*Are Black Woodpecker (*Dryocopus martius*) tree cavities in temperate Beech (*Fagus sylvatica*) forests an answer to depredation risk?*

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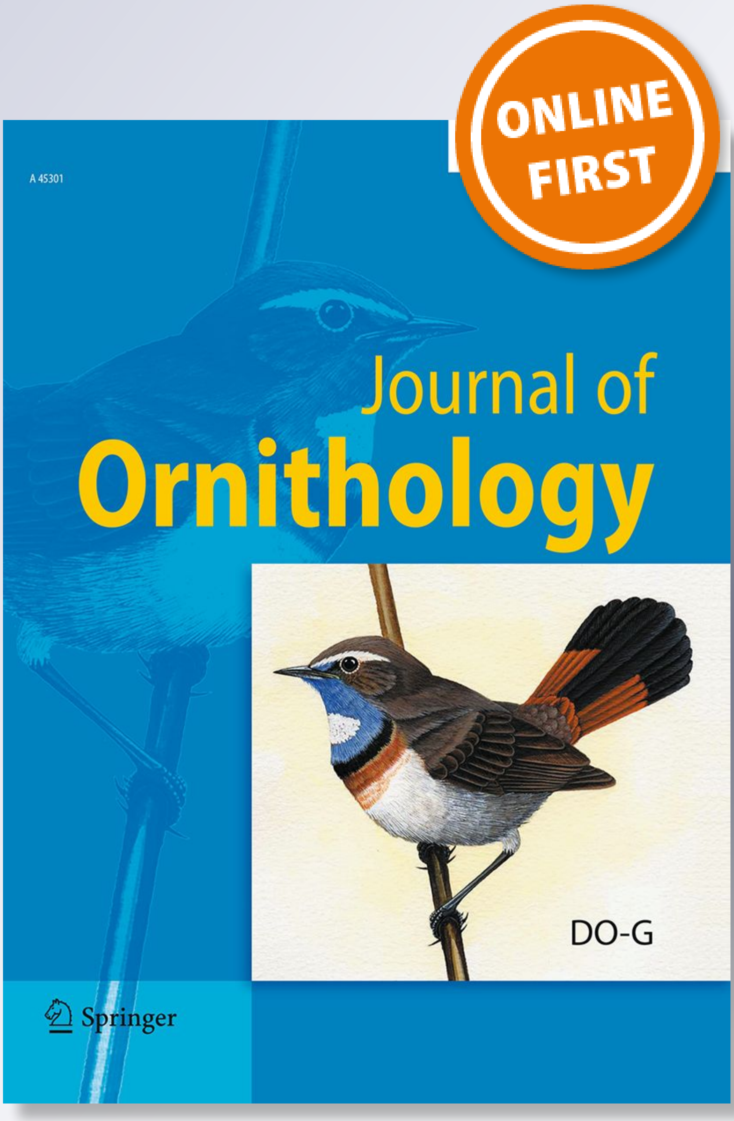
Journal of Ornithology

ISSN 2193-7192

J Ornithol
DOI 10.1007/s10336-017-1467-2



Springer

J Ornithol
DOI 10.1007/s10336-017-1467-2

ORIGINAL ARTICLE

Are Black Woodpecker (*Dryocopus martius*) tree cavities in temperate Beech (*Fagus sylvatica*) forests an answer to depredation risk?

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Received: 24 January 2017 / Revised: 22 May 2017 / Accepted: 6 June 2017

Abstract The Black Woodpecker (*Dryocopus martius*) is described as a key creator of nesting cavities. Nevertheless, data on nest depredation at Black Woodpecker cavities are scarce. We continuously monitored 72 Black Woodpecker tree cavities by means of camera trapping during one breeding season in different temperate Beech forest (*Fagus sylvatica*) areas in southern Germany. We assessed the frequency of visits of the different predator species at the tree cavities. We found that cavities visited by predators and those which remained undetected by potential predators did not differ according to factors that are assumed to drive cavity selection in order to reduce predation risk. We conclude that, under the conditions prevailing in our study regions, Black Woodpecker cavity nesters cannot substantially further reduce depredation risk by nest cavity site selection.

Keywords Cavity nesters · Depredation · Camera trapping · Temperate beech forests

Zusammenfassung

Untersuchungen zum Prädationsrisiko an Schwarzspechthöhlen (*Dryocopus martius*) in Buchenwäldern (*Fagus syvatica*) der gemäßigten Zone

Der Schwarzspecht (*Dryocopus martius*) ist in der Lage, große Bruthöhlen zu erstellen und gilt deshalb als eine Schlüsselart in den Waldlebensräumen der Paläarktis. Informationen zur Nestprädation in Schwarzspechthöhlen liegen bislang jedoch nur in geringem Umfang vor. Mit Hilfe von Fotofallen konnten in verschiedenen Buchenwäldern (*Fagus sylvatica*) Süddeutschlands insgesamt 72 Schwarzspechthöhlen durchgehend während einer kompletten Brutsaison überwacht werden. Hierbei wurden deren Besetzung durch verschiedene Höhlenbrüter sowie die Besuchsfrequenzen unterschiedlicher Prädatorenspezies an den jeweiligen Bruthöhlen erfasst. Zudem wurden verschiedene Lage- und Umgebungsparameter an den Höhlen untersucht, die als maßgeblich für die Prädationsvermeidung gelten. Dabei zeigte sich kein Unterschied zwischen Höhlen, die von Prädatoren besucht wurden, und solchen, die von potentiellen Nesträubern unentdeckt blieben. Hieraus schließen wir, dass die Potentiale zur Prädationsvermeidung, die sich für den Schwarzspecht durch die Auswahl von Höhlenstandorten ergeben, unter den in unseren Untersuchungsgebieten herrschenden Habitatbedingungen nicht weiter gesteigert werden können.

Communicated by F. Bairlein.

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Published online: 20 June 2017

Introduction

Nest predation is a major cause of nest loss and accounts for up to 80% of all nest failure (Martin 1995a, b; Lima 2009; Paclik et al. 2009). The selection of an appropriate nest site is therefore an important determinant of fitness in many species (Lima 2009). Through nest site selection and adjusting their behavior, birds can significantly lower their risk (Alatalo and Lundberg 1984; Wesołowski 2002; Forstmeier and Weiss 2004; Paclik et al. 2012). Species nesting in cavities show reduced nest predation rates and increased nest survival compared to open nesters (Fontaine and Martin 2006). The Black Woodpecker (BW) is able to excavate tree cavities even in hardwood trees. As it provides tree cavities for secondary cavity users, the BW is described as a key species in forest habitats (Kühlke 1985; Kosiński et al. 2010). The largest woodpecker species in the Palearctic, the BW depends on large-dimensioned trees for cavity construction. In temperate forests, Beech is the tree species mainly preferred by BW as a cavity tree (Kühlke 1985; Lange 1996; Kosiński et al. 2010, 2011). Beech seems to provide the most favorable conditions for the cavity breeder, including reduction of predation risk (Lange 1996; Kosiński et al. 2010, 2011; Zahner et al. 2012). However, intensive forestry is assumed to critically restrict the availability of sufficiently dimensioned trees (Wesolowski and Tomialojc 2005). Against this background, our study initially aimed to assess the different predator species and particular behavior relating to cavity tree conditions in order to improve our understanding of factors relevant for predation exposure of BW cavities in temperate forests.

Methods

The study was carried out in seven woodland areas of southern Germany: Northern Steigerwald (49°54N, 10°34′E), Southern Steigerwald (49°47N, 10°32′E), Gelnhauser Forst (50°22N, 10°47′E), Hienheimer Forst (48°54′N, 11°48′E), Bavarian Forest Nationalpark (48°56N, 13°24′E), Freisinger Forst (48°25N, 11°43′E), and Landsberg am Lech (47°54N, 10°55′E). Sizes of the study areas range from 7 to 12.5 km^2. Beech is a relevant tree species in all study sites with proportions ranging from 20% (Bavarian Forest) to 98% (Steigerwald). The second most important tree species is Norway Spruce (*Picea abies*).

BW cavities were recorded in our study areas in previous years by the forest administration and as part of our research. The cavity density ranged from 13 to 36 cavities per 10 km^2 over the study areas (mean: 17 cavities per 10 km^2). In addition to the available data, we checked the areas for fresh BW cavities. We focused on fresh cavities and on cavities known to be used by the BW in the previous year. In order to inspect the cavities, the trees were climbed before the breeding season started. We measured cavity dimensions, and ensured that fresh cavities were completed by the BW, as well as inspecting previous year's cavities for suitable nesting conditions for the BW. We excluded all cavities showing signs of rotting, wetness or water inside, or providing more than one cavity entrance. Of the cavities that met the conditions described, we selected 10–12 cavities per study area for the camera survey. For each of the selected cavity trees, we recorded diameters at breast height (dbh) as well as tree diameter at the cavity position. These measures were taken with 80-cm calipers. Further, we measured cavity heights, crown heights and the distances between the cavities and tree crowns. All the heights were measured with a Vertex L5 Bluetooth Laser. Height of vegetation cover was assessed within an area of 500 m^2 around each cavity tree. During 2012 and 2013, we selected 72 different BW cavities from throughout our seven study areas in which to install camera traps. We used Cuddeback Attack IR ($n = 65$), and RECONYX HC 600 ($n = 10$) Camera Traps for the survey. Cameras were fixed to the tree with a tension belt at between 2 and 4 m above the entrance of the cavities. In order to reduce potential disturbance at the cavities, cameras were mounted on a sledge-system, which allowed moving the cameras up and down the tree for monthly inspection of SD-cards and battery changes without climbing the tree during nesting periods. We monitored the cavities continuously from the middle of March until the middle of July. The images produced were in color during daylight and black and white at night-time. The digital camera images were inspected with the program Lightroom 4 (Adobe Photoshop) to identify cavity visitors. Except for bats, identification at species level was always possible.

We counted several visits of a distinct predator species to the same cavity during a single day (24 h) as one event. Conversely, different predators visiting the same nest were counted as separate visiting events. As predators, we regarded those mammal species, raptors, and owl species that are known for potentially preying on the species nesting in the respective cavity. The omnivorous Greater Spotted Woodpecker (*Dendrocopos major*) was regarded as a predator of eggs and small nestlings.

We tested cavities selected for breeding by BW and Stock Doves (*Columba oenas*) according to characteristics supposed to be relevant for predator avoidance. The Stock Dove broods in the fresh cavities were used as a test organism to enlarge our sample size of inhabited cavities suitable for the BW. We compared cavities selected for breeding with those not used for breeding by these species. We also compared breeding cavities visited by predators versus breeding cavities where no predator occurs. The Shapiro–Wilk normality test was applied to evaluate the different variables for normal distribution. Comparisons of means of two samples were carried out by the Welch two-sample *t* test, whereas to compare several sample means we performed analyses of variances (ANOVA). In order to identify factors influencing the timespan a cavity remains undetected by predators, we tested for potential correlations between the length of the period until the first occurrence of a predator at the cavity and the characteristics of the cavity or cavity tree. For that reason, we calculated Spearman's rank correlations rho and Pearson's product moment correlation. The variable 'rejuvenation to cavity distance' can potentially remain two factors. On the one hand, rejuvenation can provide concealment. On the other hand, a short distance between rejuvenation and cavity makes it easier for predators to reach the cavity. Therefore, we additionally tested for potential non-linear correlations of 'rejuvenation to cavity distance' and the occurrence of predators at the cavities using logarithmic regression models and polynomial regression models. All statistical calculations were carried out with R (Law and Wiener 2015; R Core Team 2015).

Results

Cavity users and potential predators

We observed 72 BW cavity trees during the breeding season with remote camera traps. All cavities were found in living Beech. The average cavity height was 12.3 m (max. = 20.3; min. = 5.7; SD = 3.3). The mean dbh of cavity trees was 63.6 cm (max. = 83 cm; min. = 41 cm; SD = 10).

We found 69 out of 72 cavities were temporarily used or occupied for breeding, respectively, by 20 bird species and 8 mammal species (Table 1). Breeding BW were detected in 13 of the cavities, whereas 45 cavities were occupied by breeding Stock Doves.

At 29 cavities we recorded at least one visit of a potential predator. In other words, predators were recorded at 42% of the used cavities. During the observation period from mid-March until mid-July, the average number of predator visits in relation to all inhabited cavities ($n = 69$) was 2.1 (min. = 0; max. = 15; SD = 2.6). We recorded one mammal species and five bird species visiting inhabited cavities (Table 2). The Great Spotted Woodpecker is the potential predator that visited the largest number of different breeding cavities, whereas the most frequent visits at breeding cavities (including repeated inspections at the same cavity) were recorded for the Northern Goshawk (*Accipiter gentilis*). The Common Buzzard (*Buteo buteo*) was revealed to visit breeding cavities in five out of seven study areas, even at cavity trees located within closed forest stands.

Cavity selection and potential depredation

Breeding cavities of BW and those BW cavities used by Stock Doves for breeding did not differ in terms of height, distance of rejuvenation to the cavity, and distance from cavity to the crown of the tree. Also, the frequencies of predator visits did not significantly differ between breeding cavities used by BW and Stock Doves (Fisher's exact: $p = 0.346$; 95% confidence interval 0.501; 10.860; odds ratio 2.125). Thus, by concentrating on cavities used for breeding by BW and Stock Doves, we tested parameters potentially relevant for cavity selection by cavity users and potentially important for predation avoidance.

According to our data, the distance of rejuvenation to the cavity did not have a significant influence on cavity selection or on the number of predator visits at a cavity (Table 3). This finding is also true concerning the space between the cavity and the crown of the tree (Table 3). In addition, rejuvenation height, cavity height, distance of rejuvenation to the cavity and distance of rejuvenation to the crown did not affect the time span within which a breeding cavity was initially detected by a potential predator (Table 3).

Discussion

The photo trapping enabled a continuous survey of tree cavities in seven different areas of southern Germany during a whole breeding season. The technique helped to reveal all movements at the cavity entrances and enabled determination of breeding activities of the cavity users as well as identification of visitors to the cavities. The identification of 20 bird species and 8 different mammal species using BW cavities confirm the role of BW as a keystone species in temperate forests. The number of different nesting species we found is in accord with previous studies (e.g. Kühlke 1985). However, the proportion of inhabited cavities in our study (96%) was very high. Most of these cavities were used by Stock Doves (65%). Similar high proportions of cavity dwelling by Stock Doves have already been found by other European studies (Kühlke 1985; Möckel 1988; Lange 1993; Sikora 2008). The photo trapping in our study reveals that it mostly takes between less than an hour and a day until Stock Doves occupy a cavity after it was left by the last fledgling of a BW brood.

In previous studies, the identification of predator species at tree cavities has mainly depended on direct observation or the interpretation of traces and remains (Walankiewicz

Table 1 Camera traps at 72 Black Woodpecker (*Dryocopus martius*) cavities documented 28 different vertebrate species visiting the cavities

Species recorded	Number of different cavities where the species was recorded	Cavities with reproduction
Black Woodpecker *Dryocopus martius*	29	13
Grey-faced Woodpecker *Picus canus*	6	
Green Woodpecker *Picus viridis*	7	
Middle Spotted Woodpecker *Dendrocopos medius*	6	
Great Spotted Woodpecker *Dendrocopos major*	19	
Tawny Owl *Strix aluco*	8	2
Ural Owl *Strix uralensis*	2	
Boreal Owl *Aegolius funereus*	2	
Northern Goshawk *Accipiter gentilis*	9	
Common Buzzard *Buteo buteo*	11	
Stock Dove *Columba oenas*	52	45
Jackdaw *Corvus monedula*	2	2
Great Tit *Parus major*	9	
Coal Tit *Parus ater*	2	
Blue Tit *Parus caeruleus*	3	
Marsh Tit *Pocille palustris*	1	
Nuthatch *Sitta sitta*	7	1
Common Starling *Sturnus vulgaris*	3	
Jay *Garrulus glandarius*	2	
Collared Flycatcher Ficedula albicollis	2	
Pine Marten *Martes martes*	10	1
Red Squirrel *Sciurus vulgaris*	4	3
Yellow-necked Mouse *Apodemus flavicollis*	1	
Edible Dormouse *Glis glis*	3	2
Brown Long-eared Bat *Plecotus auritus*	3	
Greater Mouse-eared Bat *Myotis myotis*	1	
Bechstein's Bat *Myotis bechsteinii*	1	
Common Noctule *Nyctalus noctula*	1	
Total	206	69

At 3 out of the 72 cavities, neither breeding activity nor predator visits were recorded

Table 2 Predator visits recorded by camera trapping at Black Woodpecker cavity trees

	Total no. of recorded visits at any cavity	Mean visit frequency per pred. species (min./max./SD)	Total no. of visits at cavities/no. of visits at different cavities		
			Inhabited by Stock Doves	Inhabited by BW	Inhabited by other species
Northern Goshawk (*Accipiter gentilis*)	63	7.0 (1/15/3.90)	60/8	3/1	–
Great Spotted Woodpecker (*Dendrocopos major*)	31	1.6 (1/3/0.81)	27/15	1/1	3/3
Tawny Owl (*Strix aluco*)	24	3.0 (1/5/1.10)	18/6	3/1	3/1
Common Buzzard (*Buteo buteo*)	14	1.3 (1/1/0.33)	12/10	–	2/1
Pine Marten (*Martes martes*)	12	1.5 (1/3/0.79)	9/7	1/1	2/2
Total	144		126/46	8/4	10/7

BW Black Woodpecker, *STD* stock dove (*C. oenas*), *pred.* predator

2002; Weidinger 2008a; Paclik et al. 2009; Barnett et al. 2013; Gregory et al. 2014). Thus, the attempts of raptors like Northern Goshawk and Common Buzzard to get access to fledglings within the cavities remained previously undetected. In parallel, we revealed a variety of different potential predator species repeatedly visiting nest cavities.

Table 3 Cavity characteristics, cavity selection and predator visits

Variable [min/max/mean/ SD (m)]	Testing constellation/model	Statistics
Height of cavity (5.7/20.3/ 12.3/3.3)	Heights of breeding cavities vs. heights of non-breeding cavities	Welch two-sampled: $t = 1.43$; $df = 36$; $p = 0.162$
Height of cavity	Breeding cavities visited vs. non-visited by predators	Welch two-sampled: $t = -0.46$; $df = 56$; $p = 0.649$
Rejuvenation to cavity distance (0/12/3.5/2.9)	Predvis vs. nonPred vs. breedC vs. emptyC vs. BWbreed vs. STDbreed vs. totalC	ANOVA: $df = 6$; sum sq = 26; mean sq = 4.39; $F = 0.339$; Pr (>F) = 0.916
Cavity to crown distance (1.3/11.4/4.6/2.4)	Predvis vs. nonPred vs. breedC vs. emptyC vs. BWbreed vs. STDbreed vs. totalC	ANOVA: $df = 6$; sum sq = 24; mean sq = 4.00; $F = 0.771$; Pr (>F) = 0.594
Height of rejuvenation	Time until first visit by a predator	Spearman's rank correlation rho: $\rho = 0.247$; $S = 2467$; $p = 0.214$
Height of cavity	Time until first visit by a predator	Spearman's rank correlation rho: $\rho = 0.117$; $S = 2893$; $p = 0.562$
Rejuvenation to cavity distance	Time until first visit by a predator	Spearman's rank correlation rho: $\rho = -0.010$; $S = 3307$; $p = 0.963$
Rejuvenation to cavity distance	Time until first visit by a predator = 3.1 (dist rej. cav) − 0.2 (dist. rej. cav)^2 + 41.6	$F = 0.150$; $df = 24$; mult. $R^2 = 0.0123$; $p = 0.862$
Rejuvenation to cavity distance	Time until first visit by a predator = −0.8 ln (dist. rej. cav.) + 51.9	$F = 0.007$; $df = 25$; mult. $R^2 = 0.0003$; $p = 0.935$
Rejuvenation to crown distance	Time until first visit by a predator	Pearson's product-moment correlation: $r = 0.153$; $t = 0.777$; $df = 25$; $p = 0.444$

Predvis predator presence, *nonPred* no predator was present, *breedC* cavity was used for reproduction, *emtyC* cavity not used, *BWbreed* Black Woodpecker used cavity for breeding, *STDbreed* Stock Dove used cavity for breeding, *totalC* all cavities assed by the study

Research on depredation on open nests carried out by means of camera trapping did not indicate adulterating effects (Weidinger 2008b). According to our knowledge, no experience is available concerning the aspect of predator attention that may be attracted towards breeding cavities because camera traps are visible relatively close to the cavity entrances. Information on visiting frequencies of raptors is not available from other studies. However, the frequencies of visits of Pine Marten (*Martes martes*) that we recorded with our study are in accord with findings concerning depredation rates from other research (Lange 1995, 1996). Thus, we do not believe that the cameras traps at the trees substantially affected our results.

Since we could not survey the interior of the cavities with our technique, the consequences of predator visits could not be entirely determined. Therefore, the number of predator visits served as a measure of the exposure of a particular cavity to predators. We recorded the occurrence of predators at 42% of cavities inhabited by breeding species. Information on depredation rates at BW cavities is in general very scarce, and the reported data ranges from 9 to 74% losses (Johnsson 1994; Lange 1996). Even the approach of exploring seven different study areas intensively provided only a relatively small number of BW broods for our survey. To extend our data, we additionally included cavities that had been freshly built or recently used, respectively, by the BW but inhabited by Stock Doves during the study period. By climbing the trees and inspection, we ensured that all these cavities provided conditions similarly suitable to newly built BW cavities. Since the visitation rate of predators did not differ between the cavities used by BW and Stock Doves, this supports our approach to use the Stock Dove as a test organism in order to explore predator behavior towards newly built and inhabited BW cavities.

Beside the height of the cavity position at a tree, rejuvenation height beneath the cavity tree has been mentioned as a factor of cavity selection in some studies (Möckel 1988; Lange 1993). For other species, like the Yellow Warbler (*Dendroica petechia*), microhabitat structure reduced the likelihood of predation (Latif et al. 2012). Thus, we explored the impact of factors determining concealment (e.g. rejuvenation to crown distance) or reachability (height of the cavity at the tree, distance of rejuvenation to cavity).

However, our study did not distinguish any cavity features or cavity tree characteristics determining cavity selection by the breeding species and nor could we reveal factors influencing the frequency of predator visits within our samples (Table 3). This result suggests the following interpretation: it seems that, in relation to the prevailing conditions in our study areas, the BW somehow optimized predator avoidance. Moreover, at trees where suboptimal conditions for predator avoidance were prevailing (e.g.

lack of possibilities to build cavities in higher positions above the ground), the BW did not excavate cavities.

The distance from cavities to the ground is a relevant factor influencing exposure to mammalian predators, mainly the Pine Marten (Möckel 1979; Rolstad et al. 2000), whereas protection against avian predators is achieved through the limited size of the cavity entrance and the depth of the cavities. Distances between the entrances and bottoms of the cavities in our study areas ranged from 28 to 50 cm (mean 38.2 cm), making it difficult for larger raptors e.g. Northern Goshawk or Common Buzzard to reach the fledglings. According to several articles (Kühlke 1985; Nilsson et al. 1991; Rolstad et al. 2000; Uphues 2003; Kosiński et al. 2011), the Pine Marten is the most significant predator at BW cavities in terms of its impact on the breeding success of the users of larger tree cavities.

Some research from Scandinavia suggests that older tree cavities are more vulnerable to predators than freshly built cavities (Korpimäki 1987; Nilsson et al. 1991; Rolstad et al. 2000; Uphues 2003; Kosiński et al. 2011). The predator species known to visit BW cavities are mostly the same in temperate forests and in boreal habitats (Lange 1996; Rolstad et al. 2000; Uphues 2003; Kosiński et al. 2011). In both habitats, success in avoiding predators is likely to depend on the most efficient combination of defense mechanisms against the predation pressure resulting from the predator community in total. However, in Scandinavian boreal forests, BWs are forced to use mainly conifers for cavity construction, and, due to tree dimensions, the breeding cavities are positioned lower to the ground than is the case in temperate Beech forests (Möckel 1979; Korpimäki 1987; Nilsson et al. 1991; Rolstad et al. 2000; Kosiński et al. 2011; Zahner et al. 2012). Thus, temporally restricting the use of a distinct cavity, e.g. to one breeding season, seems to be an efficient anti-predation strategy in regions where larger tree cavities can only be excavated at a relatively small distance above ground (Nilsson et al. 1991; Rolstad et al. 2000). In temperate forests with longer vegetation periods, large Beeches allow the excavation of cavities at greater heights. With cavity positions at greater heights combined with a smooth bark, which is more difficult to climb, large-dimensioned Beeches can provide efficient protection against the Pine Marten (Möckel 1979; Kosiński et al. 2011; Zahner et al. 2012).

Our study underlines the important role of old Beech forests providing suitable breeding conditions for the BW and a large number of secondary cavity users. Since the BW is described as a key species of forest diversity, a better understanding of the underlying mechanisms of BW behavioral ecology can improve forest conservation schemes in the Palearctic zone. Against this background, we would like to encourage intensifying comparative research of BW ecology in different habitats within the boreal and temperate zones.

Acknowledgements We thank J. Müller and K. Weingart, Bavarian National Park, for their help and provision of ten camera traps. For a prototype of our surveillance sledge, we thank G. Sauerbrey and A. Brumer. N. Wimmer and B. Rückert, E. Engesser, N. Stöger, K. Zeimentz, A. Fuchs, H. Rudolf, M. Reuther, and U. Mergner considerably supported our studies in the different areas in South Germany. We are grateful to R. Reiter, P. Jägemann, S. Lion, J. Buhl, P. Goeder, and D. Honold for their assistance in fieldwork and in installing and maintaining the cameras. G. Pasinelli and H. Robles improved a former version of the manuscript with valuable comments. Financial support was provided by the German Federal Environmental Foundation (DBU) and the Bavarian State Ministry for Food, Agriculture, and Forestry. We are grateful to two anonymous reviewers for substantial and detailed comments.

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