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RESEARCH ARTICLE

Failed predator attacks: A direct test of security of tree cavities used by nesting Marsh Tits (*Poecile palustris*)

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ABSTRACT

Birds that nest in tree cavities, despite being relatively safe, are still threatened by predators, which not only can destroy broods but also can kill the parents. Therefore, using safe cavities is crucial for the survival of parents and nestlings. Safe cavities should simultaneously have the smallest entrance (yet large enough to admit the cavity occupant), walls made of hard wood, and depth sufficient for the nest to be placed beyond the reach of predators. I studied nests of Marsh Tits (*Poecile palustris*) that were attacked by predators and compared cavity features of nests that survived the attack with those that did not. Observations were gathered in pristine conditions (Białowieża National Park, Poland) over 30 yr. There was no direct human interference, and cavities were superabundant. I observed 169 attacks on Marsh Tit broods by a diverse set of predators. Nests survived ~30% of these attacks. Only 10% survived when a predator entered the cavity, but 29% survived if the predator attempted to pluck the nest from the cavity and 39% survived if the predator tried to remove the cavity wall. The probability of surviving an attack depended on predator identity and cavity attributes; the smallest predators passed through even the narrowest entrances, but small entrances combined with walls of sound wood were effective in stopping larger predators. Nests situated closer to the cavity entrance were less likely to survive attack than nests farther away, but nests were seldom placed beyond the predators' reach, which suggests the existence of some constraints. The probability of surviving an attack strongly increased with the nestlings' age; larger young survived attacks more often, demonstrating that, even in cavity-nesting birds, early development of locomotor capacity might be at premium. I discuss constraints on antipredator adaptations in cavity structure and trade-offs between opposing requirements.

Keywords: Białowieża National Park, breeding hole, Marsh Tit, *Poecile palustris*, primeval forest

Ataques de depredación fallidos: un estudio de las cavidades de anidación en árboles usadas por seguridad por *Poecile palustris*

RESUMEN

Aunque permanecen relativamente a salvo, las aves que anidan en cavidades de árboles aún tienen la amenaza de depredadores que no solo pueden destruir camadas sino también matar a los padres. Por esta razón, usar cavidades seguras es crucial para la supervivencia de los padres y los polluelos. Las cavidades seguras deberían, simultáneamente, tener la entrada más pequeña posible (suficientemente grande para permitir la entrada de su ocupante), paredes hechas de madera dura y una profundidad suficiente para que el nido sea ubicado por fuera del alcance de depredadores. Estudié los nidos de *Poecile palustris* que fueron atacados por depredadores y comparé las características de las cavidades de los nidos que sobrevivieron ataques con las de los nidos que no lo hicieron. Las observaciones se hicieron en condiciones prístinas (Parque Nacional Białowieża, Polonia) a lo largo 30 años. No hubo interferencia humana directa y las cavidades fueron muy abundantes. Observé 169 ataques a las camadas de *P. palustris* por un conjunto diverso de depredadores. Los nidos sobrevivieron aproximadamente a un 30% de estos ataques. Solo el 10% sobrevivieron cuando el depredador entró a la cavidad, pero el 29% sobrevivieron si el depredador intentó sacar el nido de la cavidad y el 39% sobrevivieron si el depredador intentó remover la pared de la cavidad. La probabilidad de supervivencia a un ataque dependió de la identidad del depredador y de los atributos de la cavidad; los depredadores más pequeños pasaron a través de incluso las entradas más estrechas, pero entradas pequeñas junto con paredes de madera firme fueron efectivas para detener los depredadores más grandes. Fue menos probable que los nidos situados cerca de la entrada de la cavidad sobrevivieran a ataques en comparación con nidos más lejanos, pero rara vez los nidos fueron ubicados fuera del alcance de los depredadores, lo que sugiere algunas restricciones. La probabilidad de supervivencia a un ataque se incrementó fuertemente con la edad de los polluelos; los polluelos más grandes sobrevivieron ataques más frecuentemente, lo que demuestra que aún en aves anidantes de cavidades el desarrollo temprano de la capacidad locomotora es primordial. Discuto las restricciones en las adaptaciones antidepredatorias de la estructura de la cavidad y los compromisos entre requerimientos opuestos.

Palabras clave: bosque antiguo, cavidades para reproducción, *Poecile palustris*

INTRODUCTION

Nest predation is a key component of offspring mortality in birds (Lack 1954, Nice 1957, Ricklefs 1969, Payevski 1985), and parents use diverse techniques to avoid it, ranging from changes in habitat distribution to direct behavioral interactions with predators (Thiollay 1988, Newton 1998, Caro 2005, Lima 2009). Breeding in tree cavities is one such frequently used solution, adopted by numerous taxa of forest birds on all continents (Newton 1998, Cockle et al. 2011). The relative breeding success of cavity-nesting birds tends to be higher than that of open-nesting species, and—as shown by broad-scale comparisons of nest success data (Wesołowski and Martin 2017)—this difference is, to a large extent, caused by varying nest predation rates. The higher relative safety of nests in tree cavities is also confirmed by comparisons of the nest success of birds breeding side by side in the same forests but using different nest types. Both in Arizona (Li and Martin 1991, Martin and Li 1992) and in Poland (Białowieża National Park; Wesołowski and Tomiałojć 2005), the nesting success of cavity breeders was the highest among all types of locally used nest sites.

Even for nests in tree cavities, however, predation is the major cause of nesting failure (Paclík et al. 2009, Wesołowski and Martin 2017). Nest predators not only destroy broods, but—even more importantly—may also kill parent birds in cavities (Czeszczewik et al. 2008, Wesołowski and Rowiński 2012, Maziarz et al. 2016). Therefore, using safe (predator-proof) cavities is of paramount importance for the parents.

Hunting consists of a sequence of events that have to be accomplished consecutively to result in success. A predator has to encounter prey, detect it and recognize it as a quarry, decide to attack, and finally strike and kill it. The threat that the would-be victim will lose its life increases with each successive stage (Endler 1986). The prospective prey, though, may avoid being killed by preventing the completion of just one step in this hunting sequence. It can avoid being attacked by using primary (indirect) defenses, and, if attacked, it can use secondary (direct) defenses (Edmunds 1974). The range of possible defenses depends on the size and strength of the organism. Large and well-armored birds, such as owls, can aggressively chase away most of their would-be nest predators, so they can afford to rely mostly on direct defenses, whereas smaller birds have to rely on indirect means—that is, the security provided by the nest site itself. Given that a predator could either enter a cavity or insert its paw or beak through the entrance—or even remove a part of the cavity wall to gain access to the eggs, nestlings, or adults—small birds selecting secure nest sites should choose cavities that simultaneously have (1) an entrance just large enough to admit the hole's occupant, (2) walls made of hard wood, and (3) sufficient depth for the nest contents to be placed beyond the predator's reach ("nest security hypothesis"; Wesołowski 2002).

Such adaptive hypotheses are usually tested by comparing features of successful and depredated nests, to see whether attributes of their sites differ in the predicted fashion (Söderström 1999, Burke et al. 2004, Thompson and Burnhans 2004, Weidinger 2009). However, there is a methodological problem with this type of comparison. While depredated nests clearly did not pass the security check, it may be unclear whether the successful ones did so. Some of the latter may indeed have survived a predator attack because of cavity properties, but the success of others may be attributable to other factors (e.g., no predators around, nests undetected or ignored by predators). A stronger test of nest security hypotheses requires comparing features of cavities between nests that were depredated and nests that were attacked but survived. Here, I provide such a test, comparing characteristics of trees and cavities between Marsh Tit (*Poecile palustris*) nests that survived predator attack and nests that did not survive. In particular, I scrutinize whether the surviving nests were located in trees and cavities that fulfilled the specifications for a "secure" cavity (see above).

The Marsh Tit (a chickadee) is a small (about 10–11 g), sedentary bird that lives in mature broad-leaved forests of the Palearctic (Cramp et al. 1993, Glutz von Blotzheim and Bauer 1993). It is a non-excavating cavity breeder that relies on existing cavities, though adults are able to remove debris from existing cavities before building a nest (Wesołowski 1999, 2013). Adults do not actively chase predators away from their nests; instead, they usually stay in the vicinity of the cavity, uttering alarm calls (T. Wesołowski personal observation).

Here, I report observations gathered during a long-term study on a population living in the middle of a large ($\sim$1,500 km^2) expanse of the Białowieża Forest, where the last remnants of the primeval forests of temperate Europe are protected (Tomiałojć et al. 1984, Wesołowski 2007). Observations were carried out in the strictly protected part of the Białowieża National Park (BNP), where an abundance of diverse nest sites, combined with an intact assemblage of predators, creates ideal conditions for studying antipredator adaptations of organisms in pristine conditions (Tomiałojć et al. 1984, Wesołowski 2002, Tomiałojć and Wesołowski 2005). Free of direct human interference, Marsh Tits breeding there can choose their preferred nest sites from a diverse array of superabundant tree cavities (Wesołowski 1996, 2001, 2002). The efficacy of their choices is put to the test by an intact assemblage of nest predators, which use diverse detection and attack techniques. The set of predators known to attack birds in cavities in BNP consists of an array of mammals—from the smallest, bank voles (*Myodes glareolus*) and weasels (*Mustela nivalis*), to the largest, European red squirrels (*Sciurus vulgaris*) and pine martens (*Martes martes*). The Great Spotted Woodpecker (*Dendrocopos major*) is the only bird species that regularly attacks nests in cavities, but Eurasian Pygmy-Owls (*Glaucidium passerinum*) may sometimes attack such nests. Eurasian Jays (*Garrulus glandarius*) could presumably be involved as well, but no case of their attacks on nests in cavities has been recorded in >30 yr of study. No nest-attacking snakes or arthropods have been recorded (Walankiewicz 2002, Wesołowski 2002, Czeszczewik et al. 2008, Maziarz et al. 2016). Conspecific nest attacks, such as recorded in House Wrens (*Troglodytes aedon*; Belles-Isles and Picman 1986), are not known for this species.

METHODS

Study Area

The Białowieża Forest complex is situated in the middle of the European plain, at the Polish–Belarusian border. The western part of the forest (613 km^2, ~45% of the area) lies in Poland and represents a remnant of the vast lowland forests that once covered large parts of temperate Europe. Its present unique features result from its considerable size and an exceptionally good state of preservation (Tomiałojć and Wesołowski 1990, Wesołowski 2005, 2007). The majority of the tree stands in the Polish part are now under management, but a 47.5 km^2 block of the best-preserved primeval old-growth stands, situated in the center of the forest, has been retained within the strictly protected part of BNP. The preserved primeval stands are multistory, mixed-species, and uneven-aged. They contain many veteran trees, reaching 50 m in height and 2.35 m in diameter at breast height (Niechoda and Korbel 2011). They also contain large amounts of standing dead timber and fallen trees (20–25% of total wood volume; Bobiec 2002). For more information and photos, see Tomiałojć and Wesołowski (1990, 2004), Wesołowski (2007), and Wesołowski et al. (2016).

Data on Marsh Tit breeding were gathered in 4 sample plots of 33–54 ha within BNP, spaced 1–2 km apart and covering a total area of ~185 ha. Three plots (C, M, and W) were situated in oak–lime–hornbeam *Tilio-Carpinetum* forest composed mostly of hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), pedunculate oak (*Quercus robur*), spruce (*Picea abies*), and continental maple (*Acer platanoides*). The fourth plot was located in a swampy riverine forest made up mainly of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and spruce; it also contained some drier, hornbeam-covered "islands" along the edges (for detailed descriptions, see Tomiałojć and Wesołowski 1990, 2005, Wesołowski et al. 2002). No artificial food or nest boxes were available, and birds bred exclusively in tree cavities (Wesołowski 1996).

Field Data Collection

Observations were carried out in 1987–2016. Every spring, except in 1990–1991, intensive searches for nests, aimed at finding all cavities used for breeding, were made in the 4 plots described above. To gather data on the course of breeding, and on the fate of nests, the cavities were checked regularly (mostly from the ground). The nests were examined with a small bulb on a bendable wire and a small mirror—those in lower-situated cavities from the ground or a ladder, and higher ones by climbing. These observations allowed evaluation of the expected fledging dates.

At every visit, any signs of predator attack, whether successful or not, were recorded (see below). Around the expected fledging date, the cavities were observed from a distance every ~24 hr, up to the day on which no parents were observed bringing food to the cavity. If, on the previous day, young were ≥18 days old (the youngest age of fledging of undisturbed broods; Wesołowski 2000) and no signs of attempted predation were detected, the nest was considered successful. If no feeding was observed at a cavity containing young about to fledge (16–17 days old), the observers searched for parent birds (most of them color banded) to check whether they were collecting food for prematurely fledged young. If they were, the nest was classified as successful. All other cases of premature cessation of parental activity (i.e. no signs of parent presence during a 1 hr observation session) were treated as nest failure. All nests, except a few inaccessible cavities with lost nests, were checked to ascertain the possible causes of failure. The hole interior, the trunk in the vicinity of the entrance, and the ground around the nest tree were thoroughly inspected in search of the remains of eggs, young, adult birds, removed nest material, and/or traces of predators. Nests emptied prematurely were classified as depredated, even if there were no apparent signs of damage to the nest or cavity (Wesołowski 2002).

Attributes of cavities were recorded in varying detail in different years. The species of tree containing the cavity, the height of the entrance above ground (visually estimated for low holes, measured with a clinometer for holes higher than ~10 m), the type of cavity (woodpecker-excavated or non-excavated), and the substrate in which the cavity was situated (live or dead) were recorded throughout the entire study period. Dimensions of cavities were assessed systematically in 1993–2001 and 2012–2014, and less regularly in other years. Of several measurements taken at each cavity (Wesołowski 1996), only 2, relevant to the study of predation, are included here. These are the entrance diameter (either height or width, whichever was smaller) and "safety distance," the distance between the outer edge of the entrance and the nest center at the nest rim level (this shows how far a predator has to reach to touch eggs or nestlings). Details of measurement techniques are given in Wesołowski (1996). The measurements were usually taken during the nestling period, but on a few occasions they were taken after the young had fledged.

Data Analysis

Instances of successful nest defense (1–5 season^{-1}) were recorded in 19 of the 30 yr of the study. The pressure of nest predators in BNP fluctuated strongly across years (Walankiewicz 2002, Czeszczewik et al. 2008, Wesołowski and Maziarz 2009); thus, the chance of a Marsh Tit nest being depredated could vary across years for reasons independent of the birds' actions. Therefore, it would be worthwhile to include "year" as a separate factor in the analysis. However, given the low numbers of cases observed in individual seasons, this was not feasible and data from all years were pooled in the analysis. To remove the potential impact of years in which no cases of successful defense were observed, those years were excluded, and the study is based on a comparison of nests that survived predator attack and those that did not survive predator attack (i.e. were depredated) in 19 seasons in which the former were observed. Of 38 nests attacked at the egg stage, only one survived, so the analysis is restricted to attacks that occurred at the nestling stage.

For all attacked cavities, the state of the entrance was classified as "intact" or "damaged" (including cases in which the original entrance remained intact and a completely new hole was made; see Figure 1). The state of the nest material was classified as "intact" when there were no traces of removal, as "tousled" when the nest remained in the cavity but the nest structure was damaged and the material was mixed up, or as "plucked up" when the whole nest or part of the nest was removed through the original entrance or through a new hole. These signs were combined to represent 3 different predatory techniques: "entered"—predator passed through the entrance and consumed the broods inside (entrance intact and nest intact or tousled); "plucked up"—predator used paws or beak to remove nest contents through the entrance (entrance intact and nest plucked up); and "wall destroyed"—original opening enlarged or a completely new entrance excavated (entrance damaged).

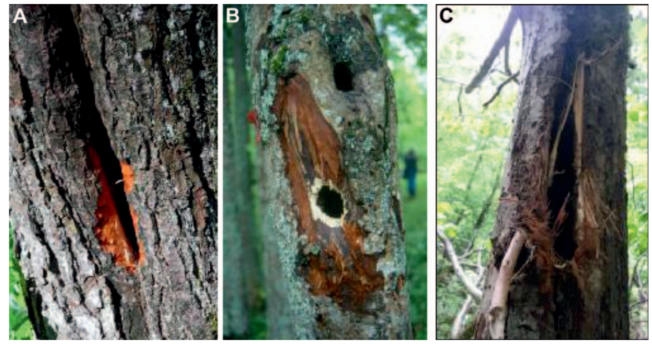

FIGURE 1. Marsh Tit cavities after predator attack. (**A**) A woodpecker attempted to enlarge the entrance but was unable to remove the nestlings. (**B**) A woodpecker removed nestlings through a newly excavated opening in a decayed cavity wall. (**C**) A mammal tore off pieces of bark and bast to gain access to nestlings.

In most cases, it was impossible to recognize the species of predator involved, but 2 classes of predators left unmistakable traces. Great Spotted Woodpeckers left fresh pecking traces on the entrance rim (Figure 1A) or at the new entrance (Figure 1B), fresh wood chips in the nest, and/or remnants of pulled nestling quills. Forest dormice (*Dryomys nitedula*) left behind nestlings or adults with eaten-out brains, scat (dark or black tapering rolls, 1–2 cm long), and tousled nest material (Nowakowski and Boratyński 2000).

Sample sizes of variables differ between individual analyses because collecting a full set of measurements was not possible in every case. For statistical calculations, nonparametric tests were used, following formulas in Statistica 12.0 (StatSoft 2014). All probability values shown are 2-tailed.

RESULTS

Of 169 Marsh Tit broods that were attacked by predators in BNP, 50 (29.6%) survived the attack, partially or totally. It was possible to count the number of surviving young in only 32 of the surviving broods; in 23 (72%) of these cases, the predator managed to remove no or only one nestling.

The locations of Marsh Tit broods that survived predator attack ($n = 50$) were similar to those of broods that were depredated ($n = 119$). They were mostly found in trunks (96% vs. 92%, respectively) of living (90% vs. 94%) limes (50% vs. 62%) and hornbeams (24% vs. 21%). These were chiefly non-excavated, decay-formed (96% vs. 92%) cavities. None of these differences approached significance (Yates's corrected χ^2, $P = 0.24$–0.61). Also, height above the ground did not differ between nests that survived an attack (median = 3.5 m) and those that did not survive (median = 3.0 m; Kruskal-Wallis analysis of variance [ANOVA], $H_{1,169} = 0.001$, $P = 0.98$). Timing of egg laying did not differ between nests that survived an attack and

TABLE 1. Condition of nest material, state of the cavity entrance, and fate (depredated or survived) of Marsh Tit nests that were attacked by predators in Białowieża National Park, Poland.

	Intact entrance		Damaged entrance [a]	
Nest material	Depredated ($n = 76$)	Survived ($n = 18$)	Depredated ($n = 43$)	Survived ($n = 25$)
Intact	38%	22%	33%	68%
Tousled	20%	6%	7%	8%
Plucked up	42%	72%	60%	24%

[a] Including cases in which the original entrance remained intact and a completely new hole was made (see Figure 1).

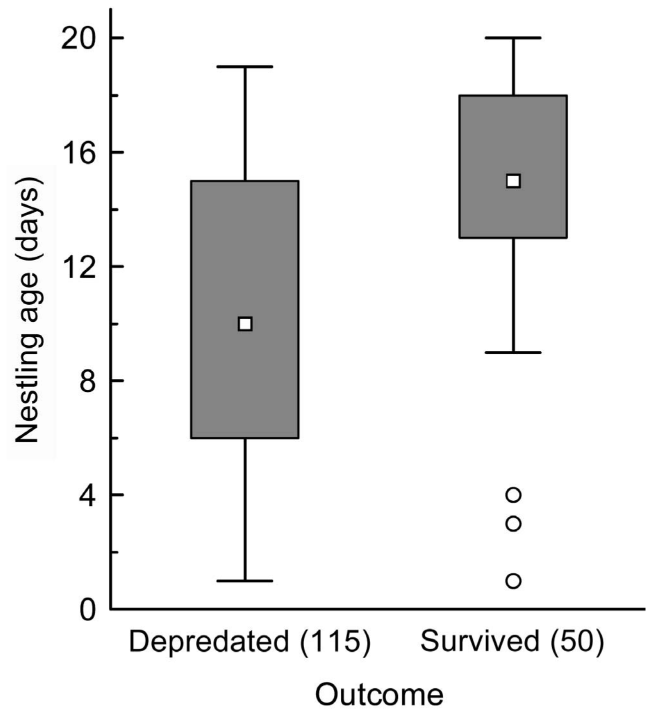

FIGURE 2. Age of nestlings when attacked for Marsh Tit broods that survived and did not survive predator attacks in Białowieża National Park, Poland. Shown are medians (small squares), 25–75% quartiles (boxes), non-outlier ranges (whiskers), and outliers (circles); sample sizes are given in parentheses.

those that did not; mean relative laying dates in both groups equaled the yearly medians (Kruskal-Wallis ANOVA, $H_{1,168} = 0.4$, $P = 0.52$).

The chances that a Marsh Tit brood would survive an attack depended on the technique employed by the predator. Survival was lowest (10%) when the predator managed to enter the cavity without damaging the entrance (Table 1: entrance intact and nest intact or tousled). It was higher (29%) when the predator used paws or beak to pluck up nest contents through the entrance (Table 1: entrance intact and nest plucked up). It was highest (39%) when the predator tried to enlarge the original opening or make a completely new hole at nestling level (Figure 1 and Table 1: entrance damaged; $\chi^2_2 = 10.48$, $P = 0.005$). Additionally, the proportion of broods surviving predator attack increased with the age of the brood (Figure 2; Kruskal-Wallis ANOVA, $H = 29.9$, $P < 0.001$).

Cavity entrances of depredated nests most often (64%) bore no traces of predator activity, whereas predator signs, such as attempted enlargement of entrances or newly excavated entrances (Figure 1), were more often (58%) found in cavities with broods that survived (Table 1). The smallest predators were able to pass through even the narrowest (1.7 cm) entrances of cavities used by Marsh Tits and, once inside, they could reach broods even in the deepest cavities (27 cm from the entrance; Figure 3D). For this type of attack, there was no difference in cavity entrance diameter, nor in the safety distance, between nests that survived attack and those that were depredated (Kruskal-Wallis ANOVA, $H = 0.06$, $P = 0.80$ and $H = 1.25$, $P = 0.30$, respectively). When predators attempted to "pluck up" nests, those nests that survived the attack had similar entrance dimensions to nests that were depredated (Figure 3B; $H = 1.10$, $P = 0.30$), but they were situated ~5 cm farther from the entrance, a difference that approached significance (Figure 3E; $H = 3.77$, $P = 0.052$). Overall, the broods in cavities from which the predators managed to pluck nest material, independent of the broods' fates, were ~3 cm closer to the entrance than the broods in cavities where predators entered (cf. Figure 3D, 3E; $H_{1,52} = 8.52$, $P < 0.04$). In the cases where predators damaged walls, safety distances did not differ between nests that survived attack and nests that were depredated (Figure 3F; $H = 0.04$, $P = 0.84$), but the cavity entrances were narrower at nests that survived than at nests that were depredated (Figure 3C; $H = 9.41$, $P = 0.002$).

Several species of woodpeckers occur in BNP, but only Great Spotted Woodpeckers were ever observed to attack Marsh Tit broods in cavities (3 causal observations). These woodpeckers were usually too large to pass through the cavity entrance, because the entrance diameter of ~85% of Marsh Tit cavities was below the minimum size (4.5 cm; Wesołowski 2002) passable by this species. Woodpeckers could probably pluck up some nests through the entrance without damaging cavity walls (and then they could not be differentiated from other predators), but in 40 cases they left quite unmistakable traces of their attacks—fresh peckings at the entrance rim, fresh wood chips in the nest, or an additional new hole (Figure 1A, 1B). Marsh Tit nests survived 40% of the woodpecker attacks. Nests that survived woodpecker attack had narrower openings (median = 2.2 cm) than nests depredated by woodpeckers (median = 3.8 cm, Kruskal-Wallis ANOVA, $H_{1,21} = 6.6$, $P = 0.01$), but their safety distances were similar (median = 14 cm in each case).

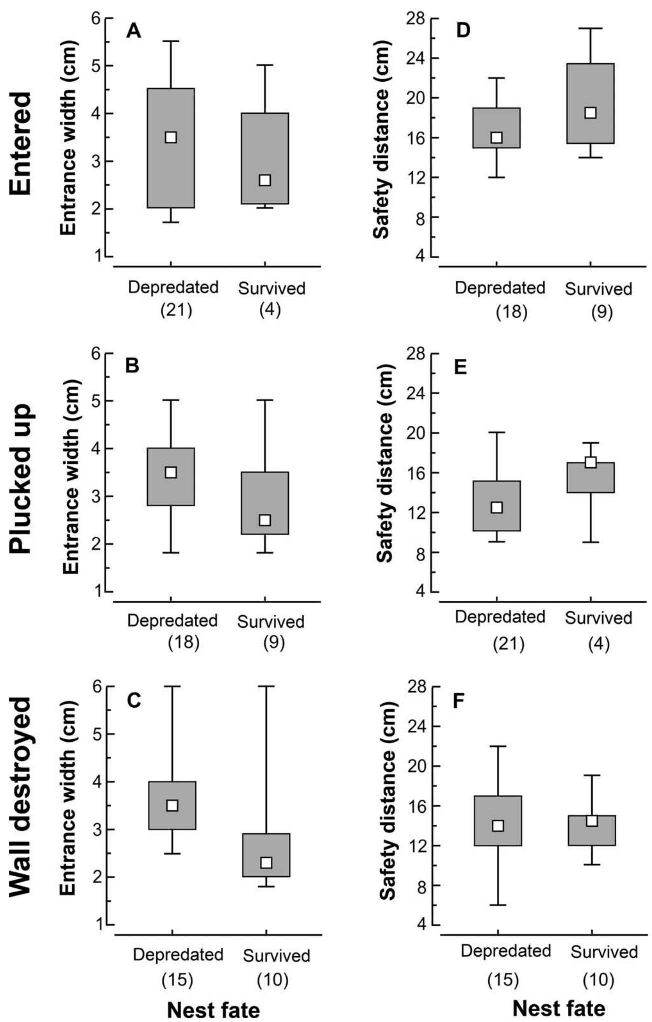

FIGURE 3. Variation in entrance diameter (**A**–**C**) and "safety distance" (**D**–**F**) of cavities in which Marsh Tit broods survived or did not survive predator attacks in Białowieża National Park, Poland. The 3 predatory techniques ("entered," plucked up," and "wall destroyed") are described in the text. Squares indicate medians, boxes indicate 25–75% quartiles, and whiskers indicate non-outlier ranges; sample sizes are in parentheses.

Broods destroyed by forest dormice ($n = 8$, none of which survived) contained remnants of nestlings (and in one case an adult) with removed brains, contained scats (dark or black tapering rolls, 1–2 cm long), and the nest material was often tousled. In all cases the rodents entered the cavities, passing through their entrances (as narrow as 1.8 cm) and reaching nests far from the entrances (down as far as 21 cm).

DISSCUSSION

To fledge their young, Marsh Tits have to avoid or survive attacks by a diverse assemblage of predators (see above). The results of the present study show that they achieve this with variable efficiency. Overall, Marsh Tit nests survived ~30% of predator attacks that were recorded in BNP. However, the chance of surviving an attack was only 10% when the predator managed to enter the hole; it was 29% when the predator attempted to pluck the nest, and 39% when the predator tried to get access by removing the cavity wall. Great Spotted Woodpeckers depredated only 60% of attacked broods, whereas the onslaughts of forest dormice appeared to be 100% efficient. These findings clearly demonstrate that a suite of antipredator measures used by Marsh Tits are efficient to a varying extent against different predators' tactics.

In BNP, locations of Marsh Tit broods were very similar between nests that survived a predator attack and nests that were depredated. Nests were mostly in non-excavated cavities, in trunks of living broad-leaved trees, and at similar heights above the ground. Thus, once a predator had already launched an attack, cavity placement was unimportant in determining the brood's fate. This is not to say that the features of cavity location were unimportant; as shown in an earlier study (Wesołowski 2002), the nesting success of (few) Marsh Tits breeding in woodpecker-made cavities, or in cavities in dead wood, was much lower than the success of those breeding in non-excavated cavities, surrounded by strong walls (trunks of living trees). Therefore, these features of cavity localization probably acted mostly as indirect defenses (Edmunds 1974), and cavities that were structurally well protected were presumably less frequently attacked.

By using cavities with narrow entrances, Marsh Tits could prevent larger predators from entering their cavities, but this was an inefficient barrier for smaller predators. Even the smallest entrances of cavities used by Marsh Tits (18 mm) were still passable for a set of dangerous enemies, including adult-killing forest dormice (Wesołowski 2002). Marsh Tits were barely able to pass through such small entrances; they were forced to squeeze through them, damaging plumage in the process (T. Wesołowski personal observation). Given that the birds could not gain much by using cavities with such small entrances (they could not prevent smaller nest predators anyway), they used mostly cavities with somewhat larger entrances (~25 mm; Figure 1), through which they could easily pass.

Because of the presence of small predators, entrance diameter had no effect on nest success for several other cavity-nesters breeding in BNP (Czeszczewik and Walankiewicz 2003, Wesołowski and Rowiński 2012, Maziarz et al. 2016). However, cavities of Collared Flycatchers (*Ficedula albicollis*) and Wood Nuthatches (*Sitta europaea*) with smaller entrances were less frequently depredated (Walankiewicz 1991, Wesołowski and Rowiński 2004). Smaller entrances also increased nest success in Mountain Chickadees (*Poecile gambeli*) in western Canada (Norris 2012) and in several smaller cavity-nesters in a subtropical forest in Argentina (Cockle et al. 2015). Also in woodpeckers, predation rates on broods tend to increase with the entrance size of their cavities (Paclík et al. 2009). Thus, it seems that the efficiency of small entrance size as an antipredator safety device is context dependent. One can envisage that it will be less efficient in areas like BNP, where small predators prevail (Czeszczewik et al. 2008), but it could be more profitable in places in which larger predators are the main threat.

Small entrances are practical as an antipredator defense as long as they are combined with walls of living or only slightly decomposed sapwood that cannot be destroyed by larger predators. The results of the present study strongly demonstrate the adaptive value of such solid defensive walls, thus agreeing well with data on other cavity-nesters in BNP that mostly use cavities in trunks of living trees (Maziarz et al. 2016). The importance of strong hole walls was also confirmed in studies of non-excavators elsewhere (Ludescher 1973, Alatalo et al. 1990, Albano 1992, Christman and Dhondt 1997, Cockle et al. 2015). Similarly, woodpecker broods are often immune to large predators when located in tree cavities with sound wood, but destroyed when located in decayed wood (Paclík et al. 2009, Tozer et al. 2012).

Marsh Tit nests that survived attack were located farther from the cavity entrance than those that were depredated, which demonstrates that placing a nest far from the opening was an efficient tactic to avoid those predators that were able to remove nest contents through the entrance. This relationship also holds for several other cavity-nesters in BNP, whose nests were more often depredated when situated closer to the cavity entrance (Czeszczewik and Walankiewicz 2003, Wesołowski and Rowiński 2012, Maziarz et al. 2016). In Białowieża Forest, nest contents could be pulled through the entrance if the safety distance was below ~17 cm (Wesołowski 2002). Similarly, successful broods of Pied Flycatchers (*F. hypoleuca*) in Sweden (Alatalo et al. 1990) and of Carolina Chickadees (*P. carolinensis*) in Illinois (Albano 1992) were situated farther from cavity entrances than depredated nests of the same species. The safety distance of successful broods (16–17 cm on average) was similar to that found in BNP.

Marsh Tits built nests with a bulky foundation of moss (15 cm thick in extreme instances; Wesołowski 1996, 2013). Therefore, they could adjust the safety distance of their nests by varying the amount of nest material brought to the cavities: Less moss would increase the safety distance. Despite the clear selective advantage, they only seldom placed their nests beyond the reach of predators, which strongly suggests that there could be constraints on building nests that are too low and/or on breeding in cavities that are too deep. Such constraints might include insufficient insurance against flooding (important in rainy seasons in BNP; Wesołowski et al. 2002), not enough light in the nest (Löhrl 1977, Wesołowski and Maziarz 2012), or problems with cavity ventilation or movement within the nest chamber. In cavities with smaller entrances, Marsh Tits located their nests closer to the entrance (Wesołowski 1996), which suggests that by shortening the distance to the entrance, the birds could try to compensate for poor illumination in such cavities.

The chance of a Marsh Tit brood surviving a predator attack strongly increased with the nestlings' age. This cannot be attributable to the increased intensity of nest defense of larger young, because Marsh Tits do not actively chase predators (T. Wesołowski personal observation). This suggests that nestling size or behavior may play an important role in surviving attacks. Small young, being virtually immobile, had no means to defend themselves, but larger nestlings, with eyes open and functional legs, could escape and hide in cavity recesses or hook on nest material, hindering their removal by a predator (T. Wesołowski personal observation). These observations demonstrate that, even in this cavity-nesting altricial bird, early development of legs may be at a premium.

The results presented here demonstrate the existence of limits on adaptations. Despite constant selective pressure exerted by nest predators, Marsh Tits do not have much room to improve their antipredator tactics; they already use cavities with strong walls (with no way to upgrade), and they could not use cavities with yet smaller entrances (which could eliminate predation by small rodents) without reduction of their own body size. Although they could increase the safety distance of their nests by locating them farther from the cavity entrance, they often place them closer to the entrance than the security requirements would demand. It seems, thus, that some trade-offs between security and other requirements (see above) do exist.

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