



## The European mantis *Mantis religiosa* (Linnaeus, 1758) (Mantodea: Mantidae) in Poland – the present status and changes in range

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**Abstract:** This paper presents the past and present occurrence of *Mantis religiosa* in Poland and discusses range changes of this species during the last 100 years (1923–2021), basing on 2664 records, 2029 of these unpublished. Up to 1994, the species was restricted to a relatively small area in the south-eastern part of Poland (3.3% of the country's area). During 27 years (1995–2021), *M. religiosa* spread from there to the north, west and south, increasing its range more than 20 times, to 77% of Poland's area. At present, only north-western part of the country and central part of mountainous belt in the south are not occupied or sparsely occupied by this species. The average annual increase in European mantis range in Poland in the years 2013–2021 was eight times faster than during the earlier period (1995–2012).

**Key words:** range expansion, population increase, expansive species, thermophilous insect, threats, protection

### INTRODUCTION

The European mantis *Mantis religiosa* (Linnaeus, 1758) is the most widespread species of the mantids (Mantodea), and with the most northern distribution border. It occurs from southern and central Europe through vast parts of Asia to southern Siberia and Far East, as well as in Africa as far as Cape of Good Hope, New Guinea and Australia (Battiston et al. 2010). It has also spread to North America as an alien species (Bazyluk 1977). In Central Europe the European mantis occupies open habitats, often of an ecotone character, such as forest clearings, firebreaks, heaths, sandy and xerothermic grasslands, and fallow land. Sometimes it can also be found in peat bogs and wet meadows (Liana 2004, 2007).

The European mantis was reported from Poland for the first time at the end of the 18th century, however it had not been recorded again until the beginning of the 20th century. Newer mentions from the area of the present borders of Poland (after the Second World War) come from the 1920s, 1930s and 1940s (Bazyluk 1976, 1977). Until the end of the 20th century

*M. religiosa* was reported only from few localities in the southeastern parts of Poland, where its entire population was estimated at several hundred to several thousand individuals (Liana 2004, 2007).

Since the beginning of the 21st century an increase in numbers and range expansion has been observed throughout Central Europe, including Poland (Liana 2004, 2007, Zieliński et al. 2018b). In this study we have compiled all the available records of *M. religiosa* within the present Polish borders, both published and unpublished, in order to present the current range of the European mantis in Poland and changes in its range distribution within the last 100 years.

## MATERIALS AND METHODS

The data on the occurrence of European mantis in Poland used in this study come from 63 publications (marked with an asterisk in the reference list), as well as from unpublished records obtained personally by the authors in the field or provided by 430 people (professional and amateur naturalists) listed in the Acknowledgements section. For the purpose of this study, a record is defined as a sighting or a collection of at least one individual at a specified locality and year (or time period – explained below). Some of the unpublished data was acquired from open internet databases: iNaturalist (<https://www.inaturalist.org>), ornitho.pl (<https://www.ornitho.pl>), GBIF.org (2022), Biodiversity of Ukraine (<http://dc.smnh.org>), from internet nature forums: Polskie Forum Entomologiczne (<https://www.entomo.pl/forum/>) and Forum Jurajskie (<https://www.forumjurajskie.pl>), from Facebook nature groups: Przyrodnicy (<https://www.facebook.com/groups/przyrodnicy>) and Prostoskrzydłe (Orthoptera) Polski (<https://www.facebook.com/groups/2067331400149811>), and from several other internet websites (<http://archiwum.dukla.pl>, <http://biologiaolsztyn.blogspot.com>, <https://echodnia.eu>, <https://insektarium.net>, <http://natura.wm.pl>, <https://nto.pl>, <https://sudawcy.blogspot.com>). We have also included information on European mantis occurrence presented in a wildlife documentary film entitled “Roztoczański Park Narodowy” (directed by K. Nowakowski and M. Janiszewski, Warszawa 2005). We have ignored records, whether published or unpublished, obtained in circumstances indicating alien origin (e.g., European mantis found in vehicles or transport containers arriving from other parts of Poland or abroad). Most of the unpublished records were documented by photos verified by the authors of this paper. All together in this study we included 2664 European mantis records (635 published and 2029 unpublished) gathered in the years 1923–2021 within the present Polish borders, whose location could be assigned to 10 × 10 km squares of the MGRS (Military Grid Reference System) spatial coordinate grid (a derivative of the UTM [Universal Transverse Mercator] system).

The range expansion analysis is based on the earliest records assigned to the UTM squares occupied by the European mantis. The records were assigned to five periods (1923–1994, 1995–2006, 2007–2012, 2013–2017, 2018–2021); the length of the periods is not equal due to the periodisation of the data in the two earlier papers on European mantis expansion in Poland, in which data is assigned to multi-year periods rather than to a specific year (Liana 2007, Zieliński et al. 2018b). For each period, two basic parameters were calculated: Extent of Occurrence (EOO) and Area of Occupancy (AOO), both described by Wilk et al. (2020). The extent of occurrence (EOO), which measures the extent of the occupied area including the area stretching between known sites of occurrence, was determined in QGIS 3.4 using the concave envelope tool (alpha shape) with a threshold of 0.3, basing on the occupied 10 × 10 km UTM squares. AOO is the area of occurrence calculated as the sum of the area of the occupied UTM squares within Poland.

The distribution of occurrence of imagines during the year (section Phenology) was presented as a histogram with observations assigned to five-day periods (pentads). Only records of live

imagines with the known exact date of observation were used. A total of 1245 records from 1979–2021 were included, although most of this data was collected between 2012 and 2021 (at least 10 records per year). All records collected on a given day at a particular UTM square were considered a single observation in the calculations. In this way, 443 unique observations were used to generate the histogram.

Habitat information was available for 449 out of the 2029 unpublished records. We have taken into account only habitat information from the period 2013–2021 so that it can be compared with historical data from the literature. This yielded habitat information for 417 records. We assigned the habitats (as described by the observers) to the following categories: unspecified dry habitats, sandy habitats, semi-natural dry grasslands, peat bogs, meadows (moist, periodically wet, and wet), forests, heaths, fallow land, and urban habitats (in proximity or on buildings, in private gardens, on urban terrain). This let us with 263 records, because not all habitat descriptions could be assigned to the categories. Some records had multiple types of habitats given and some habitat descriptions could be assigned to multiple categories, e.g. habitats described as dry and sandy. For this reason the percentages of different habitat types do not sum up to 100 percent.

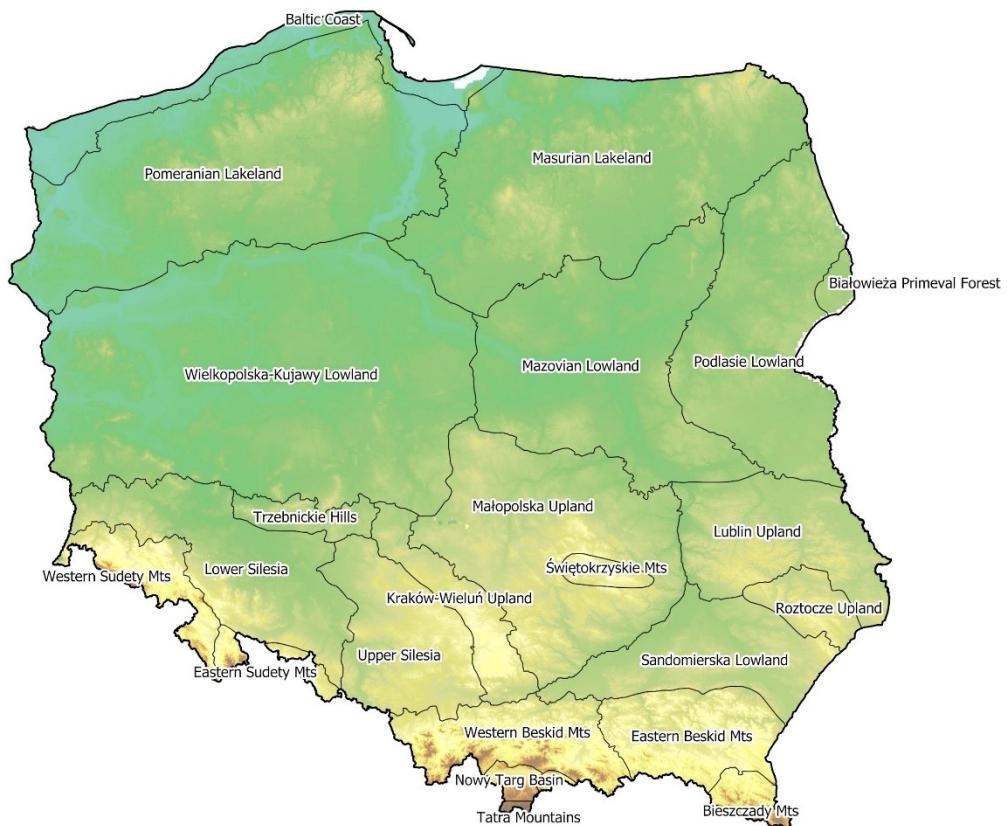


Fig. 1. Regional division of Poland used in this paper (after Bazyluk 1976).

## RESULTS

### Occurrence of European mantis in Poland

In this section we present the occurrence of the European mantis in Poland according to the faunistic regionalization of this country used in “Catalogue of the Fauna of Poland” (Bazyluk 1976) (Fig. 1). The data is presented chronologically, i.e. from the regions populated earlier to the regions populated in recent years. After the English name of the region, the following information is given in square brackets: UTM – the total number of UTM squares in the region (including partial squares, i.e. squares shared between regions), UTM(Mr) – the number of UTM squares in which European mantis was recorded, P(Mr) – percentage of UTM squares with European mantis records. Finally, the European mantis records from the respective region are presented in chronological order with UTM square id-numbers in square brackets. The results are summarised in Table 1 and presented on maps (Fig. 2). The sum of the occupied squares within all regions is higher than the total number of squares with European mantis in Poland given in the next section (Table 2) because some squares are shared between two or more regions.

**Mazovian Lowland** [UTM=328, UTM(Mr)=115, P(Mr)=35.1%]. From this region comes the earliest European mantis record in Poland, from the area of Warsaw at the end of the 18th century (Bazyluk 1976). Subsequently the species was recorded in Garbatka in 1953 and 1955 [EC40] (Bazyluk 1956, Michalski 1959), and after a long break in 2008 in the area of Grójec [DC84, DC95] (unpublished data of Grójec Forest Inspectorate) and Radzymin [ED10] (A. G. Gabi, pers. obs.), in 2009 and 2010 in the vicinity of Świerże Górne [EC32] (Falencka-Jabłońska 2009; W. Piątek, pers. obs.). In the years 2011–2021 the European mantis was found in the region at more than 200 sites (Marczak & Skalski 2016, Zieliński et al. 2018b, Miłkowski & Chmielewski 2019, Kutera 2021, and unpublished data) (Figs 2a–e).

**Lublin Upland** [UTM=170, UTM(Mr)=67, P(Mr)=39.4%]. Earliest data comes from 1923 from the area of Borowo [EB62] (Bazyluk 1947) and from 1954 from the area of Modliborzyce [EB91] (Michalski 1959). Subsequently the species was found in Zaklików [EB72] (Cmoluch 1971, Czarniawski et al. 1999) in 1968 and 1997, and at 17 other sites in the years 1995–2006. From 2007 to 2012 European mantis was recorded at five new localities, and in the years 2013–2021 at 100 more sites (Kozina & Łopucki 2016, 2017, Zieliński 2016, Zieliński et al. 2018a, b and unpublished data) (Figs 2a–e).

**Sandomierska Lowland** [UTM=157, UTM(Mr)=93, P(Mr)=59.2%]. The first site with European mantis was found in 1925 in Rudniki, and several more in the years 1927–1950 in the area of Nisko and Biłgoraj [EA88, EA89, FB20] (Bałut 1953, Prüffer 1955, Michalski 1959, Bazyluk 1960), in 1938 in the area of Tarnowska Wola [EA58] (Karczewski 1955), in the years 1952–1955 in Dęba Rozalin, Kolbuszowa, Krzatka, Mielec i Nisko [EA36, EA46, EA46, EA58, EA68, EA84] (Razowski 1953, Bazyluk 1956, 1957) and in the years 1956–1958 in the area of Rozwadów and Stalowa Wola [EB70, EB81] (Michalski 1959, Bazyluk 1960). Subsequently the species was recorded in 1994 from Wilcza Wola [EA67] (Kawa 2001). In the years 1995–2006 European mantis was known to occur at ca. 80 sites (Czarniawski et al. 1999, Kata 2004, Zięba 2004, Liana 2007, Pączka 2008, Trzeciak 2010), and in the years 2007–2021 at as many as 200 sites (Trzeciak 2010, Ćwik et al. 2012, Kołodziej et al. 2012, Krawczyk et al. 2012, Durak et al. 2018, Zieliński et al. 2018b, Kutera et al. 2021, and unpublished data) (Figs 2a–e).

**Roztocze Upland** [UTM=47, UTM(Mr)=27, P(Mr)=57.4%]. The earliest records come from 1938 and the first half of the 1940s (Skuratowicz 1946, Bazyluk 1947, Michalski 1959). Further sites were found in 2005 in Goraj [FB21] (Buczyńska et al. 2006) and Bukowa Góra [FB30] (K. Nowakowski, M. Janiszawski, pers. obs.), in 2009 in Panasówka [FB30] (W. Michałczuk, pers. obs.), and in 2011 in Józefów [FA49] (R. Cymbała, pers. obs.). One hundred and twenty

more sites were found in the years 2012–2021 (Durak et al. 2018, Zieliński et al. 2018b, and unpublished data) (Figs 2a–e).

**Małopolska Upland** [UTM=316, UTM(Mr)=151, P(Mr)=47.8%]. First records come from the area of Skarżysko (Bałut 1953), in 1956 and 1958 from Góry Wysokie [EB52] (Bazyluk 1960), in 1968 from Chotel Czerwony [DA78] (Witkowski 1992), in the years 1979–1980 from Jelonek [EB46] (J. Ślupek, pers. obs.), in the years 1980–1985 from the area of Wola Korzeniowa [DB87] and Barak [DB97] (data of Nadleśnictwo Skarżysko – Skarżysko Forestry), in 1981 from Krępa Kościelna [EB36] (J. Ślupek, pers. obs.), and in 1993 from the vicinity of Końskie [DB56] (unpubl. data). In the years 1995–2006 European mantis was recorded at 19 sites (Sępioł 2005, Liana 2007, Bonk & Kajzer 2009, Łazarski 2016, and unpublished data), and in the years 2007–2021 in occurred already at ca. 250 sites (Bonk & Kajzer 2009, Walczyk & Lis 2009, Bonk et al. 2011, Sępioł 2012, Łazarski 2016, Durak et al. 2018, Zieliński et al. 2018b, Miłkowski & Chmielewski 2019, Kajzer-Bonk 2020, and unpublished data) (Figs 2a–e).

**Pieniny Mts** [UTM=12, UTM(Mr)=1, P(Mr)=8.3%]. The only record of European mantis in this region was made in 1968 in the vicinity of Nowa Góra peak, 902 m a.s.l [DV57] (Witkowski 1992) (Fig. 2a). Currently European mantis seems to be absent in this region (E. Zajac, pers. obs.).

**Bieszczady Mts** [UTM=30, UTM(Mr)=8, P(Mr)=26.7%]. The earliest records come from Cisna [EV95] from the years 1995–2006 (Liana 2007). Subsequently it was found in 2012 in Baligród [EV96], in 2012 and 2014 in Rabe [FV26] (M. Scelina, pers. obs.), in 2017 nearby the peak of Riaba Skała Mt., 1192 m a.s.l. (Bury & Bury 2018), in 2019 and 2020 in Roztoki Górne (M. Ślusarczyk, pers. obs.), in 2020 in Wetlina [FV04] (G. Bistuła-Prószyński, pers. obs.), and in 2021 in Radoszyce (A. Malkiewicz, pers. obs.) (Figs 2b–e).

**Eastern Beskid Mts** [UTM=113, UTM(Mr)=55, P(Mr)=48.7%]. First sites were discovered in 2002 in the Magurski National Park [EV37] (Pawełec & Basista 2003), in 2003 in Glinik Górnny [EA21], Krośno [EA50], Pietrusza Wola [EA51], Beskid Niski [EV38, EV48], Katły [EV39], Magurski National Park [EV39], Myscowa [EV49], and Ustrzyki Dolne [FV17] (Pawełec & Basista 2003, Zięba 2004, Liana 2007). In the years 2004–2021 ca. 120 sites were known (Liana 2007, Pączka 2008, Pawłowski 2009, Durak et al. 2018, Zieliński et al. 2018b, unpublished data) (Figs 2b–e).

**Wielkopolska-Kujawy Lowland** [UTM=670, UTM(Mr)=54, P(Mr)=8.1%]. In this region the European mantis was first recorded in 2004 in Warta [CC33] (M. Szwedka, pers. obs.), subsequently in 2014 in Mała Nieszawka [CD37] (unpubl. data), in the years 2013–2016 in the eastern parts of the region [CC14, CC31] (Zieliński et al. 2018b), and in 2017 in Police [XT60] (Kadej et al. 2021). The westernmost records come from 2020 from Mielno [VT73], Wielotów [VT74], Suchodół [VT83] (K. Kilian, pers. obs.), Tuplice [VT82] (A. Woźniak, pers. obs.), and Gubin [VT85] (J. Lewandowski, pers. obs.). In the years 2018–2021 *M. religiosa* was found at ca. 75 sites, mostly in the eastern and southern parts of the region (Kadej et al. 2018, 2021, Kutera 2019, Żurawlew et al. 2019, Rosińska 2020, Szymański et al. 2020, 2021, and unpublished data) (Figs 2b–e).

**Upper Silesia** [UTM=152, UTM(Mr)=41, P(Mr)=27.0%]. The species was first recorded in 2005 in Sławków [CA87] (D. Lorek, pers. obs.), in 2013 in Markowo Duże [BB95], and in 2015 in Błotnica Strzelecka-Doryszów [CA19] and Rędzin [CB22] (Biwo 2016). In the years 2016–2021 it was recorded at 60 other sites (Biwo 2016, Kadej et al. 2018, 2021, Zieliński et al. 2018b, Kopij 2021, and unpublished data) (Figs 2b–e).

**Świętokrzyskie Mts** [UTM=22, UTM(Mr)=9, P(Mr)=41.0%]. The first record comes from 2007 from Kielce [DB73] (M. Gwardjan, pers. obs.), and the next from 2014 from Świętokrzyski National Park (Błoński 2015). More sites were discovered in the years 2015–2021, mostly in the area of Kielce, Jaworze, Zachełmie, and in Świętokrzyski National Park (Błoński 2015, Zieliński et al. 2018b, and unpublished data) (Figs 2c–e).

**Western Beskid Mts** [UTM=127, UTM(Mr)=3, P(Mr)=2.4%]. Only three records are known: in 2009 from Muszynka [EV06] (Ćwik et al. 2012), in 2020 from Tokarnia [DA10] (J. Kijak, pers. obs.), and in 2021 from Bielsko-Biała [CA52] (Ł. Gierlasiński, pers. obs.) (Figs 2c–e).

**Lower Silesia** [UTM=210, UTM(Mr)=43, P(Mr)=20.5%]. First records come from 2009–2011 from Opole [YS01, YS11] (Królik 2010, Kopij 2021) and Brzezie [YS02] (Biwo 2016). In 2012 European mantis was observed in the area of Górażdże [BB80] and Suchy Bór [BB91] (Biwo 2016), and in 2013 in the vicinity of Gogolin [BA89], Lubienia [XS93], Żywocice [YR19], and Brzezie [YS02] (Biwo 2016, M. Brodacki, M. Pastrykiewicz, pers. obs.). In the years 2014–2021 ca. 60 sites were known (Biwo 2016, Kadej et al. 2018, 2021, Zieliński et al. 2018b, Kopij 2019, 2021, and unpublished data). In 2021 first localities in the western part of the region were found: Golnice (former military training ground) [WS38, WS39] (A. Berezowski, Ł. Skoczylas, pers. obs.) (Figs 2c–e).

**Podlasie Lowland** [UTM=270, UTM(MR)=82, P(Mr)=30.4%]. Earliest records come from 2010 from Orchówek [FC71] (M. Hołowiński, pers. obs.), from 2011 from Międzyrzec Podlaski [FC26] (P. Mikołajczuk, pers. obs.), from 2012 from the area of Tarasiuki, Okuninka, and Orchówek [FC70, FC71] (M. Hołowiński, pers. obs.), from 2013 from Biebrzański National Park (FE24) (W. Emonutow, pers. obs.), and from 2014 from Sitno [FC26] (P. Mikołajczuk, pers. obs.), Siemiatycze [FD21] (A. Banach, pers. obs.), and Białystok [FD38, FD48] (Zieliński & Łazarecki 2018, and unpubl. data). In the years 2015–2021 European mantis was discovered at more than 120 new sites (Sielezniew & Dziekańska 2015, Kozina & Łopucki 2017, Zieliński et al. 2018b, Miłkowski & Chmielewski 2019, and unpublished data) (Figs 2c–e).

**Białowieża Primeval Forest** [UTM=18, UTM(Mr)=6, P(Mr)=33.3%]. Earliest obervations come from 2010 (unpubl. data) and 2014 from Białowieża [FD94] (M. Jeliński, pers. obs.), where the species was recorded every year from 2015 to 2021. Further sites were recorded in the years 2016–2021 in Orzeszków [FD73], Hajnówka, Górniańskie Łąki, Judzianki [FD74], Stare Budy [FD84], Narewka [FD85], Grudek [FD94], Cisówka [FD96], Marusza, Pasieki, and at Siemaniówka lake [FD96] (Zieliński & Łazarecki 2018, Zieliński et al. 2018b, and unpublished data) (Figs 2c–e).

**Kraków-Wieluń Upland** [UTM=91, UTM(Mr)=11, P(Mr)=12.1%]. In this region the European mantis was first recorded in the years 2013–2015 in Kraków [DA24], subsequently in 2016 in Masłońskie [CB71] (P. Huber, pers. obs.), and in 2017 in Olsztyn [CB72] (unpubl. data). Further sites were recorded in the years 2018–2021 in the following localities: Góra Biakło in Olsztyn, Częstochowa, Dzibice, Góra Zborów nature reserve, Janów, Jaroszów, Korwinów, Olsztyn, Podlesice, Siedlec, Więckowice, Włodowice, Zawodzie, Złoty Potok, and in Błędów Desert (unpubl. data) (Figs 2d–e).

**Eastern Sudety Mts** [UTM=39, UTM(Mr)=3, P(Mr)=7.7%]. Earliest records come from 2014 from Nowa Wieś [XR26] (P. Szczuko, pers. obs.). Further sites were discovered in 2017 in Strachocin [XR37], in 2007 and 2018 in Międzygórze [XR26], and in 2019 in Goworów [XR25], and Stronie Śląskie [XR37] (Kadej et al. 2021, A. Balcer, M. Mol, P. Szczuko, pers. obs.) (Figs 2d–e).

**Masurian Lakeland** [UTM=456, UTM(Mr)=60, P(Mr)=13.2%]. First records come from 2014 from Olsztyn [DE65] (P. Odoj, pers. obs.), further from 2015 from Okółek [FE57] (Zawadzki et al. 2018) and Boksze-Osada [FF40] (unpubl. data), and in 2016 at the Krzywe lake by Suwałki [FE39] (H. Stojanowski, M. Stojanowski, pers. obs.). In the years 2017–2021 ca. 80 more sites were discovered (Zawadzki et al. 2018, Zieliński & Łazarecki 2018, Zieliński et al. 2018b, Miłkowski & Chmielewski 2019, and unpublished data) (Figs 2d–e).

**Western Sudety Mts** [UTM=84, UTM(Mr)=7, P(Mr)=8.3%]. First records from this region come from 2015 from Lubań [WS16] (Kadej et al. 2016), and from 2018 from Karkonosze Mountains [WS95] (Torzewski & Dobrzański 2019). Further records are from

2019: Miszkowice [WS61], forest district Sokołowsko [WS81], Szczawina [XR17] (Kadej et al. 2021), Dobromyśl [WS71] (B. Schneider, pers. obs.), and Gniewoszów [XR16] (K. Zaremba, pers. obs.) (Figs 2d–e).

**Trzebnickie Hills** [UTM=47, UTM(Mr)=8, P(Mr)=17.0%]. *M. religiosa* was first reported in 2017 from Leśnictwo Turze [YS08] and in 2018 from Oleśnica [XS67] (Kadej et al. 2018). It was subsequently recorded in 2020 in Piaski [CB07] (Z. Pokora, pers. obs.), Chobanin [CB08], Bagatelka [CB18] (S. Pawlak, pers. obs.), Oborniki Śląskie [XS38] (P. Jagodziński, pers. obs.), and Poręby [XT70] (L. Matacz, pers. obs.), and in 2021 in Pasikurowice and Pierwoszów [XS47] (Z. Gołębska, L. Tobolska, pers. obs.) (Figs 2d–e).

**Pomeranian Lakeland** [UTM=508, UTM(Mr)=4, P(Mr)=0.8%]. Only few sites are known: 2019 in Grudziądz [CE52] (K. Kustusch, pers. obs.), 2020 in Zlew [CE27] (G. Bistuła-Prószyński, pers. obs.), and 2021 in Kwidzyn [CE65] (P. Olszewski, S. A. Zgorzałek, pers. obs.) and Jagatowo [CF41] (G. Gierlański, pers. obs.) (Figs 2e).

**Baltic Coast** [UTM=143, UTM(Mr)=3, P(Mr)=2.1%]. In 2019, the species was recorded three times in Gdańsk: city center [CF42], and on the beach in Stogi and Sobieszewo [CF52] (B. Feledyn-Szewczyk, P. Szewczyk, D. Przybytkowska, pers. obs.). In 2021 it was observed in Elbląg [CF90] (M. Mikułowski, pers. obs.) (Figs 2e).

*Mantis religiosa* was never recorded in the Nowy Targ Basin and the Tatra Mountains from 1923 to 2021 (Figs 2a–e).

Table 1. Number of UTM squares with *M. religiosa* records in regions of Poland (Figure 1) for five time periods from 1923 to 2021.

Region	Number of UTM sq.	1923–1994	1923–2006	1923–2012	1923–2017	1923–2021	% UTM with <i>M. religiosa</i>
Sandomierska Lowland	157	12	32	52	77	93	59.2
Roztocze Upland	47	2	4	8	16	27	57.4
Eastern Beskid Mts	113	0	11	18	41	55	48.7
Małopolska Upland	316	7	18	46	96	151	47.8
Świętokrzyskie Mts	22	0	0	1	6	9	41.0
Lublin Upland	170	3	15	18	45	67	39.4
Mazovian Lowland	328	1	1	5	60	115	35.1
Białowieża Primeval Forest	18	0	0	0	4	6	33.3
Podlasie Lowland	270	0	0	3	41	82	30.4
Upper Silesia	152	0	1	1	16	41	27.0
Bieszczady Mts	30	0	2	4	5	8	26.7
Lower Silesia	210	0	0	6	17	43	20.5
Trzebnickie Hills	47	0	0	0	1	8	17.0
Masurian Lakeland	456	0	0	0	9	60	13.2
Kraków-Wieluń Upland	91	0	0	0	3	11	12.1
Western Sudety Mts	84	0	0	0	1	7	8.3
Pieniny Mts	12	1	1	1	1	1	8.3
Wielkopolska-Kujawy Lowland	670	0	1	1	5	54	8.1
Eastern Sudety Mts	39	0	0	0	2	3	7.7
Western Beskid Mts	127	0	0	1	1	3	2.4
Baltic Coast	143	0	0	0	0	3	2.1
Pomeranian Lakeland	508	0	0	0	0	4	0.8
Nowy Targ Basin	0	0	0	0	0	0	0
Tatra Mts	0	0	0	0	0	0	0

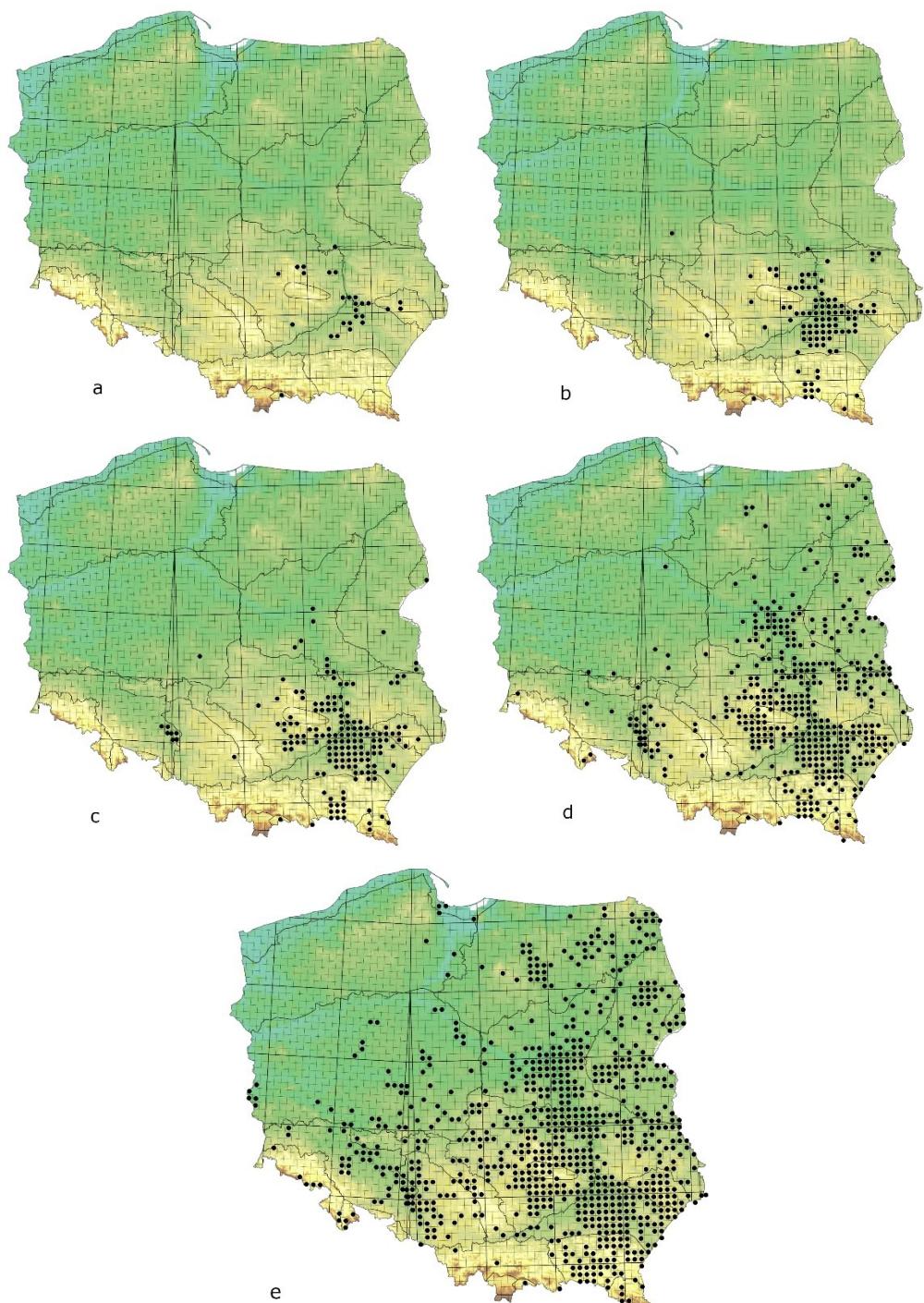


Fig. 2. Records of the European mantis *Mantis religiosa* in Poland in the  $10 \times 10$  km grid of the MGRS (UTM) coordinate system from 1923 up to 1994 (a), 2006 (b), 2012 (c), 2017 (d) and 2021 (e). Black lines denote regions of Poland (Fig. 1).

### Range expansion of European mantis in Poland

By 1994, the range (EOO) of the European mantis covered 3.3% of the country's area, and the total number of  $10 \times 10$  km UTM squares where the species was observed at least once during this period was 27 (out of 3388 squares located wholly or partially within Polish borders) (Table 2, Fig. 2a). For most of the 20th century the European mantis occurred in a restricted area, inhabiting there a narrow range of habitats. In this study we refer to this area as the reference range (Fig. 3). At the end of this period the first signs of expansion were already noticed. Between 1995 and 2012 the range (EOO) change was about  $2500 \text{ km}^2$  per year, so that in 18 years the species' range increased 5–6 times to about 18% of the country's area and the number of known occupied UTM squares increased to 169 (Table 2, Fig. 2c, Fig. 3). During the next period (2013–2021), which was only half as long (9 years), the average annual increase of European mantis range (EOO) in Poland was over  $20\,000 \text{ km}^2$  (8 times faster). This resulted in colonisation of 77% of the country's area with records of the species in 815 UTM squares (Table 2, Fig. 2e, Fig. 3). During 27 years (1995–2021), *M. religiosa* increased its range in Poland (in relation to the reference range) about 23 times considering EOO, or ca. 30 times with regard to AOO or the number of occupied UTM squares.

Table 2. Expansion parameters of *M. religiosa* in Poland up to 2021; \* – in relation to the previous period,  
\*\* – cumulative with previous periods.

Period	N of years in period	Range of occurrence (EOO) [ $\text{km}^2$ ]	Percentage of the country's area [%]	Change in range [ $\text{km}^2$ ]*	Mean annual change in range [ $\text{km}^2$ ]	N of occupied UTM squares**	Area of occurrence (AOO) [ $\text{km}^2$ ]**
up to 1994	-	10432.2	3.3	-	-	27	2680.3
1995–2006	12	40799.6	13.1	30367.4	2530.6	97	9580.9
2007–2012	6	55266.8	17.7	14467.2	2411.2	169	16457.2
2013–2017	5	161675.9	51.7	106409.1	21281.8	431	41794.0
2018–2021	4	241477.2	77.3	79801.3	19950.3	815	79087.7

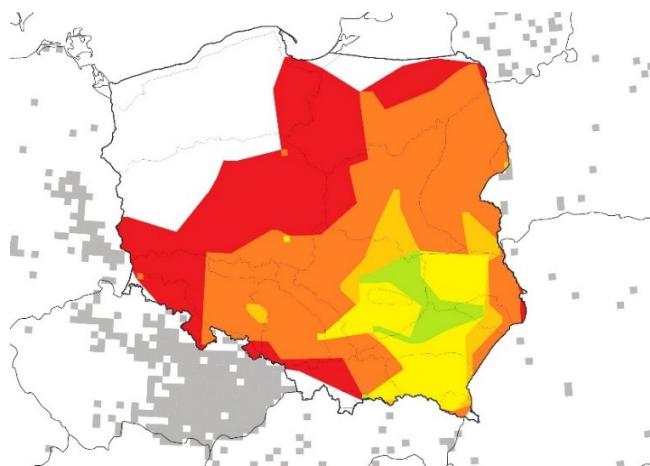


Fig. 3. Range expansion of *Mantis religiosa* in Poland during 1995–2021. Green: reference range (up to 1994), yellow: area colonised in 1995–2006, pale orange: area colonised in 2007–2012, orange: area colonised in 2013–2017, red: area colonised in 2018–2021 (source of data: present work). Grey squares: occurrence of *M. religiosa* in neighbouring countries up to 2021 (source of data: GBIF 2022, Chobot 2022).

### Phenology and habitat

Live adult European mantis individuals were observed from the 1<sup>st</sup> July to the 8<sup>th</sup> November, i.e., over the period of four months. However, there are very few records (less than five per pentade) in the first and second decades of July and from the third decade of October onwards. The highest number of observations (more than 30 per pentade) was made from the second decade of August to the second decade of September, with the peak in the last pentade of August (Fig. 4). Therefore, we conclude that the typical period of appearance of *M. religiosa* imagines in Poland lasts from the third decade of July to the second decade of October.

The European mantis was recorded 27 times in unspecified dry habitats (10.0% of records) and 60 times (22.8%) in sandy habitats. In semi-natural dry grasslands 70 observations (26.6%) were made. The species was observed 34 times (12.9%) in moist to wet habitats from which 21 (8.0%) were peat bogs and 13 (4.9%) were moist, periodically wet, and wet meadows. On abandoned arable land 35 records (13.3%) were made. From forests come 11 (4.2%) and from heaths 7 (2.7%) records. *M. religiosa* was observed 53 times (20.2%) in urban habitats.

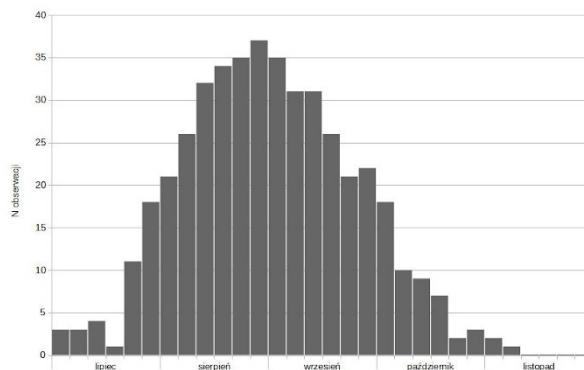


Fig. 4. Seasonal distribution of records of imagines of *Mantis religiosa* in Poland in the years 1979–2021 (N=443).

### DISCUSSION

This work is the most recent study in the 21<sup>st</sup> century dealing with the occurrence and range expansion of *M. religiosa* in Poland. In comparison to two previous papers from the 21<sup>st</sup> century (Liana 2007, Zieliński et al. 2018b), much more occurrence data was compiled and analysed. The study by Liana (2007), covering occurrence data up to 2006, reported 54 UTM squares occupied by the European mantis. The data from the same period gathered by us yielded 97 squares. The paper by Zieliński et. al. (2018b), presenting observations from 2013–2016, reports 159 UTM squares with European mantis. Our data for a slightly longer period (2013–2017) revealed 269 UTM squares. Differences in square numbers between previous papers and this study are due to wider range of data sources used by us, including online open databases and social media. Data quality is similar, with finds of single individuals and oothecae as well as records of established populations included in all three studies (finding a single individual or ootheca does not guarantee that there is a viable population at a particular site).

### Changes in the range of the European mantis in Poland and other European countries

As shown by Liana (2007), Zieliński et al. (2018b) and this study, until the 1990s the range of *M. religiosa* in Poland was relatively stable and limited mainly to the Sandomierska Lowland, Roztocze Upland and the eastern part of the Małopolska Upland in the south-eastern part

of the country (Fig 2a). The number of known sites and population size were relatively small, the species inhabited heathlands and sandy grasslands within forest clearings and was found at edges of pine forests (Liana 2004, 2007).

Data presented by Liana (2007) and in this paper indicate that at the turn of the 20th and 21st centuries the number of sites and the abundance of local populations in the area defined above began to increase (Figs 2b). At this time the species also appeared quite numerously in the Eastern Beskid south of its main range. In the following years the range in eastern Poland expanded northwards. At the end of the first decade of the 21st century, an isolated metapopulation of the European mantis appeared in Lower Silesia in south-western Poland (Królik 2010) (Fig. 2c). As shown by Zieliński et al. (2018b) and this study, in the second decade of the 21st century the range of the European mantis expanded rapidly north and west (Figs 2d–e). By 2021, only the north-western part of Poland (Baltic Coast, Pomeranian Lakeland and the western part of the Wielkopolska-Kujawska Lowland) and the central part of the mountainous belt in the south of the country (Western Beskids, Nowy Targ Basin and the Tatra Mountains) remained unoccupied or sparsely occupied (Fig. 2e). The species is now found in diverse habitats, both natural and anthropogenic, such as various types of dry, moist and periodically wet grassland, fallow land, ruderal vegetation at roadsides and along railroad embankments, and even urban green areas.

The observed amount of range expansion suggests that in the next several years European mantis may colonise the whole north-western part of the country up to the Baltic coast. A similar direction and timing but somewhat faster rate of expansion was shown for another orthopteroid insect – the common sickle bush-cricket *Phaneroptera falcata* (Poda, 1791), whose range in Poland in the 20<sup>th</sup> century was also confined to the south-eastern part of the country. Currently, this bush-cricket is found commonly throughout the entire country, including the Pomeranian Lakeland and Baltic Coast (Żurawlew et al. 2017, 2022).

Overall, the expansion of the European mantis in Poland is similar to that observed in other European countries. In Germany, the first records of the European mantis come from the middle of the 18th century, when the species was observed in different areas of the country (Berg et al. 2011). However, as in Poland, its range shrunk through the 19th and the first half of the 20th century and until the end of the 20th century the European mantis was only present at xerothermic grassland sites (Berg et al. 2011, Schwarz et al. 2017). The intensification of agriculture and the resulting decline in dry grasslands and fallow land (main European mantis habitats) probably caused its decline in this period (Schwarz et al. 2017). Until the year 2016 the European mantis occupied two areas in Germany: south-western part of the country (mainly the Rhine valley) and its eastern part, reaching nearly as far as the 53<sup>rd</sup> degree of latitude (Schwarz et al. 2017), which roughly corresponds to the 54<sup>th</sup> degree of latitude reached in Poland by 2017.

In the Netherlands, European mantis was first recorded in 2020 (Noordijk & Swart 2021) which is also the time when this species reached the Baltic Sea in Poland. In Latvia, which is located further north than the aforementioned countries, it was first recorded in 2008 (Pupiņš et al. 2012). These records are much earlier than any records from northern Poland. However, the observed individuals may be of anthropogenic origin or originate from the northernmost Russian sites located in the surrounding of Moscow and in the Kostroma province, indicating a possible westward range expansion (Bolshakov et al. 2010).

South to Poland, in the Czech Republic the European mantis had been considered a species restricted to the warmest xerothermic grasslands until the end of the 1990s. However, as of 2008 it already spread over vast parts of Bohemia (Janšta et al. 2008).

The present distribution of *M. religiosa* in Poland and neighbouring countries is shown in Fig. 3.

### Possible causes of expansion

The expansion of the European mantis range in Poland in the 21st century is probably caused by main 3 factors:

**1. Climate warming.** According to IMGW data, the average annual air temperature in Poland in the period 1961–1990 was 7.5 C while in 2011–2020 it increased to 9.1 C (Instytut Meteorologii i Gospodarki Wodnej – Państwowy Instytut Badawczy 2022, Fundacja Edukacji 2022). *Mantis religiosa* is a thermophilic species (Bazyluk 1977). Warmer summer-autumn temperatures presumably facilitate faster development and maturation of larvae, especially in north-eastern parts of Poland, where the climatic conditions are least favourable. The climate change may influence the spread of European mantis also indirectly. Mantis oothecae detached from plants, with packets of eggs probably still alive, have been observed transported by wind (M. Kutera & P. Radzikowski, pers. obs.). The climate warming, apart from rising temperatures, results in an increase in the frequency of violent weather events, such as gales and storms, which presumably facilitate the spread of the European mantis oothecae in this way.

**2. The abandonment of agricultural use of large areas of cultivated lands in the 1990s,** caused by the unprofitability of farming after economical changes that occurred in Poland at the beginning of this period. As a result, many abandoned crop fields and grasslands turned into fallow land, becoming secondary habitats suitable for the European mantis and facilitating its initial expansion until further natural succession or reclaiming of the land made these areas less suitable for the species.

**3. Construction of new roads, highways and railways.** New roads and railway lines constructed in Poland after the country joined the European Union in 2004, especially those leading through dense forest areas, have created new secondary habitats for European mantid (grassy roadsides and railway embankments) which may have become migration routes facilitating the spread of this species.

### Role of introductions

Factors favouring the range expansion of European mantis in Poland and worldwide possibly include accidental introduction of various development stages of this species (oothecae, larvae, imagines) to new locations, e.g. with imported plants. This way, *M. religiosa* is believed to have found its way to North America at the end of the 19th century, where it became part of the local fauna (Bazyluk 1977).

In the literature we found one case of European mantis arriving within the present (post World War 2) borders of Poland from abroad: at the end of the 19th century in Wrocław (an individual brought with imported foods) (Dietl 1895). At the beginning of the 20th century the European mantis was found near Chorzów in Upper Silesia (Pax 1920). According to Bazyluk (1977), the circumstances of this record also indicate accidental introduction.

Among data collected by the authors for this study, two cases of accidental introduction of mantids into or within Poland were identified. In 2004, in Suwałki, a mantis of unknown species was found in a shipping container brought from Turkey (unpubl. data). In 2020 in Wolin, a female *M. religiosa* was found in a transport vehicle arriving from an unknown location (K. Wrzecionkowski, unpubl. data). These records, as well as the literature data mentioned in the previous paragraph, were not included in the analyses of the species distribution in Poland presented in this paper.

Despite of the small number of documented accidental introductions, the spread of European mantis within Poland by road and rail transport is possible. It has been noted that towards the end of the vegetation season, thermophilous insects like mantids and orthopterans search for warm places, including interiors of dwellings and vehicles. This may result in the relocation of the

insects over long distances (Grobelny et al. 2019). European mantis oothecae may be carried along with transports of seedlings of forest, ornamental and fruit trees from places of their deposition to new locations. Among the available data, isolated findings of *M. religiosa* occurring far from its main range are noteworthy, e.g. in 1968 in Pieniny Mts. (Witkowski 1992), in 2004 in Warta (M. Szweda, unpubl. data) and in 2014 in Mała Nieszawka near Toruń (unpubl. data) in Wielkopolska-Kujawy Lowland, in 2010 in Białowieża Primeval Forest (unpubl. data), and in 2015 in Lubań in Western Sudety Mts. (Kadej et al. 2016) (Figs 2b–d & Fig. 3). It is possible that these records result from such events. Accidental introductions have also been suggested to contribute to the establishment of European mantis near Opole in Lower Silesia in the 2000s (Królik 2010).

European mantises are sometimes collected from natural habitats and bred in terraria, despite being legally protected in Poland. Oothecas are also easily obtained from natural sites. Such cases were recorded most often in large cities, e.g. Warsaw in the period 2010–2020. This was evidenced by videos and photos on social networking sites and comments on entomological forums. Informing the involved persons that collecting and keeping the protected species violates law resulted in the removal of the entry, thus obliterating evidence of such actions. The number of European mantis kept and reproduced in captivity is unknown. No information was found that these individuals were reintroduced into the wild. Nevertheless, the first observations of European mantis in Warsaw may have concerned individuals translocated and bred by amateurs (A. Liana, personal communication to P. Radzikowski).

As the accidental and intentional introductions cannot be ruled out, it is possible that not only the native Central European population of the European mantis (Czech Republic, Slovakia, Hungary) is present in Poland, but also admixtures from Western European (France and West Germany) and Eastern European (Eastern Ukraine) populations. This issue could be clarified by genetic studies. Such research helped to explain the origin of European mantis populations in Germany (Linn & Griebeler 2016).

### Protection and threats to European mantis in Poland

The need for protection of *M. religiosa* in Poland had been pointed out as early as in 1929 (Sprawozdanie 1929). However, the species was not included in the list of protected species until 1984 (Rozporządzenie 1983). In 2001 the European mantis was placed under strict species protection, which is still in force today (Rozporządzenie 2001 and further amendments).

Until now *M. religiosa* has been categorised as a critically endangered (CR) or endangered (EN) species in Poland (Liana 2002, 2004). In view of its significant range expansion described in this paper, we suggest that the current red-list status of the European mantis in Poland is rather least concern (LC). However, a meticulous assessment is required (IUCN Species Survival Commission 2012). In spite of that, we argue that the European mantis should still enjoy legal protection in Poland. The following facts support this statement: 1) The regression of the population in the 19<sup>th</sup> and first half of the 20<sup>th</sup> century in Poland as well as in Germany was attributed to land use change (Schwarz et al. 2017). 2) In spite of the current range expansion in Central Europe, a study found that in a scenario of continuous climate change the range of the European mantis will start contracting (Steger et al. 2020). 3) Ongoing loss of open and half-open habitats with low and sparse vegetation (Linn & Griebeler 2016). These habitats, even though still abundant, are among the most endangered in Poland, disappearing fast from the landscape due to the abandonment of traditional agricultural practices (Török et al. 2018, Hanczaruk & Bąba 2020). 4) Even though currently the European mantis is common through most of the occupied range and shows high habitat variability, the wide spectrum of occupied habitats may be a result of the ongoing expansion.

Maintaining the protection status for the European mantis in Poland may also have a positive impact on other endangered species occupying dry open and half-open habitats. As a large and charismatic insect, arousing public interest, it is an umbrella species. Its presence provides a justification for the protection of valuable sites of psammophilous and xerothermic vegetation with associated rare plants and animals.

#### SUMMARY AND CONCLUSIONS

1. Until the 1990s the occurrence of *M. religiosa* in Poland was restricted to a relatively small area in the centre of the south-eastern part of the country. At the end of the 20th century the first signs of range expansion were observed. In the following years the species started to spread north, west and south. In the second decade of the 21st century the rate of expansion clearly accelerated.

2. In 1995–2021 the area settled by the species in Poland increased more than 20-fold, from circa 3% to 77% of the country's area. The average annual change in settled area ranged from about 2,500 km<sup>2</sup> in the first years of the expansion to over 20,000 km<sup>2</sup> in recent years. During the expansion the habitat variability of the European mantis increased.

3. Despite of the ongoing expansion, the European mantis should be still considered a potentially threatened species in Poland. It is an umbrella species whose protection favours preservation of valuable natural habitats (sandy and xerothermic grasslands) and associated endangered plant and animal species. For this reason, the legal protection of *M. religiosa* in Poland should continue.

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#### STRESZCZENIE

#### [Modliszka *Mantis religiosa* (Linnaeus, 1758) (Mantodea: Mantidae) w Polsce – stan obecny i zmiany w zasięgu]

Praca podsumowuje informacje o występowaniu modliszki *Mantis religiosa* w Polsce w latach 1923–2021. Wykorzystano materiał obejmujący 2664 rekordy: 635 opublikowanych i 2029 niepublikowanych, których lokalizację można było przypisać do kwadratów  $10 \times 10$  km (według siatki układu UTM). Do początku lat 90. XX wieku zasięg *M. religiosa* ograniczony był do obszaru południowo-wschodniej Polski (Nizina Mazowiecka, Wyżyna Lubelska, Nizina Sandomierska, Roztocze i Wyżyna Małopolska). Pod koniec XX wieku zaobserwowano pierwsze oznaki ekspansji zasięgu, a w kolejnych latach gatunek zaczął rozprzestrzeniać się na północ, zachód i południe. Modliszka zasiedlała kolejno następujące krainy: Bieszczady, Beskid Wschodni, Nizinę Wielkopolsko-Kujawską, Śląsk Górnny, Góry Świętokrzyskie, Beskid Zachodni, Śląsk Dolny, Podlasie, Puszcę Białowieską, Wyżynę Krakowsko-Wieluńską, Sudety Wschodnie, Pojezierze Mazurskie, Sudety Zachodnie, Wzgórza Trzebnickie, Pojezierze Pomorskie i Pobrzeże Bałtyku. W drugiej dekadzie XXI wieku tempo ekspansji wyraźnie przyspieszyło, a w latach 1995–2021 zasięg gatunku zwiększył się ponad 20-krotnie, z 3% do 77% powierzchni kraju. Średnia roczna zmiana zasiedlanej powierzchni wahala się od około  $2500 \text{ km}^2$  w pierwszych latach ekspansji do ponad  $20\,000 \text{ km}^2$  w ostatnich latach. W trakcie ekspansji wzrosła różnorodność zasiedlanych przez gatunek siedlisk. Za główne przyczyny ekspansji uważa się: ocieplenie klimatu środkowej Europy pod koniec XX w., zaniechanie użytkowania dużych obszarów rolniczych w latach 90. XX w. i rozpoczęcie na dużą skalę budowy nowych dróg, autostrad i linii kolejowych w następnej dekadzie. Wyższe temperatury letnio-jesienne przypuszczalnie sprzyjają szybszemu rozwojowi i dojrzewaniu larw, zwłaszcza w północno-wschodniej części Polski, gdzie warunki klimatyczne są najmniej korzystne. W latach 90. XX w. wiele opuszczonych pól uprawnych i łąk zmieniło się w ągory, stając się wtórnymi siedliskami odpowiednimi dla modliszki i ułatwiającymi jej początkową ekspansję. Nowe drogi i linie kolejowe wybudowane w Polsce po wstąpieniu kraju do Unii Europejskiej w 2004 r., szczególnie te prowadzące przez zwarte obszary leśne, stworzyły nowe siedliska wtórne (trawiaste pobocza dróg i nasypy kolejowe), które mogły stać się szlakami migracyjnymi ułatwiającymi rozprzestrzenianie się tego gatunku. Pomimo trwającej ekspansji, modliszka powinna być nadal uważana za gatunek potencjalnie zagrożony w Polsce. Jako, że jest to gatunek parasolowy, jej ochrona sprzyja zachowaniu cennych siedlisk przyrodniczych (murawy napiaskowe i kserotermiczne) oraz związanych z nimi zagrożonych gatunków roślin i zwierząt. Postulujemy, aby nadal kontynuować jej ochronę prawną w Polsce.