrates in tropical and subtropical systems, mostly to groups with aquatic stages, such as amphibians. To fill the knowledge gap on the use of WHs by vertebrates in temperate forests, we conducted a camera study in three sites across Germany. We identified a total of 28 vertebrate species including 11 mammal, 17 bird and one amphibian species using the WHs. The recorded videos showed that vertebrates use the WHs mainly for nutrition and hydration. With an expected future increase in frequency and intensity of dry spells in central Europe, these microhabitats may sustain healthy forest ecosystems by providing resources for wildlife. Reliable, updated data about the importance of WHs for vertebrates is required to urge forest managers and stakeholders to enforce the preservation of these microhabitats.

Keywords: birds, dendrotelmata, forest, habitat tree, mammals, microhabitat, tree-related microhabitats

Water-filled tree holes (hereafter WHs) may constitute an integral part of forest ecosystems by providing space for development, prey and a source of freshwater to forest organisms (Kitching 2000). Due to water accumulation in open crevices, tree stem cavities and root systems, these WHs, also referred to as dendrotelmata, may carry water throughout the year or only during distinct time periods. Leaves and detritus accumulate in WHs, enriching them with organic material and nutrients (Fish and Carpenter 1982). So far, research on the use of WHs by organisms primarily focuses on invertebrates developing in these aquatic microhabitats (Fashing 1975, Schmidl et al. 2008, Gossner et al. 2016). Invertebrates without aquatic life stages may also use WHs for drinking (e.g. wasps, bees and

beetles, Gossner 2018, Petermann unpubl.). Vertebrates are sometimes targeted in WH studies from tropical and subtropical regions (Yanoviak 2001, Walters and Kneitel 2004, Vickers et al. 2014, Sharma et al. 2016), but to our knowledge, there is no study carried out in temperate regions on the use of WHs by vertebrates.

In the tropics and sub-tropics, researchers reported mainly amphibians, reptiles, marsupial gliders and primates using the WHs. Possible uses include life cycle development, typical for amphibians (Yanoviak 2001); drinking, which is documented for primates (Sharma et al. 2016) and suggested for bats (Boyles et al. 2006); and bathing, as it has been observed for birds (Baker 1983). A field study by Gossner et al. (2020) in temperate beech forests revealed that fake larvae displayed in WHs are frequently attacked by small mammals and birds, indicating WHs are used and harbor potential food resources.

To document the use of WHs by vertebrates in temperate forests, we performed a field study, with the aim of providing a first inventory of vertebrate species using WHs, including notes on their behavior.

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Methods

The field study included two different data collections located in three study areas in Germany: the UNESCO Biosphere Reserves Schwäbische Alb (ALB; south-west) and Schorfheide-Chorin (SCH; north-east), two sites that are part of the Biodiversity Exploratories project (Fischer et al. 2010); and the southern Black Forest (BF), a site of the ConFoBi project (Storch et al. 2020). The forests of ALB were either dominated by European beech *Fagus sylvatica* or Norway spruce *Picea abies*, those in SCH by either *F. sylvatica*, Scots pine *Pinus sylvestris* or sessile oak *Quercus petraea*, and those of BF by *P. abies*, silver fir *Abies alba* and *F. sylvatica*.

WHs were observed at ALB and SCH (10 forests stands each) using camera-traps (Berger + Schröter 31277, Digital Trail Camera 12 MP) with a motion sensor, night vision and a 32 GB SD-card. Recording began in April 2015 and ended in August 2015, totaling 143 and 116 days at ALB and SCH, respectively. WHs included a total of 48 pan (ALB 25, SCH 23) and 8 rot holes (ALB 7, SCH 1) of different origin from ground level to 23 m height in the canopy. All cameras were moved to a new tree hole in each forest stand after three to four weeks. At the BF site, 16 Bushnell Trophy Cam Aggressor cameras with passive infrared motion sen-

sor were deployed in five forest plots equipped with 32 GB SD-cards. The study was conducted in June and July 2019. All cameras were recovered after a recording timeframe of four weeks. The total in-field study period at the BF site was 44 days. WHs included nine pan and two rot holes at the base of the tree. Cameras were mounted on nearby trees and wooden poles facing the tree hole.

Results and discussion

Importance for vertebrates in temperate forests

A total of 184 interaction events between vertebrates and WHs were observed at BF, 246 (ground \leq 2 m: 160; canopy $>$ 2 m: 86) at ALB and 176 (111; 65) at SCH.

In total, we found 28 vertebrate species visiting WHs (Table 1), including one amphibian, 17 bird and 11 mammal species. We provide information on the frequencies of observation per day and tree. Among mammals, at BF and ALB the Eurasian squirrel was among the most frequently observed species (observed on average 0.3 times per WH and day). Yellow-necked mouse was the most frequently observed mammal at BF (0.4), and edible dormouse at SCH (0.6).

Table 1. Vertebrates inventoried at water-filled tree holes in three forests of Germany. Numbers show the frequency of observation per day and tree hole (based on tree holes that were visited at least once by the species). Behavior shows the share (%) of observations for a given behavior. Sites: ALB=Schwäbische Alb; SCH=Schorfheide-Chorin; BF=Black Forest. Observed behavior: EAT=eating; DRI=drinking; BAT=bathing; UNK=unknown.

Species	Scientific name	Site			Observed behavior		
		ALB	SCH	BF	EAT/DRI	BAT	UNK
Amphibians							
European tree frog	<i>Hyla arborea</i>		0.03				100
Birds							
Stock dove	<i>Columba oenas</i>		0.19				100
Tawny owl	<i>Strix aluco</i>	0.12			59.3		40.7
Great spotted woodpecker	<i>Dendrocopos major</i>	0.04	0.21		100		
Eurasian jay	<i>Garrulus glandarius</i>	0.06		0.01	100		
European robin	<i>Erithacus rubecula</i>	0.17	0.10	0.1	97.9		2.1
European blackbird	<i>Turdus merula</i>	0.04	0.06	0.06	60.0		40.0
Great tit	<i>Parus major</i>	0.08	0.09	0.03	35.0	19.1	45.9
Blue tit	<i>Cyanistes caeruleus</i>	0.05	0.15		80	20	
Crested tit	<i>Lophophanes cristatus</i>	0.04			100		
Eurasian nuthatch	<i>Sitta europaea</i>	0.07	0.09	0.03	65.7	20.6	13.7
Treecreeper	<i>Certhia sp.</i>	0.21	0.09		63.6	16.2	20.2
Eurasian blackcap	<i>Sylvia atricapilla</i>			0.12	100		
Brambling	<i>Fringilla montifringilla</i>		0.05		100		
Bullfinch	<i>Pyrrhula pyrrhula</i>	0.34			100		
Common chaffinch	<i>Fringilla coelebs</i>	0.11	0.29		100		
Hawfinch	<i>Coccothraustes coccothraustes</i>	0.05	0.05		100		
Mammals							
Eurasian squirrel	<i>Sciurus vulgaris</i>	0.28	0.03	0.31	97.8		2.2
Edible dormouse	<i>Glis glis</i>	0.04	0.58		73.3		26.7
Hazel dormouse	<i>Muscardinus avellanarius</i>	0.04			100		
Bank vole	<i>Myodes glareolus</i>			0.05	89.6		10.4
Unidentified mouse		0.26	0.25		100		
Yellow-necked mouse	<i>Apodemus flavicollis</i>			0.43	87		13
Shrew	<i>Sorex sp.</i>			0.01	33.3		66.7
Red fox	<i>Vulpes vulpes</i>	0.03			100		
Raccoon	<i>Procyon lotor</i>		0.04		100		
European pine marten	<i>Martes martes</i>			0.04			100
Stone marten	<i>Martes foina</i>			0.01			100
Unidentified marten	<i>Martes sp.</i>		0.06				100
Unidentified bat	(<i>Myotis sp.</i> or <i>Pipistrellus sp.</i>)		0.03				100

Among birds the treecreeper (ALB, 0.3), bullfinch (ALB, 0.2), European robin (SCH 0.3), great spotted woodpecker (SCH, 0.2) and Eurasian blackcap (BF, 0.1) were observed most frequently. Interestingly, a bat was found in our study, representing probably the first evidence of use of temperate WHs by this taxon (Supplementary material Appendix 1). We identified two main activities at the WHs (Table 1): 1) direct use in form of drinking (Supplementary material Appendix 2) or feeding (either larval or plant seeds, Supplementary material Appendix 3); 2) bathing (Supplementary material Appendix 4). In addition, we observed species sitting (European robin, Eurasian blackcap, great tit, tawny owl, treecreeper, edible dormouse, unidentified mouse) or sleeping in a hole (great tit), and intra-specific interactions for pine martens (Supplementary material Appendix 5). Previous studies have suggested martens defending their territories quite vividly (Genovesi et al. 1997). The study was conducted during hot and dry summer months. The frequent consultation with numerous visits per day suggests the WHs' importance as a hydration source in an otherwise dry environment, which may lead territorial animals to actively defend them as a potentially limited resource. Differently from the tropics (Yanoviak 2001), we did not record reptiles visiting the WHs. The activities carried out at WHs by other vertebrate species, however, resembled those recorded in the tropical and subtropical environment, including drinking, bathing and feeding (Yanoviak 2001, Walters and Kneitel 2004, Vickers et al. 2014, Sharma et al. 2016). The importance of vertebrate predation on the aquatic insect larvae in WHs have recently been shown by experiments with fake larvae in European beech forests (Gossner et al. 2020). In contrast to the tropics and subtropics (Scheffers et al. 2013), we did not find evidence of life cycle development of amphibians in these microhabitat. However, the observation of frog development in a big dendrotelm of a lying deadwood log in the National Park Hainich suggest that large dendrotelmata on trees might serve as suitable habitats for amphibian development (Nöllert 2012).

Coping with drought and management

Various studies modeling climatic scenarios predict more intense and longer-lasting droughts in the future which will put stress on ecosystems worldwide (Ciais et al. 2005, Bolte et al. 2009, Forzieri et al. 2014). Accordingly, Germany is experiencing increasingly dry summers with prolonged periods without or only with minimal rainfall and above-average temperatures (Mühr et al. 2018). These climatic extremes will affect vertebrates as well as invertebrates and will have far reaching impacts on ecosystems including changes in the provisioning of microhabitats (Augustynczyk et al. 2019). Small water bodies such as WHs might provide one of the few available water sources during dry periods (Gossner 2018).

WHs thus not only promote biodiversity by providing specific microhabitats for a specialized invertebrate fauna with aquatic life stages (Gossner 2018) but might additionally increase the survival of terrestrial invertebrates and vertebrate species in both temperate and tropical forests. We found on average 1.3 ± 0.22 SE (BF, recorded on pre-selected trees, Storch et al. 2020), 15.7 ± 2.5 SE (ALB, with capacity

> 200 ml), 11.0 ± 2.2 SE (SCH, with capacity > 200 ml) WHs per ha that can potentially be used by vertebrates. This, in combination with the frequent visits observed, impressively shows how important these microhabitats for vertebrates likely are.

Water-filled tree holes and forest management

A promising management tool, the tree-related microhabitats typology (Larrieu et al. 2018), can be helpful to inventory WHs, mostly on the ground level as WHs in the canopy are difficult to assess. This typology is an established tool (Asbeck et al. 2019) for the selection of 'habitat trees', which have a long-lasting tradition in temperate Europe (Mölder et al. 2020). Applications of the typology can be used to assess many aspects of forest biodiversity and trade-offs between timber production and biodiversity conservation (Paillet et al. 2019, Santopuoli et al. 2019). Habitat trees and their conservation recently gained increasing attention in the context of retention forestry in temperate forests (Basile et al. 2020, Gustafsson et al. 2020). WHs are an integral selection criterion for habitat trees and their importance for insects and nematodes have repeatedly been shown (Gossner et al. 2016, Petermann et al. 2020). Our results point out the importance of WHs beyond this by providing sources of food and water for vertebrates. Increased knowledge about the role of these microhabitats for vertebrate species (e.g. the use of WHs by bats) in temperate forests could allow forest managers to explicitly consider these in their management plans to protect species relying on WHs.

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Supplementary material (available online as Appendix wlb-00786 at <www.wildlifebiology.org/appendix/wlb-00786>). Appendix 1–5.