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Expansion of the Syrian Woodpecker *Dendrocopos syriacus* in Europe and Western Asia

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Abstract: The Syrian Woodpecker has been colonizing SE Europe for more than 100 years. It has already colonized SE Poland, but northern and western Poland are still outside its regular range. Frequent nesting at the edge of stable breeding population range and incidental cases of breeding far away from its regular breeding range show that the Syrian Woodpecker expansion may be explained by a diffusion and scattered colony model. However, unsuccessful cases of establishing local populations distant from a regular breeding range suggest that there are some ecological barriers limiting adaptation capacity of this synanthropic species. The Syrian Woodpecker expansion rate slowed down at the beginning of the 21st century. Nowadays the Syrian Woodpecker west distribution range spreads out from West Poland across the central region of the Czech Republic up to the eastern part of Austria and Slovenia. It may have resulted from the population decline and lower number of immigrants supplying edge populations from the source population in the SE Poland. Currently, the colonization of new areas proceeds dynamically in eastern Europe, mainly in Russia.

Key words: Syrian Woodpecker, *Dendrocopos syriacus*, woodpeckers, expansion, colonization

Ekspansja dzięcioła białoszyjego *Dendrocopos syriacus* w Europie i Azji Zachodniej. Abstrakt: Dzięcioł białoszyi od końca XIX wieku rozprzestrzenia się w południowo-wschodniej Europie. Gatunek ten na stałe skolonizował południowo-wschodnią Polskę, a poza jego zasięgiem pozostaje obecnie północna i zachodnia część kraju. Częste gniazdowanie ptaków na skraju zwartego obszaru lęgowego oraz przypadki lęgów daleko poza jego granicami wskazują, że ekspansja dzięcioła białoszyjego to proces dyfuzyjny i skokowy. Jednak nieudane próby założenia lokalnych populacji daleko od zwartego zasięgu wskazują na istnienie barier przekraczających możliwości adaptacyjne tego synantropijnego gatunku. Obecnie zachodnia granica zasięgu przebiega od zachodniej Polski, przez środkowe Czechy do wschodniej części Austrii i Słowenii. Na początku XXI wieku tempo ekspansji dzięcioła białoszyjego w Polsce wyhamowało. Być może wynika to ze spadku liczebności populacji, skutkującego ograniczeniem dopływu imigrantów z populacji źródłowych z południowo-wschodniej Polski. Kolonizacja nowych obszarów postępuje za to dynamicznie na wschodzie Europy i dotyczy głównie Rosji.

Słowa kluczowe: dzięcioł białoszyi, *Dendrocopos syriacus,* dzięcioły, ekspansja, kolonizacja

The colonization of new biocenoses by new bird species is a phenomenon observed on all continents (Elton 1967, Nowak 1971, Mendelssohn & Yom-Tov 1999, Hatzofe & Yom-Tov 2002), as well as on a regional scale, e.g. in Poland (Tomiałojć & Stawarczyk 2003, Głowaciński et al. 2010). In Europe these processes concern primarily the expansion of southern and southeast species to the north and northwest (Głowaciński 1974, 1990,

Nikiforov 2003, Tomiałojć & Stawarczyk 2003). Changes in geographic range can be mainly linked with the spontaneous crossing of geographical and environmental barriers by a species. In many cases it is believed to be a consequence of global warming (Nowak 1971, Hatzofe & Yom-Tov 2002, Tomiałojć 2003, Tomiałojć & Stawarczyk 2003). The increased dispersion of some species is thought to be a result of human economic activities leading to changes in the environment. The emerging niches create conditions enabling many species of birds to expand their range (Yom-Tov & Mendelssohn 1988, Głowaciński 1990, Mendelssohn & Yom-Tov 1999). Species colonizing such niches are often characterized by high capacity to adapt to anthropogenic habitats. The Collared Dove *Streptopelia decaocto* is an example of such a species (Nowak 1971). The group of "winner species" (Järvinen & Ulfstrand 1980, Głowaciński 1990), whose breeding range expands northwest, includes also the Syrian Woodpecker *Dendrocopos syriacus* (Nowak 1971, Skakuj & Stawarczyk 1994). None of the remaining European woodpeckers has exhibited such a marked expansion in recent years (Glutz von Blotzheim & Bauer 1980, Cramp 1985). For more than 100 years this species has populated almost a fifth of Europe area, becoming a common breeding bird in many countries (BirdLife International 2004). In this paper I summarize all available information about the Syrian Woodpecker distribution in Europe and Asia. I also evaluate changes in the geographical range, present-day distribution and expansion of this species in Poland.

The expansion of the Syrian Woodpecker in Europe and Western Asia

The original breeding range of the Syrian Woodpecker encompassed the northern part of Western Asia (Dementiev et al. 1951, Winkler et al. 1995, Winkler & Christi 2002, Fig. 1). At the end of the 19th century this species began to colonize Europe (Nowak 1971, Cramp 1985). It was first detected in northern Bulgaria near the village of Srebarna in 1890 (Glutz von Blotzheim & Bauer 1980). Observations made far from the Straits of Bosphorus and Dardanelles, which was the most likely place this species entered Europe, suggest that the Syrian Woodpecker could have populated the continent earlier. For this reason, the start of the expansion of the species into Europe is cautiously considered to occur around 1880 (Nowak 1971). The Syrian Woodpecker began to colonize the area of former Yugoslavia already in the 19th century (Glutz von Blotzheim & Bauer 1980). In 1899 the first bird was observed in Serbia near the town of Nis, while in 1928 the species was found in the north of the country in Vojvodina, near the town of Old Vrbas (Szlivka 1957). The first reports of this species in Macedonia are from 1917. Soon, just after 1930, the Syrian Woodpecker arrived in Croatia, and in subsequent years in Slovenia (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Gorman 1997, Bačani 1998). It was only in 1969 that its presence was confirmed in Montenegro (Gorman 1997), and in 1996 in Bosnia and Herzegovina, where in 2008 it was found to be breeding in Banja Luka (Gašić 2010, but see also Matvejev & Vasič 1973). During 1910–1920 the species began to colonize the south-eastern regions of Greece, and only in the 1950s it was found in Albania (Gorman 1997). It seems that the mountainous Balkans have effectively hindered its expansion into the western part of the peninsula. The most likely the species has not still reached the Adriatic Sea shore (e.g. Gašić 2010), while the southern limit of its range reached 39°N (Handrinos & Akriotis 1997, Fig. 1).

The Syrian Woodpecker spreads much faster through the lowlands of the Great Hungarian Plain and the Wallachian Plain in a northerly direction. In eastern Romania it was already observed in 1931 near the town of Buzau (Catuneanu 1933), and by 1944 it

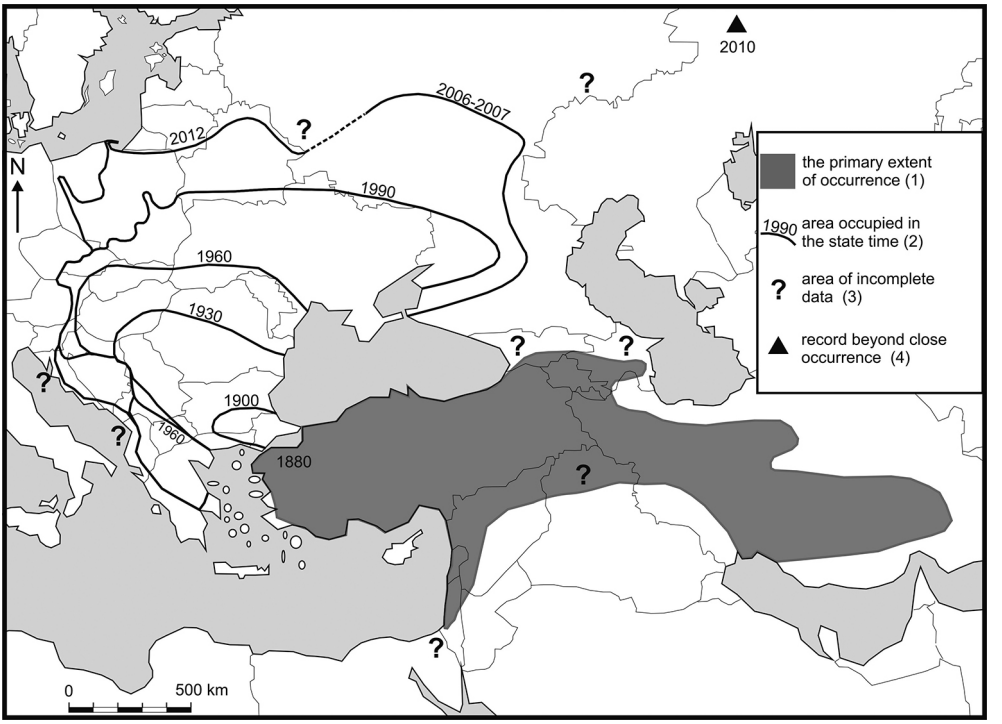

Fig. 1. The Syrian Woodpecker expansion in Europe (approximate dates based on the literature cited in the text)

Rys. 1. *Przebieg ekspansji dzięcioła białoszyjego w Europie (dane przybliżone na podstawie literatury zawartej w tekście). Objaśnienia: (1) – obszar pierwotnego występowania, (2) – regiony zasiedlone w podanym czasie, (3) – regiony o niekompletnych danych, (4) – stanowisko poza rozpoznanym zasięgiem występowania*

had spread up to the western border of the country, to the region of Banat (Glutz von Blotzheim & Bauer 1980). The species appeared in southern Hungary already around 1930, and the first brood was documented in 1937 in the town of Kiskunfélegyháza (Keve 1955, Glutz von Blotzheim & Bauer 1980, Gorman 1996). Over the next 20 years it colonized the entire country (Gorman 1996), from where it spread further to the north (Glutz von Blotzheim & Bauer 1980, Fig. 1). In 1949 the first birds were shot near the village of Senne in eastern Slovakia (Ferianc 1950). Five years later the species was observed near Bardejov in northern part of the country (Balat & Folk 1956), and by the end of the 1980s it had spread throughout Slovakia (Ferianc 1953, Pavlik 2002). Almost at the same time the species appeared in Austria; the first broods were detected in 1951 in northern Burgenland (Bauer 1952). It can be assumed that the colonization of that country began a bit earlier, which was confirmed by subsequent observations of the birds (Bauer 1954, 1955), as well as by its simultaneous appearance in the Czech Republic, where in 1952 the first individual was observed in Lednice near the Austrian border (Kren 2000). Two years later the Syrian Woodpeckers were noted in Břeclav (Czech Republic), and afterwards birds were found further away to the west and north. To date this woodpecker has colonized only the eastern part of the Czech Republic (as in Austria), and has become more common only in Moravia (Cramp 1985, Kren 2000). Observations of this species in south-eastern Germany, far from its known range (e.g. Dornbusch 1968), are considered

uncertain as they concerned an individual being probably a hybrid with the Great Spotted Woodpecker *D. major* (Munteanu & Samvald 1997).

In the same period the expansion proceeded also in a northeasterly direction (Nowak 1971, Glutz von Blotzheim & Bauer 1980, Cramp 1985, Fig. 1). The first information about the presence of the species in Moldova came from 1957 (Marisova 1965, Cramp 1985). However, it had been recorded much earlier in Ukraine. The birds were encountered for the first time in 1948 in the vicinity of Khotyn on the Dnestr and in the city of Vynohradiv at the Romanian-Slovak border (Strautman 1963). Then, in 1960 it was found in the Ternopil region, and in 1969 in Lviv (Marisova & Butenko 1976, Glutz von Blotzheim & Bauer 1980). Birds were observed during the breeding season of 1981 already near the village of Shostka in the northern part of the country near the Russian border (Afanasyev 1998) and at the eastern border, in Krasnodon, in the autumn of 1989. Up to the 1990s the species colonized the entire Ukraine, including the Crimean Peninsula (Zavialov et al. 2008). In 1980 the first birds were found in Russia at Rostov-on-Don. Currently Syrian Woodpeckers are already being observed on the outskirts of Moscow, and in 2010 the first observation was noted in the Kazakhstan province of Qostanay (Cramp 1985, Zavialov et al. 2008, Wassink et al. 2011). These are the most distant east and north populations in Asia (Fig. 1).

At the end of the 1970s the Syrian Woodpecker entered Poland (Ciosek & Tomiałojć 1982). It quickly colonized the south-eastern part of the country, arriving to the Wielkopolska region and the Baltic coast in the 1980s (see details below, Figs. 1 and 2). In 1970–1980 it began to colonize the southern parts of Belarus (Cramp 1985, Nikiforov et al. 1997), and in the next decade a permanent population was already established in Grodno. Currently it can be found almost throughout the entire country (D. Vinchevski – unpublished data) reaching Polotsk near the Russian-Latvian border in 2012 (A. Erdmann – unpublished data) and Krasnopol near the eastern border with Russia (Birdwatch. by 2013). In 2013 a male of the species was observed in Kalinkavichy in SE Belarus near the Ukraine border (A. Shevchyk – unpublished data). The Syrian Woodpecker arrived in Lithuania at the beginning of the 21st century, where on 18th April of 2002, one bird was observed near Vilnius (announcement of the Lithuanian Ornithological Society No. 490/12, K. Castren – unpublished data, Fig. 1).

The Syrian Woodpecker is also extending the area of its original range (Fig. 1). New areas of colonization have been observed in Kurdistan (at the border between Turkey and Iraq), reached by the species in 1953–1954 (Cramp 1985). In the 1970s its first records were also confirmed in north-eastern Egypt, near the border with Israel (Cramp 1985, Shirihai 1996). In the 1980s, the species began to colonize southern areas of Georgia and Azerbaijan (Cramp 1985). Currently, however, there is no new data available on this process from the aforementioned regions (Patrikeev 2004).

At present the range of the Syrian Woodpecker in Europe covers over 2 million km^2 (BirdLife International 2004). However, its rate of expansion in a westerly direction has decreased (Fig. 1), while the colonization of new areas occurs rapidly in an easterly direction, especially in the agricultural and steppe lands of the East European Plain in Russia (Zavialov et al. 2008).

Colonization of Poland

The Syrian Woodpecker was first detected in Poland in 1978 in Trzciana near Rzeszów (SE Poland), where two young birds were seen, and a year later a breeding attempt was con-

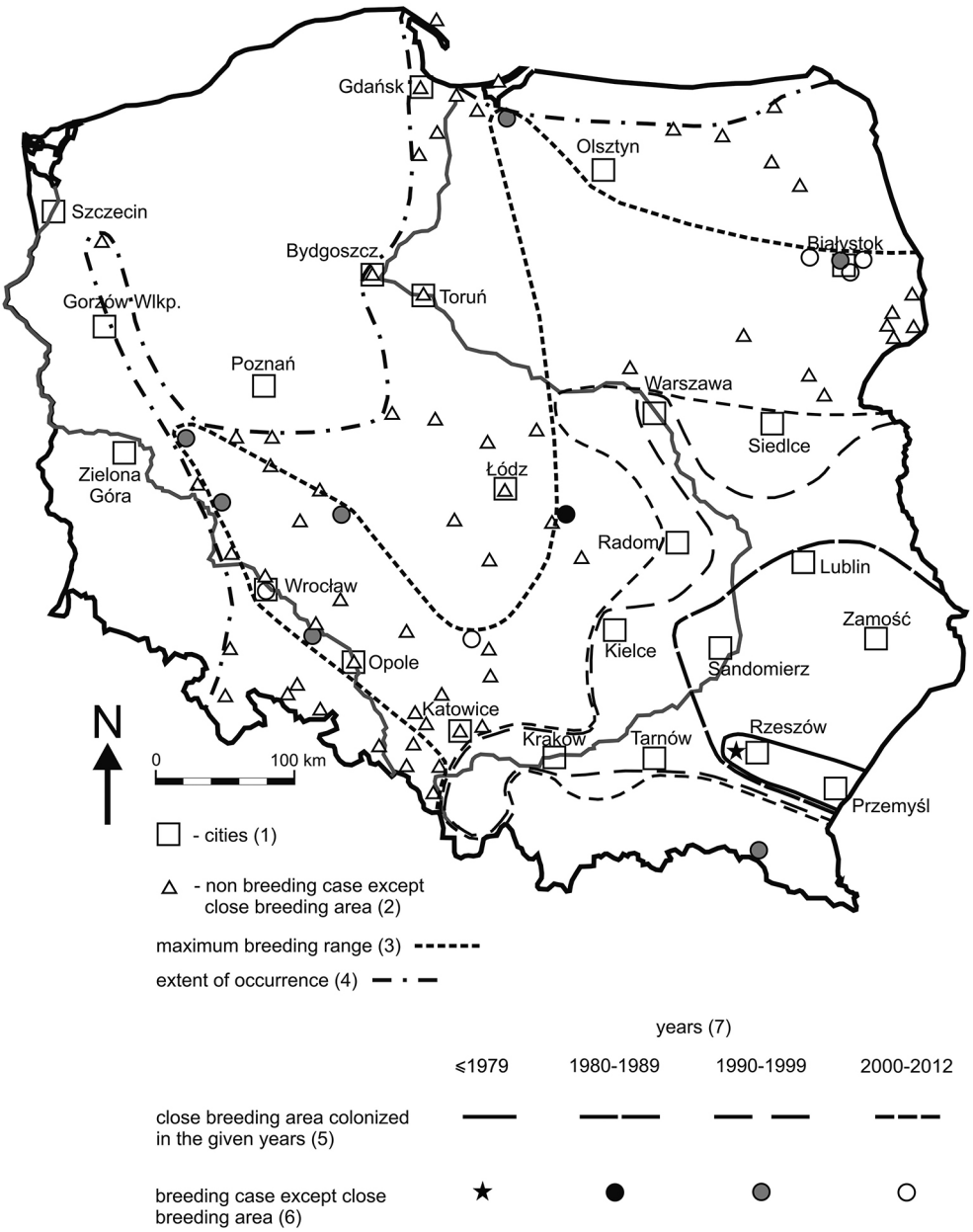

Fig. 2. Expansion and current range of the Syrian Woodpecker in Poland (based on the literature data cited in the text)

Rys. 2. *Przebieg ekspansji i zasięg występowania dzięcioła białoszyjego w Polsce (zilustrowany schematycznie na podstawie danych literaturowych zamieszczonych w tekście). Objaśnienia: (1) – miasta, (2) – stanowiska nielęgowe poza zwartym obszarem lęgowym, (3) – maksymalny zasięg lęgowy, (4) – granice zasięgu występowania, (5) – zwarty obszar lęgowy skolonizowany w podanym okresie, (6) – stanowiska lęgowe poza zwartym zasięgiem, (7) – lata*

firmed (Ciosek & Tomiałojć 1982, Fig. 2). In the early 1980s, the presence and breeding of Syrian Woodpeckers was revealed in Przemyśl and its surroundings (Kurek 1984). In the same period a male was observed in the vicinity of Pacanów in the Kielce region (Tomiałojć 1990). Subsequent observations were made in this area in 1985, and breeding was recorded only in 1988 near Sandomierz and Opatów (Komisja Faunistyczna 1986–2013, Wilniewczyc 2005). Quite soon, already in 1983, breeding records of this species were noted in central Poland, in Warsaw (Konofalski & Kamola 1985). In the same year the first birds were also observed in the village of Żelebsko in the Zamość region (E Poland). However, the Syrian Woodpecker nest holes were discovered in this region only in 1988 near Hrubieszów (Profus et al. 1992). In Lublin the first breeding was recorded in 1987, and two years later in Siedlce (Biaduń 2001, Buczek 2007). In subsequent years further colonization was observed in the northern part of Lublin region (Biaduń & Stachyra 2005, Fig. 2).

At the beginning of the 1980s the species entered Podlasie, where the first observations were made in the vicinity of Narew village (Tomiałojć 1990). However, the first breeding record in this region was noted in 1999 in Białystok, where now the species is a permanent breeder (Komisja Faunistyczna 1986–2013). Also in 1983 the first birds were seen in Silesia (SW Poland), first near Racibórz (Krotoski 1986), and in following years in other locations of the region (Karnaś 1986, Lontkowski 1986, Dyrcz 1991). In 1991 a nest was found in Piotrowice (Lorek & Durczyńska 1992). In Kraków city the first record of this species was reported in 1983, with breeding confirmed in 1988 (Tomiałojć 1990, Tomiałojć & Stawarczyk 2003). Subsequent breeding records of the Syrian Woodpecker were made in following years in this city (Fröhlich & Ciach 2013). Other breeding sites from the western Małopolska region were discovered in 1990 in Żywiec, and one year later near Bielsko-Biała (Buczek 2004, Fig. 2).

The Syrian Woodpecker colonised soon also the Wielkopolska region (W Poland). The first observations from this area were reported in 1984 from Konin town (Kosiński 2000). Though the birds were seen in other areas of this region, it was not until 1992 that a hole was found in Boruja village near Wolsztyn (Tryjanowski 1994). In 1990 nests were discovered in Batorowo near Elbląg (Buczek 2004), and other non-breeding birds were seen even farther north, for example, in the area of Gdańsk city (N Poland, Komisja Faunistyczna 1986–2013, Sikora et al. 1994, Tomiałojć & Stawarczyk 2003).

The colonization of the Carpathian foothills and adjacent regions (SE Poland) started significantly later. The first individuals were noted in Jasło in the 1990s (Stój & Dyczkowski 2002). Although 4–8 pairs were recorded at the border with Slovakia (Stój 1997) and a few territories in the Beskid Mały Mountains (Kajtoch 2012), a confirmed breeding record is still lacking for this region. Northern Wielkopolska, Pomorze Koszalińskie and the northern- and westernmost parts of Poland still remain out of the range of this species (Tomiałojć & Stawarczyk 2003, Buczek 2007, Fig. 2). So far the Syrian Woodpecker has been observed only once in Western Pomerania – in 1999 in the village of Trąbki near Stargard Szczeciński (Komisja Faunistyczna 1986–2013, Fig. 2). This is the most northwestern location of the species in its entire distribution range (Fig. 1).

Changes in the distribution of the Syrian Woodpecker in Poland

According to Nowak (1971), only areas where a species can fulfil all life functions, i.e. where it can breed, should be considered as an area colonized by the Syrian Woodpecker. During mapping the continuous range of the Syrian Woodpecker in Poland, isolated and ephemeral nests were disregarded, and only permanent territories were taken into

consideration. A breeding site was included in a continuous range when two other adjacent sites were located within a radius of at least 100 km from the focal site. In addition, they should have been stable, i.e. nesting was confirmed at least once within no less than 10 years. The expansion front and area colonized by the species in a given decade were determined by connecting such designated points. These criteria were adopted because the Syrian Woodpecker is a secretive species and its broods are very difficult to detect (Winkler 1973, Michalczuk & Michalczuk 2006a, 2006b, Michalczuk et al. 2011). The maximum range of the breeding area included all locations where the birds were found to be breeding, and its range by sites where the birds were observed (Fig. 2).

At the beginning of the 1980s, the continuous breeding area of the Syrian Woodpecker included the southern part of Sandomierz Basin at the border of the Carpathian Foothills (Fig. 2). In this area the first breeding attempt in Poland was reported (Ciosek & Tomiałojć 1982, Kurek 1984). In 1983 an increase in the number of the Syrian Woodpecker observations from different regions of Poland was noted (Tomiałojć & Stawarczyk 2003). It was recorded in sites located far away from each other, situated even in the northern and western parts of the country. By the end of the 1980s the species had colonized southern Lublin region, the eastern part of the Subcarpathian region (Hordowski 1991, Hordowski & Kunysz 1991) and Sandomierz region (Fig. 2). Over the next decade its continuous range included already southern Podlasie and south-eastern Mazowsze with breeding records noted in the vicinity of Warszawa (Komisja Faunistyczna 1986–2013, Luniak et al. 2001). During this time a stable population was established in the Podkarpacie area (Hordowski 1998, 1999, Kunysz & Kurek 1997), and the species also populated western Małopolska and eastern parts of Kielce region (Walasz & Mielczarek 1992, Tomiałojć & Stawarczyk 2003, Wilniewczyc 2005).

The continuous breeding area of the species in Poland has not changed significantly in recent years (Komisja Faunistyczna 1986–2013, Tomiałojć & Stawarczyk 2003, Fig. 2). It can be assumed that at the beginning of the 21st century the northern edge of its range extends from the southern Belarussian border through Siedlce to the area of Warszawa (Komisja Faunistyczna 1986–2013, Tomiałojć & Stawarczyk 2003), then continues through the Wisła River Valley to the south of Radom, where it changes direction to the west heading Kielce area, the Nida River Valley and back south to the Wisła River Valley (Fig. 2). Next it turns to the west, passing through Kraków area, including the Oświęcim Basin and the Beskid Mały region. In the westernmost part of its continuous range, it turns east to the border with Ukraine. The southern border runs through Sandomierz Basin lowlands and the Beskid Foothills, along a line Kraków – Tarnów – Rzeszów – Przemyśl (Fig. 2). Its maximal breeding range includes permanent territories in Białystok, incidental ones near Elbląg, Radom and the southern areas of Wielkopolska (Tryjanowski 1994), Silesia and Małopolska, where recently breeding was recorded in Wrocław and Częstochowa (Komisja Faunistyczna 1986–2013, Czyż & Celiński 2012, Fig. 2). Although the species occurs mostly in highlands and lowlands in Poland, it is also recorded at foothills and rarely in the mountains.

Status of the population

The size of the European population of the Syrian Woodpecker is not precisely known. It is estimated at 200,000–250,000 breeding pairs (BirdLife International 2004). The largest populations, reaching 45,000–50,000 breeding pairs, inhabit Ukraine and Bulgaria. Slightly smaller population, hosting 20,000–30,000 breeding pairs, occurs in Romania,

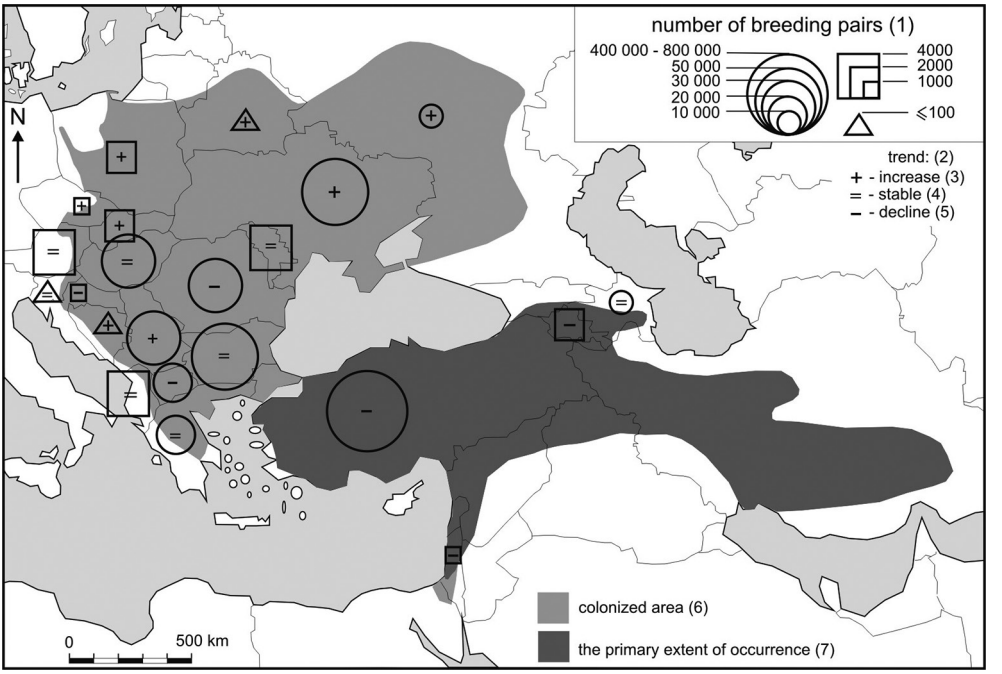

Fig. 3. Breeding population of the Syrian Woodpecker in Europe and West Asia (according to the BirdLife International 2004 and other publications cited in the text)
Rys. 3. *Stan liczebny populacji dzięcioła białoszyjego w Europie i Azji Zachodniej (na podstawie BirdLife International 2004 i innych publikacji cytowanych w tekście). Objaśnienia: (1) – liczba par lęgowych, (2) – trend liczebności, (3) – wzrostowy, (4) – stabilizacja, (5) – spadkowy, (6) – obszar skolonizowany, (7) – obszar pierwotnego występowania*

Greece, Serbia, Montenegro and Hungary. About 10,000 breeding pairs were confirmed in Macedonia and intensively colonized Russia (BirdLife International 2004, Zavialov et al. 2008, Fig. 3). In most countries, including Poland, populations of this species consist of 1,000–4,000 breeding pairs (BirdLife International 2004, Michalczuk & Michalczuk 2006a). In the Czech Republic and Croatia the estimated population consists of not more than 1000 breeding pairs (BirdLife International 2004, Lukač 2007). Small populations, not exceeding 100 nest sites, were found in Slovenia, Bosnia and Herzegovina, and Belarus (Nikiforov et al. 1997, BirdLife International 2004, Gašić 2010, Fig. 3). Little information on the abundance of this species from Asia Minor and the Caucasus is available. Counts are missing from Georgia, Syria and other Arabic countries. The only estimates are provided for large populations breeding in Turkey (400,000–800,000 breeding pairs), Azerbaijan and Armenia (5,000–10,000 and 1,000–2,000 breeding pairs, respectively) (BirdLife International 2004). In Israel the population size was assessed at about 1,000 breeding pairs in the 1980s (Shirihai 1996, Fig. 3).

In many European countries, including Poland, an increasing trend has been observed (Cramp 1985, BirdLife International 2004, Zavialov et al. 2008). This is mostly visible in countries at the edge of the species range, which currently are still being colonized (Fig. 3). Perhaps this is due to ornithologists' huge interest in new species in their country. Only in a few European countries, located mainly in the centre of the species current range, has the population size stabilized after initial rapid increase. In some countries, such as

Romania and Macedonia, a decline of this species has been reported (BirdLife International 2004, Fig. 3).

Expansion forms and routes

The pattern of the Syrian Woodpecker occurrence, as well as the course of its colonization of new areas in Poland (Tomiałojć & Stawarczyk 2003, Fig. 2), recall a process of diffusion based on expansion scattered around a source population ("diffusion" and "scattered colony model" typology of Shigesada & Kawasaki 1997). However, "jump dispersion" over long distances was also reported for the Syrian Woodpecker. After the first observations in Poland, further records proliferated and then cases of breeding were noted. Although colonization occurred the most often at the edge of the woodpecker's continuous range, sometimes single breeding attempts were recorded at sites located far away from the species main range. Such nesting records were often only occasional and did not repeat in the subsequent years, probably as a result of unsuccessful breeding due to some ecological barriers (e.g in the Elbląg area, Tomiałojć & Stawarczyk 2003). Another reason for unsuccessful colonisation may be small initial population size and stochastic processes operating in such populations. However, in some regions, including Mazowsze, Podlasie or Wielkopolska, successive nests were sometimes noted even far from the regular breeding range (Konofalski & Kamola 1985, Komisja Faunistyczna 1986–2013, Tomiałojć & Stawarczyk 2003). Usually they gave rise to new local populations, which sometimes became connected with the continuous breeding range (e.g. Konofalski & Kamola 1985, Luniak et al. 2001, Tomiałojć & Stawarczyk 2003). Such a situation may be expected to occur soon in Lower Silesia, where nesting birds were found in Wrocław after several years (Komisja Faunistyczna 1986–2013).

The colonization of new areas by the Syrian Woodpecker the most likely occurs by occupying the best habitats found mostly in built-up/urbanized areas. This species shows preferences for anthropogenic woods (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Michalczuk & Michalczuk 2011) and woods located in river valleys (Strautman 1963, Klitin et al. 1994). It is assumed that the Vistula River Valley acted as a dispersal corridor, which enabled the Syrian Woodpecker to reach quickly Warszawa (Konofalski & Kamola 1985, Luniak et al. 2001, Tomiałojć & Stawarczyk 2003). Despite the fact that clear evidence for such a hypothesis is lacking, it can be assumed that such habitat "islands" and "corridors", with a large number of trees preferred by the species, apparently become the main pathways of colonization.

In conclusion, it seems that the rate of colonization of the Syrian Woodpeckers increased at the beginning of the 21st century in Poland (Komisja Faunistyczna 1986–2013). This is probably due to its decline in the area of the continuous range, e.g. in the south-eastern part of the country. Local studies have shown that the number of Syrian Woodpeckers has decreased in recent years in the region of Tomaszów Lubelski (SE Poland) by about one-third (Michalczuk et al. 2011). According to metapopulation concept (Solarz & Zając 1998, Hanski 1999, Łomnicki 2003), a slower rate of expansion and colonization of new areas in Poland resulted probably from a reduced immigration from the source population to the sink, edge populations.

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