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Nest holes of Great Spotted Woodpeckers *Dendrocopos major* and Middle Spotted Woodpeckers *D. medius*: Do they really differ in size?

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Abstract. Great- and Middle Spotted Woodpecker nest-hole dimensions and tree diameters at hole-entrance height were analyzed in order to test the hypothesis that Middle Spotted Woodpeckers, by making use of a thinner substrate and excavating smaller nest-holes, may reduce interspecific competition for nest-sites with Great Spotted Woodpeckers. It was found that only the vertical diameter of Great Spotted Woodpecker nest-hole openings and the entrance-hole area (49.2 mm, 17.8 cm² respectively) were significantly larger than the corresponding parameters in Middle Spotted Woodpeckers (44.9 mm, 16.2 cm²). The average tree diameter at nest-height was 42.7 cm in Great Spotted Woodpeckers and 38.2 cm in Middle Spotted Woodpeckers, and did not differ between the two species. There were no correlations between the tree diameter at nest height and nest height in either species. The small variation in hole-entrance diameters (CV ≤ 10%) and the distance that a predator had to reach to plunder the nest (≥ 19 cm) are most likely to protect woodpeckers' broods against arboreal predators — mainly Pine Martens. It is concluded that the tree diameter at nest-height probably makes little or no difference with respect to avoidance by Middle Spotted Woodpeckers of competition with Great Spotted Woodpeckers. The role of nest-hole size in terms of its influence on reproduction is also discussed.

Key words: Great Spotted Woodpecker, Middle Spotted Woodpecker, *Dendrocopos medius*, *Dendrocopos major*, nest-hole dimension, substrate thickness, cavity kleptoparasitism

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INTRODUCTION

Tree species, substrate diameter and its viability, interspecific competition and predation are among the crucial factors affecting nest-site selection in woodpeckers (Short 1979, Wesolowski & Tomiałojć 1986, Hågvar et al. 1990, Stenberg 1996, Bai et al. 2005, Kosiński et al. 2006). A broad generalisation suggests that among all woodpeckers *Picidae* there is a relationship between body size and substrate diameter at nest-height (e.g. Conner et al. 1975, Hågvar et al. 1990, Stenberg 1996). It has been shown that the choice of thin stems or fragments by the smallest species is affected by a lower risk of the nest-hole being taken over and enlarged by larger species of woodpeckers (Short 1979). Moreover, some nest-hole attributes, e.g. entrance size and nest-hole depth, may protect

broods against a variety of predators (Walaniewicz 1991, Sandström 1992, Wesolowski 2002).

Middle Spotted Woodpeckers (20–22 cm; wingspan 33–34 cm, Pasinelli 2003) are ca 10% smaller than Great Spotted Woodpeckers (22–23 and 34–39 cm respectively, Michalek & Miettinen 2003). This suggests that the Middle Spotted Woodpecker nest-hole sizes should be smaller than those excavated by Great Spotted Woodpeckers. Günther (1993) suggested that the Middle Spotted Woodpecker's ability to build smaller nest-holes, excavated higher in the tree and in thinner substrate than Great Spotted Woodpeckers, might have evolved to reduce cavity kleptoparasitism (sensu Kappes 1997), and thereby enabling the co-existence of both the woodpecker species (see also Pasinelli 2003). However, this suggestion has not yet been directly tested by

a comparison of nest-hole sizes (Günther 1993). Moreover, the data covering detailed characteristics of nest-hole dimensions of each species are scarce (e.g. Yamauchi et al. 1997, Kosenko & Kaygorodova 2003, Remm et al. 2006, see also review in Michalek & Miettinen 2003, Pasinelli 2003). As yet, we have not found any study referring to the nest-hole size of Great- and Middle Spotted Woodpeckers living in syntopy.

The aims of this paper were: 1) to describe variation in nest-hole dimensions and the tree diameter at nest-height for the Great- and Middle Spotted Woodpeckers, 2) to show the hole attributes which may prevent access by predators and 3) to discuss whether nest-hole kleptoparasitism may really affect nest-site selection. We predicted that Middle Spotted Woodpecker nest-holes would have smaller dimensions than Great Spotted Woodpecker ones due to the smaller body size.

STUDY AREA

The study site, 224 ha in size, was located in the riverine forest of the Warta river valley, central Poland, near Czeszewo (17°31' E -52°09' N), 50 km south east of Poznań. The study plot encompasses 185 ha of the forest. The vegetation consists of *Quercus-Fraxinus-Ulmus* (*Fraxino-Ulmetum*) woodland in the flooded parts and *Quercus-Carpinus* (*Stallario-carpinetum*) forest on the higher grounds. A part of this area (74 ha) is covered by mature, near-natural forest stands (155–165 years old), which has been practically left unmanaged since 1959. The rest of the study plot is covered by younger stands (mainly 40–120 years old). In 2004, the whole study plot (222.6 ha) was established as a nature reserve "Czeszewski Las". A more detailed description of the study area and nesting habitats of woodpeckers is presented elsewhere (Kosiński & Winięcki 2004, Kosiński et al. 2006).

MATERIALS AND METHODS

In 2002–2004, while conducting detailed studies of the breeding biology of both the woodpecker species (Kosiński & Ksit 2006), nest-holes were described. The following measurements were taken at each accessible hole: horizontal and vertical entrance diameters in the narrowest place, thickness of the front wall at the level of the bottom of the hole entrance (length of entrance

corridor), chamber diameter at the level of the bottom of the entrance hole, chamber depth and chamber height from the bottom to the roof of the entrance hole. The latter two dimensions were measured using a thread with a weight tied to its end. The thread was passed through a tube and inserted into the bottom of the nest-hole (see also Ar et al. 2004). The area of the entrance was calculated assuming the ellipse-like shape, according to the formula:

$$A = \pi ab$$

where a and b are the semimajor and semiminor axes of the entrance. The cavity volume was calculated using cylindrical approximation (Remm et al. 2006):

$$V = \pi (c/2)^2 d$$

where c is the hole diameter, and d is the chamber height.

While plundering an woodpecker's nest, a predator that can not enter the hole has to reach the bottom of the hole. To express the distance that such a predator has to reach, a 'danger distance', we calculated a sum of the length of the entrance corridor and the chamber depth. The nest-holes were measured after the nestlings had fledged.

For technical reasons, to measure diameter at nest height (DNH), we used nest-holes found in 2005 and 2006. Since neither the diameter at breast height of the nesting trees nor the height of nest-holes in Great- and Middle Spotted Woodpeckers differed between 2002–2004 and 2005–2006 (t-test, $p > 0.05$ in all cases), as well as there were no differences in the placements of nest-holes in relation to the tree species and part of tree (trunk vs limb/branch; χ^2 test, $p > 0.05$), it is unlikely that DNH differed between both the study periods.

Trunks and limbs/branches with nest-holes were photographed using a digital camera with a 35–420 mm lens. Each photograph was calibrated based on the mean horizontal entrance diameter (4.5 cm in Middle Spotted Woodpeckers and 4.6 cm in Great Spotted Woodpeckers) which is characterised by very small variation ($CV \leq 10\%$, see below). Following this procedure the tree diameter at the nest height was measured to the nearest 1 cm using Lupa software (Lupa 2.0, UI Desmodus 2004). All nest-holes were photographed in 2006. Because some trees had fallen or nest-holes had

become sealed since 2005, the sample size is slightly smaller than the number of nest-holes previously found.

Since all nest-hole dimensions were normally distributed and had equal variances, we used the t-test for comparing the means. The tree diameter at nest height was log-transformed for comparing the means. Statistical tests were carried out using STATISTICA 7.1 (StatSoft, Inc. 2005). The values reported are means \pm standard deviations unless otherwise stated. All tests are two-tailed.

RESULTS

Nest-hole size

Except the vertical entrance diameter and area of entrance, hole dimensions did not significantly differ between Great- and Middle Spotted Woodpeckers (Table 1). In the case of Middle Spotted Woodpeckers, openings were approximately circular; the vertical and horizontal diameter of the entrance did not vary significantly when compared with each other (t test for matched pairs, $t_{30} = -0.85$, $p = 0.40$). The openings of Great Spotted Woodpeckers were elongated; the value of the vertical diameter was significantly greater than the horizontal diameter of the entrance (t test for matched pairs, $t_{62} = -5.29$, $p < 0.00001$). As a consequence, the area of the entrance for Great Spotted Woodpeckers was on average 1.6 cm² larger compared to that for Middle Spotted Woodpeckers (Table 1). The entrance width and height were the least variable (coefficient of variation $CV \leq 10\%$) of all nest-hole dimensions. The most variable characteristic was the frontal wall thickness (Table 1). The mean distance between the edge of the entrance and the back wall of the cavity, which may express a space indispensable to hole excavation, was 168.4 ± 31.5 mm (range 110–290, $n = 63$) in Great Spotted Woodpeckers and 160.2 ± 30.2 mm (range 104–250, $n = 31$) in Middle Spotted Woodpeckers and did not differ between species ($t_{92} = 1.21$, $p = 0.227$, Fig. 1).

If the 'danger distance' has an adaptive value in avoiding nesting failure, one could expect that the decrease of distance between the entrance and the chamber should result in an increase of chamber depth. However, there was no correlation between these two variables (Pearson correlation, $r = -0.20$ and $p > 0.05$ in both species).

Tree diameter at nest-height

The average tree diameter at nest-height was

Table 1. Characteristics of nest-holes of Great Spotted Woodpeckers and Middle Spotted Woodpeckers. Mean \pm standard deviation (SD), range (min-max), numbers of nest-holes measured (N) and confidence of variation (CV), t-values and their probability are given.

| Variable | Great Spotted Woodpecker | | | | Middle Spotted Woodpecker | | | | t | p |
|---|--------------------------|-----------|----|------|---------------------------|-----------|----|------|-------|--------|
| | Mean \pm SD | Range | N | CV | Mean \pm SD | Range | N | CV | | |
| Entrance: | | | | | | | | | | |
| vertical diameter (mm) | 49.2 \pm 4.9 | 38–63 | 63 | 10.0 | 45.7 \pm 3.8 | 37–51 | 31 | 8.3 | 3.48 | <0.001 |
| horizontal diameter (mm) | 46.0 \pm 4.1 | 34–56 | 63 | 8.9 | 44.9 \pm 4.3 | 31–54 | 31 | 9.6 | 1.12 | 0.265 |
| Area of entrance (cm ²) | 17.8 \pm 2.8 | 10.4–25.7 | 63 | 15.7 | 16.2 \pm 2.3 | 10.5–20.4 | 31 | 14.2 | 2.88 | 0.005 |
| Thickness of front wall below entrance (mm) | 50.8 \pm 13.3 | 22–82 | 63 | 26.2 | 48.4 \pm 15.8 | 22–95 | 31 | 32.6 | 0.79 | 0.432 |
| Hole diameter (mm) | 117.6 \pm 24.9 | 80–208 | 63 | 21.2 | 111.8 \pm 24.3 | 65–173 | 31 | 21.7 | 1.07 | 0.286 |
| Chamber depth (mm) | 240.4 \pm 47.6 | 157–354 | 57 | 19.8 | 244.5 \pm 58.7 | 144–408 | 24 | 24.0 | -0.33 | 0.745 |
| Chamber height (mm) | 292.4 \pm 50.0 | 203–408 | 57 | 17.1 | 291.1 \pm 58.9 | 186–450 | 24 | 20.2 | 0.10 | 0.918 |
| Volume (l) | 3.3 \pm 1.6 | 1.3–8.2 | 57 | 48.5 | 2.8 \pm 1.0 | 0.9–4.3 | 24 | 35.7 | 1.40 | 0.164 |
| Danger distance (mm) | 290.5 \pm 46.9 | 203–395 | 57 | 16.1 | 290.3 \pm 57.7 | 187–441 | 24 | 19.9 | 0.01 | 0.989 |

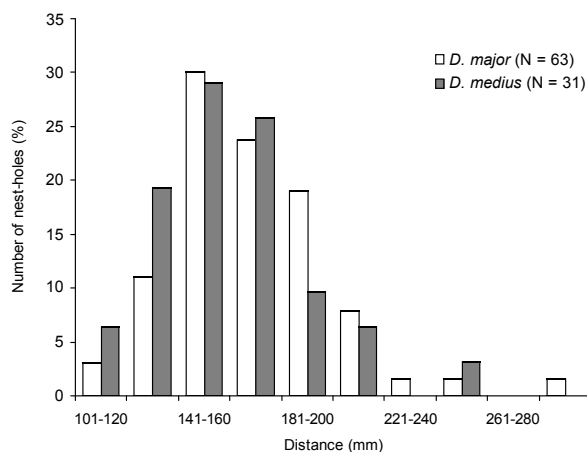


Fig. 1. Distribution of distance from the outer edge of entrance to the back wall of the nest-holes in Great- and Middle Spotted Woodpeckers.

42.7 ± 18.4 cm (95% confidence limits: 38.3–47.1, range 18–107, $n = 70$) in Great Spotted Woodpeckers and 38.2 ± 16.6 cm (95% confidence limits: 33.0–43.5, range 15–78, $n = 40$) in Middle Spotted Woodpeckers, and did not differ significantly between species ($t_{108} = 1.39$, $p = 0.167$, Fig. 2). Moreover, there were no interspecific differences in DNH between nest-holes excavated in trunks ($t_{87} = 1.63$, $p = 0.107$) and limbs/branches ($t_{17} = -1.09$, $p = 0.292$). Furthermore, comparisons within near-natural, protected forests and recently managed stands indicate no differences in DNH between Great- and Middle Spotted Woodpeckers ($t_{48} = 1.22$, $p = 0.229$ and $t_{58} = 0.83$, $p = 0.41$,

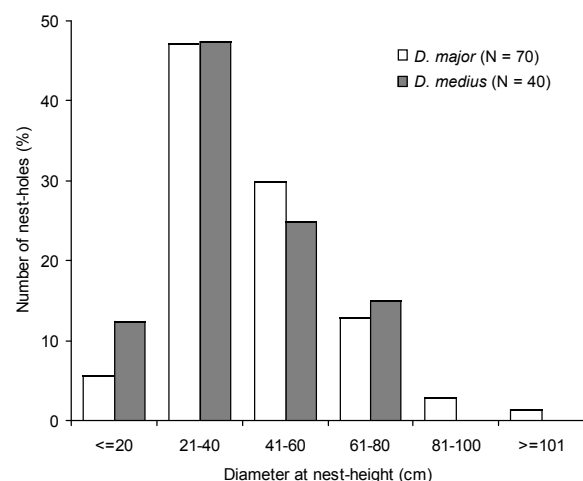


Fig. 2. Distribution of the diameter at nest-height in Great- and Middle Spotted Woodpeckers.

respectively). There was no correlation between DNH and nest height in Great Spotted Woodpeckers (Pearson correlation, $r = -0.16$, $p = 0.205$, $n = 67$) and Middle Spotted Woodpeckers ($r = -0.16$, $p = 0.33$, $n = 39$).

DISCUSSION

Nest-hole size

The characteristics of the nest-hole dimensions of both woodpecker species in our study area were similar to those reported for other populations across the range of these species in higher latitudes (e.g. Kawada 1980, Yamauchi et al. 1997, Wiesner 2001, Kosenko & Kaygorodova 2003, Remm et al. 2006, see review in Michalek & Miettinen 2003, Pasinelli 2003).

The differences between the vertical diameter of the entrance and the entrance area probably reflect a difference in body size between the Great- and Middle Spotted Woodpeckers (see Michalek & Miettinen 2003, Pasinelli 2003). The small variation in the entrance as compared to other nest-hole dimensions, is most likely to constitute an anti-predator adaptation (see below), and this has been supported by other studies (Kawada 1980, Yamauchi et al. 1997, Kosenko & Kaygorodova 2003, own calculation). In all cited studies the entry widths were the least variable of all hole characteristics.

The high variation in the distance between the edge of the entrance and the chamber in both the woodpecker species is probably influenced by substrate hardness and reflects the distance to the soft wood that must be reached before the nest-chamber can be dug out, as well as the substrate diameter at nest-height. The high variation in entrance length seems to be typical of all the populations studied in detail (Yamauchi et al. 1997, Kosenko & Kaygorodova 2003, see also Günther & Hellmann 1995).

We know of only two estimates of cavity volume in Great Spotted Woodpeckers. Carlson et al. (1998) assessed a mean volume of nest-holes at 3.7 l ($n = 8$). Cavity volumes from riverine forests in Estonia (Remm et al. 2006), calculated using cylindrical approximation, were also slightly larger (3.5 l, range 1.1–7.6, $n = 12$) than those found in our study area. However, it should be stated that all these values might be overestimated because the actual shape of the cavity of woodpeckers is not cylindrical. In fact, the shape of the cavity is rather a cone frustum or is built up

as conical bistrustum (H. Robles pers. comm., Z. Kosiński and P. Ksit unpubl. data). Based on the data reported by Ar et al. (2004), we have found that cavity volume below the entrance in Syrian Woodpeckers (structurally similar to Great Spotted Woodpeckers), calculated using cylindrical approximation, was ca. 19% larger (2.7 ± 1.0 l) than that measured using a polyethylene bag filled with water (2.2 ± 0.6 l).

It has been speculated that nest-holes of Middle Spotted Woodpeckers excavated in the thinner substrate would be smaller and in this way could not be taken over and enlarged by Great Spotted Woodpeckers (Günther 1993, see also Pasinelli 2003). This hypothesis conflicts with our results. We did not measure breeding holes situated at a great height, due to their inaccessibility to observers, nor did we directly compare the tree diameter at the nest height or the diameter indispensable for nest-hole excavation. However, it is rather unlikely that nest-holes situated higher up and in tree structures of a lower diameter, e.g. in limbs, would differ from those excavated in trunks. Moreover, since the thickness of the front wall was the most variable characteristic of nest-holes, and the space indispensable to hole excavation was similar in both species, it is most likely that nest-hole excavation in thin fragments proceeds at the cost of wall thickness. For example, in the case of a nest-hole excavated in the thinnest substrate (16 cm) the front and back wall were as thin as ca 3.5 and 2.5 cm respectively, but the internal nest-hole diameter was ca 10 cm, close to average values reported for both species. Furthermore, in all earlier studies the tree diameter at the nest-height in Middle Spotted Woodpeckers (Pettersson 1984, Günther 1993, Kosenko & Kaygorodova 2003) has been sufficiently large to provide enough room for Great Spotted Woodpecker nest-holes as well (Michalek & Miettinen 2003). Thus, substrate thickness probably makes no important difference in avoiding competition from Great Spotted Woodpeckers. The preference for highly situated substrate by Middle Spotted Woodpeckers in some areas (e.g. Wesołowski & Tomiałojć 1986, Günther 1993, Kosiński & Kempa 2007), can be explained by the limited number of tree species suitable for hole-excavation (Wesołowski & Tomiałojć 1986, Hågvar et al. 1990) and by using softer parts of the tree which are beneficial for a species with weaker excavating abilities such as the Middle Spotted Woodpecker (Jenni 1981, Shepps et al. 1999).

Anti-predator adaptations

The entrance diameters of holes excavated by the studied species are most probably sufficiently small to admit the woodpeckers but to prevent predation by Pine Marten *Martes martes* that are responsible for some nest failures of forest cavity nesting birds (Walankiewicz 2002). The minimum passable entrance size for this predator was assessed at 44 mm (Wesołowski 2002), however, other data suggest that Pine Martens should be unable to pass through holes smaller than 50 mm (Nyholm 1970). In our study area, 26% of nest-holes of Middle Spotted Woodpeckers ($n = 31$) and 54% of Great Spotted Woodpeckers ($n = 63$) exceeded this lower value in at least one of the studied planes (more frequently in vertical diameter). However, we did not find any sign of predation in the nests inspected (Kosiński & Ksit 2006), and, if any, such cases are probably incidental in both species (Pasinelli 2001, Mazgajski 2002, Kosenko & Kaygorodova 2003).

The lack of correlation between frontal wall thickness (length of entrance corridor) and chamber depth might suggest that the 'danger distance' is not adaptive with respect to the prevention of nest plundering. However, the minimum values of the 'danger distance' were no less than ca 19 cm — the safety threshold level reported from studies on some secondary hole-nesters (Wesołowski 2002, Wesołowski & Rowiński 2004, and literature cited there). Thus, it could be concluded that both the small nest-hole entrance and the 'danger distance' constitute anti-predator adaptations, and prevent woodpeckers' broods against some arboreal predators. However, the low level of brood failure may be also affected by behavioural adaptations of woodpeckers, i.e. nest-hole guarding, the low chance of dislodging adults from the nest and the relatively short time spent outside the nest by both parents (Short 1979, Woźniak & Mazgajski 2003).

Why are nest-holes similar?

It is interesting why the structurally smaller Middle Spotted Woodpeckers excavate nest-holes which are a similar-size to those of Great Spotted Woodpeckers. In our study area Middle Spotted Woodpeckers on average laid larger clutches and reared more fledglings than Great Spotted Woodpeckers (Kosiński & Ksit 2006). Therefore, it could be expected that the nest-hole dimensions of Middle Spotted Woodpeckers should be suitable for smaller but more numerous offspring. However, other studies have shown that the

reproduction parameters of Great Spotted Woodpeckers may be similar to those of the Middle Spotted Woodpeckers observed in our study area (Mazgajski & Rejt 2006). It should be pointed out that in the case of Northern Flickers *Colaptes auratus*, a woodpecker with a much more variable clutch size (4–11 eggs) than Great- and Middle Spotted Woodpeckers (see Kosiński & Ksit 2006), it was found that nest-hole size (floor area and volume) did not correlate with reproduction parameters, and the fitness consequences of overcrowding were minimal (Wiebe & Swift 2001). Moreover, the current evidence suggests that nests affect clutch size marginally (Hansell 2000, Wesołowski 2003, see also review in Wiebe & Swift 2001). The lack of differences in the majority of nest-hole dimensions between the studied species suggest that either body size of both these species does not differ sufficiently enough to influence nest-hole size or other factors affect nest-size. It could be speculated, therefore, that internal nest-hole dimension constitutes a combination or trade-offs among multiple factors such as bird size, predation risk, nest-hole microclimate and aeration during the breeding season (Wiebe 2001, Wiebe & Swift 2001, Ar et al. 2004), as well as time and energy costs of excavation.

Interspecific competition and its consequence

A recent generalisation has suggested that Middle Spotted Woodpeckers are subordinate to Great Spotted Woodpeckers during the nest-building phase, and that this relation is connected with competition for nest-holes (Pettersson 1984, Pasinelli 2003). However, the frequency of such conflicts in our study area is not sufficiently known. It is obvious, that nest-site availability and differences in spatial distribution of nest-holes reduce the frequency and severity of interactions between woodpecker species (Short 1979, Pasinelli 2003), and hole-nesting passerines (Walankiewicz 1991). We have found that in near-natural riverine forests Great- and Middle Spotted Woodpeckers differ in nest-site selection distinctly, while in simplified managed stands a convergence of some nest-site characteristics occurs (Kosiński et al. 2006). The scarcity of available substrates for nest-hole excavation and their convergence may cause an increase in competition for nest sites, particularly between similarly-sized species that overlap in nesting habitats (Short 1979, Lindell 1996), and finally reduce the abundance of subordinate (less competitive)

species. It is likely that lower densities of Middle Spotted Woodpeckers found even in very old but structurally simplified managed oak stands (Kosiński & Winiecki 2005, Kosiński & Kempa 2007), could be partly a result of the lower availability of potential nest sites and interspecific competition for nest sites.

CONCLUSIONS

We conclude that: 1) except for the vertical entrance diameter and area of entrance, hole dimensions do not differ between both woodpecker species and do not reflect expected interspecific differences in body size, 2) substrate thickness makes probably no important difference in the nest-hole parameters of Great- and Middle Spotted Woodpeckers, 3) the small variation in the hole-entrance diameters and in the 'danger distance' not shorter than 19 cm, protects woodpecker broods against some arboreal predators, and 4) the most plausible explanation for the observed patterns of nest-site selection is most likely due to the excavation morphology of Great- and Middle Spotted Woodpeckers.

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STRESZCZENIE

[Czy dziuple dzięcioła dużego i dzięcioła średniego różnią się wielkością?]

Szereg badań wskazuje, że istnieje pozytywna zależność między wielkością ciała dzięciołów i średnicą drzewa w miejscu wykucia przez nie dziupli. Wykuwając dziuple w cieńszym substracie, mniejsze gatunki dzięciołów mogą w ten sposób zmniejszać ryzyko przejścia dziupli (kleptopasożytnictwa gniazdowego) i ich powiększenia przez większe gatunki. Ponieważ dzięcioł średni jest o około 10% mniejszy od dzięcioła dużego, a jego dziuple często umiejscowione są wyżej

i w cieńszym substracie w porównaniu z dziuplami dzięcioła dużego założono, że wykuwane przez niego dziuple są mniejsze.

Celem badań było: 1) porównanie rozmiarów dziupli dzięcioła dużego i dzięcioła średniego oraz średnic drzew na wysokości dziupli, 2) wskazanie cech dziupli o znaczeniu antydrapieżniczym oraz 3) próba odpowiedzi na pytanie, czy ryzyko kleptopasożytnictwa gniazdowego wpływa na wybór miejsca gniazdowania.

Badania prowadzono w latach 2002–2006 w lasach łągowych doliny Warty w okolicach Czeszewa w Wielkopolsce (rezerwat "Czeszewski Las"). Ogółem zmierzono 63 dziuple dzięcioła dużego i 31 dziuple dzięcioła średniego.

Średnia wysokość otworu dziupli oraz powierzchnia otworu dziupli u dzięcioła dużego była istotnie większa niż u dzięcioła średniego, co prawdopodobnie odzwierciedla różnice w rozmiarach ciała obu gatunków. Pozostałe wymiary dziupli nie różniły się istotnie (Tab. 1). Wysokość i szerokość otworów dziupli u dzięcioła dużego i dzięcioła średniego charakteryzowały się najmniejszą zmiennością ($CV \leq 10\%$). Największą zmienność odnotowano w przypadku grubości przedniej ściany dziupli. Średnie odległości między otworem wlotowym a tylną ścianą dziupli u dzięcioła dużego ($168.4 \pm 31,5$ mm, $n = 63$) i dzięcioła średniego ($160.2 \pm 30,2$ mm, $n = 31$), charakteryzujące przestrzeń niezbędną do wykucia dziupli, nie różniły się istotnie (Fig. 1). Średnice drzew na wysokości dziupli u dzięcioła dużego (42.7 ± 18.4 cm) i dzięcioła średniego (38.2 ± 16.6 cm) nie wykazywały różnic istotnych statystycznie (Fig. 2). Średnica substratu była również niezależna od sposobu umieszczenia dziupli

(pień vs konar) oraz sposobu użytkowania lasu (las seminaturalny vs las gospodarczy). U obu gatunków dzięciołów nie stwierdzono zależności między średnicą drzewa na wysokości dziupli i wysokością umieszczenia dziupli.

Uzyskane wyniki wskazują, że rozmiary dziupli obu gatunków są podobne. Średnica drzewa na wysokości dziupli nie jest czynnikiem ograniczającym rozmiary dziupli dzięcioła średniego, a wykuwanie dziupli w cieńszym substracie odbywa się kosztem grubości jej ścian. Budowanie przez dzięcioła średniego dziupli w wyższych partiach drzew może być związane z ograniczoną liczbą gatunków drzew dostępnych do gniazdowania. Ponadto, w związku z ograniczeniami anatomicznymi umożliwiającymi drążenie dziupli, umiejscawianie dziupli wyżej może być dla dzięcioła średniego korzystne w związku z malejącą wraz z wysokością twardością drewna. Rozmiary otworów dziupli, ich niewielka zmienność oraz odległość jaką muszą pokonać drapieżniki sięgając do wnętrza dziupli (≥ 19 cm) mają prawdopodobnie funkcję antydrapieżniczą. Podobieństwo rozmiarów dziupli obu różniących się wielkością, gatunków dzięciołów jest prawdopodobnie efektem współdziałania wielu czynników, takich jak: wielkość gatunku, ryzyko drapieżnictwa, mikroklimat dziupli i możliwość jej wentylacji oraz czas i koszty wykucia dziupli. Konwergencja nisz gniazdowych oraz ograniczona liczba miejsc dogodnych do wykucia dziupli w lasach gospodarczych może sprzyjać wzrostowi agresywnych interakcji między gatunkami i konkurencji o miejsca gniazdowania, powodując spadek liczebności dzięcioła średniego, który jest gatunkiem słabszym w stosunku do dzięcioła dużego.