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Impact of management regimes on epigeic spider assemblages in semi-natural mesic meadows

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Adult female of *Pardosa palustris* (photo by Marzena Stańska)

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1. INTRODUCTION

1.1. Intensification of agriculture as a threat to biodiversity

Intensive development of agriculture is one of the greatest threats to biodiversity worldwide, comparable even with climate change (McLaughlin & Mineau 1995; Tilman et al. 2001; Foley et al. 2005). The process has resulted in the transformation of many natural ecosystems into agroecosystems, i.e. croplands and grasslands (meadows, pastures). The area of croplands and pastures has increased significantly over the last several decades and currently covers about 40% of the Earth's surface (Foley et al. 2005; Anderson 2006). Locally, in some areas, the percentage of agricultural land is even higher. For example, in Great Britain in 2000 it covered as much as 75% of the total country's area (Robinson & Sutherland 2002), while in Poland the agricultural land in 2016 accounted for 60.2% of the country's territory (Rozkrut 2017a). The intensive development of agriculture, caused by the increasing needs of the growing human population, will continue for many years. It is estimated that up to 2050 one billion hectares of natural ecosystems will be transformed into agroecosystems in the developing countries alone (Tilman et al. 2001).

In order to function and satisfy the growing needs of man, agroecosystems are subject to various agrotechnical and pratotechnical treatments aimed at obtaining high yields. Traditional farming methods used in the past have been abandoned in favour of modern, highly efficient methods. Since almost the beginning of the 20th century, the agricultural production has increased significantly as a result of, among others, the increasingly intensive use of fertilizers and pesticides along with agricultural mechanisation (Smil 1999; Robinson & Sutherland 2002; Dimitri et al. 2005; Dallimer et al. 2009). In Great Britain, for example, the yield of sugar beets, potatoes, wheat and barley has tripled in 50 years after 1950 (Pretty et al. 2000). While the increase in agricultural production has largely solved the world's problems related to food shortage, the environmental costs are huge (Vitousek et al. 1997; Tilman et al. 2001; Foley et al. 2005). Large-scale and intensive agricultural methods such as fertilization, the use of crop protection products and modern machinery, as well as land improvement (irrigation or drainage) contribute to the degradation of the environment and the reduction of species diversity in agroecosystems (Donald et al. 2001; Robinson & Suntherland 2002; Kleijn et al. 2009; Stoate et al. 2009; van Dyck et al. 2009). In addition, many of the treatments used in agriculture have a significant impact on natural ecosystems. For example, as a result of the increased use of fertilizers in the past few decades, the content of nitrogen and phosphorus in aquatic ecosystems has increased several times, which results in their eutrophication and consequently degradation (Carpenter et al. 1998; Foley et al. 2005). Today's "modern" agriculture involves the maximum simplification of the environmental structure over large areas and consequently, mosaics of small arable fields are transformed into large homogeneous land. This, in turn, involves the elimination of clumps of trees, hedges, field margins, ponds and other similar elements that, until recently, have been an integral part of the agricultural landscape and contributed to its heterogeneity and biodiversity (Robinson & Sutherland 2002; Benton et al. 2003). Few plant species grow in such areas and they represent only a small fraction of what would grow if the areas were still natural ecosystems. In many cases, agroecosystems are created in place of forests, thus ecosystems of high species richness (especially when they were tropical forests), which is followed by a drastic decline of biodiversity in a given area (Koh & Wilcove 2008; Gockowski & Sonwa 2011). This is perfectly illustrated by a comparison, which shows that about 70 plant species are cultivated over 1,440 million hectares of agricultural land, while more than 100 species of trees alone can be found over one hectare of tropical rain forest (Altieri 1999).

The decline in biodiversity resulting from the intensification of agriculture and the transformation of large areas into monocultures have been proved by numerous studies based on a number of groups of organisms. This is particularly well documented in the case of birds, as the range and the population size of many bird species have drastically declined (Siriwardena et al. 1998; Donald et al. 2001; Newton 2004). In Great Britain, the population size of ten bird species (including skylark *Alauda arvensis* and tree sparrow *Passer montanus*) was estimated to have declined by 10 million individuals over 20 years (Krebs et al. 1999). For thirty years, between 1980 and 2010, about 300 million farmland birds have lost their habitats in countries of the European Union (PECBMS 2012). The decline in both the size and the range of populations of many European bird species that inhabit agrocenoses, largely reflects the degree of agriculture intensification. In the countries of the “old” European Union, where agriculture was much more advanced, these negative processes are more intensive compared to the former socialist states of the Communist Bloc (Donald et al. 2001).

The drastic decline in the abundance and the number of species has also been observed among other groups of organisms (e.g. plants, butterflies, beetles), which is particularly evident for habitat specialists, while many of the taxa still common on farmland are habitat generalists (e.g. Robinson & Sutherland 2002; Baessler & Klotz 2006; Fitzpatrick et al. 2007). Robinson & Sutherland (2002) reported a decline in farmland taxa in Great Britain for about half of the plants and one-third of insects. The research conducted in central Germany revealed that the average number and cover of weed species, especially of archaeophytes, have decreased significantly over almost 50 years (Baessler & Klotz 2006).

When discussing the decline in biodiversity, the question certainly arises as to its role and the justification for maintaining it in agroecosystems at a sufficiently high level, given that the primary objective of such ecological systems is the production of food for humans and livestock. In this context, it would appear that limiting or eliminating other consumers is most desirable. However, biodiversity is not only value in itself, but it also ensures the proper functioning of ecosystems, both the natural ones and those used by man in agriculture. In terms of effective agriculture, the most important functions of the latter include ensuring adequate soil fertility, controlling the microclimate and hydrological conditions, maintaining a large number of pollinators, controlling the number of undesirable organisms considered as pests or neutralizing harmful chemical compounds (e.g. Altieri 1999; Foley et al. 2005; Klein et al. 2007; Tscharntke et al. 2007). Consequently, the biodiversity losses may lead to serious problems in agricultural ecosystems and hence measurable financial losses. It has been demonstrated, for example, that plants naturally occurring in agrocenoses, treated as weeds and hence removed from crops, affect the diversity of flower-visiting organisms, which translates into the mobility of bees and increases the productivity of sunflower plantations (Carvalheiro et al. 2011). It is estimated that pollinating insects alone provide ecosystem services worth more than 100 billion USD a year worldwide (Gallai et al. 2009). This is not surprising considering that the yield of 35% of crops and 87 of the leading global food crops depends on animal pollinators (Klein et al. 2007). Biodiversity plays a crucial role in controlling the number of animal pests in crops which, according to research, cause yield losses between 5 and 19% worldwide in the most common cereal crops alone (Oerke 2006). Letourneau et al. (2015) calculated that the decline in species diversity of organisms that act as pest control in squash and cucumber fields in only two US states could result in losses of up to 12 million USD per year. However, the total value of ecological services provided by primarily native "wild" insects in the United States for pest control amounts to as much as 4.5 billion USD per year (Losey & Vaughan 2006).

Agriculture has long been shaping the biodiversity in Europe, although in the past the agricultural exploitation of the environment led to the transformation of the environment, but not to its degradation, as is currently the case. Low-input farming over hundreds of years has given rise to many valuable semi-natural habitats (e.g. semi-natural grasslands), which have become a typical habitat for many species. It has been estimated that 50% of all species in Europe depend on agricultural habitats, including a number of endemic and threatened species (Stoate et al. 2009). As a result, many rare species and semi-natural habitats occurring in Europe are dependent on the continuation of farming, but in its extensive form (Tryjanowski et al. 2011). Therefore, cessation of land use and land abandonment may lead in many cases not only to soil erosion, desertification or an increase in the number of fires but also to a decline in biodiversity (MacDonald et al. 2000; Rey Benayas et al. 2007). Consequently, the mere protection of valuable natural areas and excluding them from the human impact does not resolve the issue of biodiversity conservation. Many human activities related to land cultivation, such as livestock grazing or mowing, contribute significantly to biodiversity preservation (Bakker et al. 2002; Zahn et al. 2007; Humbert et al. 2012; Stalenga et al. 2016). Thus, it is extremely important to find a compromise between agriculture and biodiversity conservation.

1.2. Grasslands under human management

In addition to arable fields, grasslands are the main element of agricultural land, usually used as pastures or hay meadows providing fodder for farm animals. In terms of sustainability, they are divided into temporary grasslands, which include short-term grasslands and crops of legumes cultivated only for a certain period of time in order to rotate crops, and permanent ones, i.e. used for at least five years and often much longer (Reheul et al. 2007). In Poland, over 20% of the utilised agricultural area (UAA) is covered by permanent grasslands (Rozkrut 2017a). In the European Union, permanent grasslands cover more than 30% of the UAA, however, there are huge differences between individual countries ranging from one percent of the UAA in Finland or Cyprus to over 70% in Ireland (Reheul et al. 2007).

Grasslands develop in areas where prevailing environmental conditions are not conducive to the development of forest vegetation (e.g. they are too dry or too wet) or in places where this vegetation is destroyed by natural fires, herbivores or human activity (Ellenberg 1996; Vera 2000; Isselstein et al. 2005; Pärtel et al. 2005). Grasslands in the temperate zone exist mainly owing to haymaking and the grazing of domestic animals that have replaced wild ungulates as grazers (Pärtel et al. 2005). The natural process in this climate zone is the gradual encroachment of forest vegetation on the grasslands, hence continuous human interference, usually by livestock farming, is necessary to prevent their transformation into forests. European temperate grasslands are mostly classified as “semi-natural” ecosystems, which means that miscellaneous natural processes preventing the development of forest vegetation significantly contribute to their development, in addition to human interference (van Dijk 1991; Pärtel et al. 2005).

It is difficult to indicate the exact time when the grasslands came into existence in temperate Europe, but they certainly existed here continuously for millions of years (Pärtel et al. 2005). Semi-natural grasslands, which for many years have been an integral part of Europe’s agricultural landscape, are one of the most species-rich habitats, while also serving as refugia for many species of animals (Duelli & Obrist 2003). Both flora and fauna of semi-natural grasslands are very rich and a large number of species can be found even over a small area. For example, as many as 76 species of vascular plants per 1 m^2 were found in meadows of Estonia, which is one of the highest values in the world (Sammul et al. 2003). In general, the contribution of grasslands to the overall biodiversity in the agricultural landscape of Europe is enormous (Nösberger & Rodriguez 1996) and many species of plants and animals widespread in these environments are rarely found in other habitats (Prach 2008; Wesche et al. 2012). The co-occurrence of a large number of species in semi-natural grasslands is facilitated by traditional farming consisting of grazing, mowing and burning, which results in a favourable regular moderate disturbance in this ecosystem (Poschold & WallisDeVries 2002; Pärtel et al. 2005).

Unfortunately, mainly as a result of land abandonment on the one hand and the intensification of agricultural production on the other, the area of semi-natural grasslands in Europe has drastically decreased over the last few decades (Norderhaug 2000; Hodgson et al. 2005; Prach 2008; Krause et al. 2011; Wesche et al. 2012). Many grasslands have been converted into arable fields, reforested or used for various types of investments (Gellrich et al. 2007; Walz 2008; Krause et al. 2011). In Great Britain, for example, as much as 97% of semi-natural grasslands have disappeared after World War II (van Dijk 1991). In addition, a decline in biodiversity is observed in many existing grasslands. Plant species richness in some grasslands in Germany has decreased by 30–50% over 50 years starting from the turn of the 1950s and 1960s (Wesche et al. 2012). Hülber et al. (2017) reported a decline in the number of vascular plant species at 95 sites located in semi-natural grasslands in the Wienerwald Biosphere Reserve in Austria, ranging from an average of 43 in 1990/92 to 31 in 2011, even though preventive measures were taken. The decline in biodiversity in semi-natural grasslands, as it was said above, is mostly affected by the intensification of farming, which is manifested mainly by the application of fertilisers and increasing mowing frequency (Grevilliot et al. 1998; Janssens et al. 1998; Härdtle et al. 2006), however air pollution (Stevens et al. 2004) and urbanisation (Thompson & Jones 1999) are also important in this respect. Furthermore, considerable habitat fragmentation is a major threat to biodiversity in semi-natural grasslands as well. Many grasslands are now small patches located between areas transformed by man, such as crop fields or buildings, and are crossed by roads, railway lines etc. (Hanski & Ovaskainen 2000; Soons et al. 2005). Such small patches of habitats are very sensitive to negative environmental impact and are inhabited by relatively small populations of organisms, which reduces the possibility of colonisation of unoccupied habitat patches and the gene flow between already overgrown fragments. Unfortunately, this may result in the extinction of local populations (Soons et al. 2005). As a result of these unfavourable changes, many semi-natural grasslands have currently become the most threatened habitats in Europe (van Dijk 1991; Emanuelsson 2008; Prach 2008).

In grasslands, the cultivation procedure includes a range of pratotechnical activities carried out such as grazing, mowing, manuring, undersowing, harrowing, etc. However, the prevailing types of management in grasslands are grazing and mowing. Of these two agricultural practices, the impact of mowing on grassland assemblages is stronger than that of grazing, and the latter exerts a more positive effect on the conservation value (D'Aniello et al. 2011; Tälle et al. 2016). Extensive grazing may increase the species number by increasing the habitat diversity, i.e. formation of a mosaic of ungrazed and grazed places with varying plant heights (Bonte et al. 2000; Zahn et al. 2007). The impact of grazing on grassland organisms obviously depends on its intensity and the species of grazing animals, and the effect of these factors may vary depending on the group of organisms (Dennis et al. 2001; Lenoir & Lennartsson 2010; van Klink et al. 2016). Mowing has a much greater impact on grasslands and the strength of its influence is primarily determined by the way it is carried out, i.e. how often, when and the mode used (Nyffeler & Breene 1990; Thorbek & Bilde 2004; Humbert et al. 2010). Mowing at least once a year has a positive effect on, for example, plant species richness, especially when cuttings are removed (Bakker et al. 2002). In addition, combining one cut with grazing may have a positive effect on certain groups of organisms (Mazalová et al. 2015). However, frequent mowing usually has a negative impact on invertebrates, causing significant declines in abundance, density or diversity of certain groups like orthopterans, spiders, butterflies or some beetles (Nyffeler & Breene 1990; Thorbek & Bilde 2004; Humbert et al. 2010; Rada et al. 2014; Mazalová et al. 2015). Nevertheless, individual systematic and functional groups of invertebrates respond to mowing in different ways. For example, Birkhofer et al. (2015) showed that frequent cuts caused an increase in the number of predaceous and omnivorous ground beetles and a decrease in the number of herbivorous species. Usually, less mobile, flightless arthropods like spiders, opilionids or springtails, which cannot escape during mowing, are more exposed to its negative effects (Mazalová et al. 2015).

Given the remarkable nature conservation value of semi-natural grasslands and the role they play both in nature and the economy, their preservation and maintenance in good conditions is an urgent task for our society. In order to accomplish this task, detailed knowledge about the impact of different types of farming and pratotechnical practices on the assemblages of various grassland organisms is essential.

1.3. Biodiversity loss prevention in agricultural areas – agri-environment schemes

The designation of legally protected areas is undoubtedly one of the most effective ways of conserving biodiversity by protecting not only threatened and endangered species belonging to different groups, but also the entire ecosystems. However, effective biodiversity conservation must not solely be based on protected areas but should apply to all areas on our planet that are used in different ways, and this requires systematic measures based on a well-thought-out strategy (Margules & Pressey 2000). Particular attention in this respect should be paid to agricultural areas due to its huge contribution to the landscape structure. The dramatically deteriorating conditions of the natural environment as a result of agricultural intensification have imposed such actions as well as the introduction of systemic solutions in many countries. In Europe, agri-environment schemes (AESs) are the basic tool to serve this purpose. They were introduced in accordance with the Agricultural Structures Regulation of 1985 (European Union Regulation 1985). This act has reformed the EU agricultural policy and allowed the member states to pay national aid in environmentally sensitive areas to farmers and other landholders. In 1992, the European Union introduced agri-environment schemes under Regulation 2078/92 as compulsory for all member states, but voluntary for individual landowners. Similar schemes to those in force in the European Union have also been introduced in some European countries that are not EU member states, e.g. Norway and Switzerland. In Poland, AES called agri-environmental programme was implemented for the first time in 2004 as part of the Rural Development Programme (RDP 2007). The second edition of the agri-environmental programme was implemented in 2007–2013 and was extended until 2014. The third edition, called agri-environment-climate measures, started in 2015 and will end in 2020.

Agri-environment schemes are intended to encourage farmers to use environment-friendly farming practices that meet the requirements of agricultural production while minimising their negative impact on the environment. Financial compensation for the potential loss of profit resulting from the implementation of these measures is intended to provide an incentive for their implementation.

Agri-environment programmes vary considerably in different countries in Europe (Kleijn & Sutherland 2003). Their objectives reflect not only the most important environmental and ecological problems but also social and economic issues in a given country. For example, in Switzerland, the Netherlands and the United Kingdom of Great Britain, schemes available to farmers focused primarily on the protection of animal species and habitats. In France, the programme aimed at preventing land abandonment in agriculturally marginal areas. In Denmark and Germany, on the other hand, the schemes aimed at reducing agrochemical emissions. In Ireland and Austria, the objectives of the schemes addressed both biodiversity and landscape conservation.

A farmer joining the agri-environment programme may decide to implement a selected package and its variant and take actions required for its implementation. Practices aimed at minimising the environmental losses on grasslands include: reducing the number of cuts, delaying the first cut, leaving uncut grass fragments, the obligation to harvest hay or reducing fertilisation and livestock grazing.

The amounts of money spent on AESs are large and in many countries exceed the amounts allocated for wildlife protection by other methods (Batáry et al. 2015). Total financial expenditure on agri-environment payments in the EU in 2007–2013 was over EUR 30 billion. The total expenses executed on AES in Poland in this period was about EUR 2 billion (Batáry et al. 2015; ENRD 2018). Given the huge expenditure incurred under the agri-environment schemes, it is crucial to know to what extent they support the preservation of biodiversity. The benefits resulting from agri-environment schemes and the optimisation of related costs have been discussed for quite a long time (Kleijn & Sutherland 2003; Baylis et al. 2008; Burton & Schwarz 2013; Batáry et al. 2015). Research to determine the effectiveness of agri-environment schemes in preserving the biodiversity has started since their introduction (Kleijn & Sutherland 2003; Kleijn et al. 2006; Knop et al. 2006; Batáry et al. 2011; Batáry et al. 2015). Unfortunately, the results obtained are often ambiguous. Based on the literature review, Kleijn & Sutherland (2003) concluded that it is difficult to answer the question whether AESs are effective in conserving and promoting the biodiversity. The authors indicated that the response to agri-environment schemes differed between the analysed groups of organisms. While reviewing the studies conducted on arthropods, they showed that 11 out of 17 studies demonstrated a positive effect, three studies displayed positive and negative effects, and yet another three studies showed no effect of the schemes. In the case of birds, only four out of 19 studies demonstrated positive effects, two studies showed negative effects, and nine studies reported both positive and negative effects. In the case of plants, on the other hand, 11 out of 20 studies showed positive effects of agri-environment schemes, while two studies reported negative effects. Kleijn et al. (2006) studying the impact of AES on vascular plants, birds, bees, orthopterans and spiders in five European countries indicated that in all of them the programmes had minor to moderately positive effects on the biodiversity. The most pronounced positive effects were found for plants, as their increased densities were noticed on AES plots in all countries compared to control plots. In the case of spiders, significantly higher densities on AES plots were found only in Spain.

Scientists have been trying to investigate the causes of mixed effects of AESs on biodiversity. In their meta-analysis, Batáry et al. (2011) indicated that studies of AES impact on plant and animal species richness should take not only agricultural practices into account, but also the structure of the landscape surrounding the experimental plots. The authors showed that agri-environment schemes were effective in simplified landscapes, but not in the complex ones.

In the context of the ambiguous effects of AESs in biodiversity conservation, discussions are increasingly focusing on agri-environment schemes based on the results achieved (result-oriented agri-environment schemes) (Burton & Schwarz 2013; Moxey & White 2014; de Sainte Marie 2014). In such programmes, farmers are not paid for the mere application of environmentally friendly measures (e.g. delayed mowing or reduced fertilisation), but for achieving specific results. These may include, for example, the protection and support for threatened and endangered species, or the preservation of specific species composition of the particular group of organisms.

The results of many surveys indicate that agri-environment programmes and the related system of subsidies for farmers should be adapted to special needs, particular regions, landscape type and agricultural economy that dominates in a given area, as well as organisms to be protected (Schmitzberger et al. 2005; Batáry et al. 2011). That is why it is extremely important to carry out research in various regions with different farming methods, which will enable us to prepare recommendations for appropriate agrotechnical and pratotechnical measures adapted to specific needs of biodiversity conservation in the area, on a local scale.

It is obvious that scientists see the need to conduct regular surveys monitoring the effects of AES on the natural environment and individual groups of organisms, including spiders. This group of animals is often used as a model in this type of research, which for many years has been carried out in the European countries (Kleijn et al. 2006; Knop et al. 2006; Concepción et al. 2012; Buri et al. 2016). Unfortunately, no such studies have been conducted in Poland and the presented book is the first one on this subject.

1.4. Spiders as a research model

Spiders (order Araneae) belong to the phylum Arthropoda and together with harvestmen, mites, pseudoscorpions and other closely related groups form the class Arachnida. At present, there are almost 48,000 spider species described from all over the world (World Spider Catalog 2018), and more than 800 species have so far been recorded in Poland (Kupryjanowicz 2008; Rozwałka & Stańska 2008; Nentwig et al. 2018). Spiders are ubiquitous and abundant organisms inhabiting all the continents (except the Antarctic) and almost all habitats and climate zones on Earth (Wise 1993). They are generalist feeders and the majority of them are strictly carnivorous (Wise 1993; Pekár et al. 2012). Spiders belong to the polyphagous group feeding on a wide range of prey and their diet consists mostly of arthropods (including spiders), especially insects such as springtails, dipterans or true bugs (Nentwig 1987; Nyffeler 1999; Pekár et al. 2012). The diet of spiders living in agrocenoses largely consists of various species of dipterans, aphids or other insects that are pests to cultivated plants. Spiders can not only reduce the abundance of harmful organisms but also prevent their rapid increase. Thereby, they play an important role in natural protection against crop plant pests (Marc et al. 1999; Nyffeler & Sunderland 2003). Moreover, Marc & Canard (1997) proved that the preservation of the diversity of spiders in agroecosystems may not only increase their efficiency against one particular pest but also lead to the capture of more pest species, therefore mitigating overall crop damage and serve as an effective pest control tool.

Spiders are abundant in almost all terrestrial ecosystems, including permanent grasslands which are the subject of this study. For example, de Keer & Maelfait (1987, 1988) reported, based on their research conducted in Belgium, that the maximum density of *Oedothorax fuscus*, spider belonging to the family *Linyphiidae*, on intensively grazed pastures reached 150 individuals/m^2, and densities of *Erigone* species from the same family, were even above 300 individuals/m^2. Research conducted in Poland does not confirm such high densities, but Kajak (1978) in her research carried out in meadows reported spider densities reaching over 70 individuals/m^2.

Spiders, although numerous in many ecosystems are extremely sensitive to changes in the parameters of their habitats, such as temperature, humidity, wind, insolation, vegetation structure, the food supply, the presence of competitors and enemies (Wise 1993). For that reason, they are often used as bioindicators of changes occurring in the environment, resulting both from natural processes such as succession (Haase & Balkenhol 2015) or human activity (Maelfait & Hendrickx 1998; Rypstra et al. 1999; Pearce & Venier 2006; Diehl et al. 2013). Spider assemblages are particularly sensitive to disturbances in the spatial structure of their habitats (Uetz 1991; Duffey 1993; Bell et al. 2001). Such alterations occur as a result of numerous agricultural practices carried out in agrocenoses, especially those involving agricultural machinery, such as ploughing, harrowing or harvesting. In the case of grasslands, mowing is the commonly used treatment that completely modifies the habitat structure. This practice often negatively affects spider assemblages, causing their abundance, density and species richness to decrease (Nyffeler & Breene 1990; Baines et al. 1998; Polchaninova 2003; Thorbek & Bilde 2004; Mazalová et al. 2015). Different elements make up the mowing effect, including one of the most important ones, i.e. changes in the habitat structure. This results not only from the alteration of the vegetation structure (i.e. the reduced height of plants) caused by mowing but also from the soil damage induced by machines during the operation and during hay transportation. Such a drastic transformation of the living space may also translate into a reduction of food resources available for spiders (including the abundance of springtails that are the basic food for many spider species), the possibility of constructing webs, as well as the loss of places where spiders reproduce, hide, overwinter or spread through ballooning (Purvis & Curry 1981; Robinson 1981; Uetz 1991; Wise 1993). Furthermore, the change in the habitat structure has a significant impact on such factors as temperature, moisture or the presence of predators and competitors (Guido & Gianelle 2001; Gardiner & Hassall 2009). Moreover, other agricultural practices carried out on grasslands, such as fertilisation, the use of herbicides, burning or livestock grazing are also important for spider assemblages (Bell et al. 2001; Andrey et al. 2014).

As evidenced by a number of studies, epigeic spiders are very sensitive to changes occurring in the habitat under the influence of agricultural practices. Due to their dynamic response to any transformations, they are used as an important model group to assess the impact of management regimes in meadow habitats (e.g. Polchaninova 2003; Knop et al. 2006; Schmidt et al. 2008; Batáry et al. 2012; Buri et al. 2016; Lessard-Therrien et al. 2018).

1.5. Research assumptions and hypotheses

The main objective of this study was to investigate how different management regimes implemented in semi-natural mesic meadows, used as hay meadows, affect assemblages of epigeic spiders. Differences in the use of meadows were mainly due to different mowing regimes (varying number of cuts, different timing of the first cut, leaving or not leaving unmown fragments of meadows). The study plots were located in hay meadows where four different management regimes have been implemented: one of them involves a conventional use, i.e. a traditional agricultural method applied in the surveyed region, with no restrictions imposed, while the three other regimes were based on applied agri-environment packages and their variants, which differed in terms of the number of cuts and the timing of the first cut. Such a selection of management regimes made it possible, firstly, to check whether the set of treatments applied under the framework of agri-environment packages is effective in biodiversity preservation, and secondly, to compare the effectiveness of each package.

By assumption, the presented research was not based on an experiment and was carried out in the realities of typical farming for the Lublin region. The timing and the number of cuts, the method of mowing and other agricultural treatments were not agreed with farmers using meadows. The only requirements adopted by the farmers were those resulting from an implemented agri-environment package.

The fact that the Lublin region is an area with the complex structure of the landscape, where extensive farming predominates, was not without significance. In the case of intensively used agricultural areas situated in the simplified landscape, it can be assumed with high probability that imposing certain restrictions on the implementation of specific agricultural treatments brings tangible effects in maintaining high biodiversity (Bengtsson et al. 2005; Batáry et al. 2011). However, it is interesting whether the introduction of such restrictions, through the implementation of agri-environment packages in areas where extensive agriculture dominates, will produce positive results. The results of the previous studies do not provide a clear answer to the question about the effect of such actions (Knop et al. 2006), which was one of the reasons for undertaking this research.

The second important premise which was encouraging to deal with this subject was the fact that even though the research assessing the effectiveness of agri-environment schemes is conducted relatively often in Europe, it is extremely rarely undertaken in Poland. Furthermore, given the fact that the effectiveness of agri-environment schemes may vary depending on the taxonomic groups and landscape composition (Batáry et al. 2011), it is very important to carry out several studies involving different model groups and areas with varying structure and farming intensity. This will allow the selection of requirements imposed by agri-environment packages for the use of hay meadows, which could be tailored to both groups of organisms that we want to protect as well as to a specific place where this protection is to be applied. This study is the first attempt to compare and assess the effectiveness of the agri-environment programme in Poland based on the fauna of spiders occurring in meadows in an area where extensive farming prevails.

The impact of meadow use on spiders was assessed on the basis of comparison of parameters, such as abundance, species richness and species diversity of their assemblages. The study also included the analysis of abundance and species richness of selected families and functional groups (guilds) and rare species. This resulted from the fact that individual taxonomic and functional groups of spiders have different requirements in terms of ecological niches, different hunting strategies, different dispersal methods, as well as from the fact that their maximum abundance occurs at different times.

Consequently, individual groups of spiders can respond differently to agricultural treatments implemented in meadows.

The first part of analyses involved checking how the parameters mentioned above respond to different management regimes (taking into account different periods of meadow use in the year, i.e. from May to the end of August). Their objective was to investigate which management regime is the most beneficial for preserving high abundance and biodiversity, and thus to check whether implementation of agri-environment programme brings notable effects. The second part of analyses was to assess the direct impact of mowing on spider assemblages, based on a comparison of the above-mentioned parameters. These analyses were performed regardless of the management regime implemented in the studied meadows, independently for the three research periods. Unmown meadows were compared with meadows that were already mown. In the case of the last two periods, also timing was taken into account what was intended to enable a possible assessment whether the impact of mowing on spider assemblages is short- or long-term.

Another important objective of this study was to develop recommendations for agricultural management on how to use hay meadows in order to preserve rich fauna of spiders, which is extremely important to agricultural ecosystems, given the huge role of spiders in pest control (Marc & Canard 1997; Nyffeler & Sunderland 2003; Chatterjee et al. 2009). The obtained results should also be useful in assessing the effectiveness of the agri-environment programme, and thus the usefulness of their implementation, especially in areas where extensive farming predominates.

The following hypotheses were tested:

1) The management regime has a significant impact on epigeic spider assemblages. The abundance, species richness and species diversity will be significantly higher in those management regimes where management intensity is lower – fewer cuts and the first cut is carried out later in the growing season. Therefore, these parameters will be lower in conventionally used meadows compared to meadows under agri-environment packages. This will also apply to abundance and species richness of particular families and guilds of spiders. Meadows included in the agri-environment programme will also favour a larger number of rare species, due to the lower

intensity of use. The number of individuals and the number of rare species will be here higher compared to conventional meadows.

2) Mowing will have a negative impact on spider assemblages. Abundance, species richness and species diversity will be lower in mown meadows compared to meadows that were not mown within the same time frame. Species richness and abundance of particular spider families and guilds will be lower in mown meadows, similarly to the species richness and abundance of rare species.

2. STUDY AREA

2.1. Lublin Province

The research was carried out in the Lublin province (E Poland) in the area of seven districts: Biała Podlaska district, Chełm district, Włodawa district, Lubartów district, Parczew district, Puławy district and Ryki district.

The province covers an area of over 25,000 km^2 and is the third largest province and one of the least populated regions in Poland (85 people/km^2, while the average population density in the country is 123 people/km^2) (Rozkrut 2017b). It is also one of the least developed and poorest regions in the country. The Gross Domestic Product (GDP) per capita in 2016 was PLN 33,349, which is only 68.9% of the national average (Central Statistical Office 2017).

Agricultural land dominates in the Lublin province and accounts for almost 71% of the region's total area, which is the highest value in Poland (Rozkrut 2017a; Ściborek-Rycyk 2017). In 2017, permanent meadows covered 249,124 ha and permanent pastures 74,338 ha, which accounts for 9.9% and 3.0% of the total area of the Lublin province, respectively (Rozkrut 2017a). Small farms with an area ranging from 1 to 10 ha predominate and constitute as much as 80.2% of all farms; the average size of a farm (individual agricultural holding) is 8.0 ha (Ściborek-Rycyk 2017). Cereals (33.3%) and fruit (23.6%) contribute the most to the crop production in the Lublin province (Ściborek-Rycyk 2017). The province is the national leader in the production of soft fruit and hops (Suszek et al. 2014).

The region has a temperate continental climate, more humid in the north-eastern part and drier in the south-western part. The average annual temperature in 2015 was 9.5ºC and the total annual precipitation is 476 mm on average. The growing season lasts for 205–210 days (Jakubowski et al. 2017).

The Lublin Province is characterised by high biodiversity and considerable landscape heterogeneity, which makes it one of the most valuable regions in Poland in terms of nature. The nature conservation values of this region are determined both by its physiographic diversity and extensive farming prevailing over most of its area (Jakubowski et al. 2017). The most valuable ecosystems are found in the valleys of large rivers: the Vistula, the Bug and the Wieprz which serve as ecological corridors. Large wetland areas in the Łęczna-Włodawa Lakeland, alkaline fens near the town of Chełm and large forest complexes such as the Solska Forest, Janów Forests, Włodawa Forests or Parczew Forests also represent a significant natural value (Jakubowski et al. 2017). Many areas in the Lublin Province are legally protected, e.g. two national parks (Polesie NP and Roztocze NP), 16 landscape parks, 17 protected landscape areas, 86 nature reserves, as well as areas included in the Natura 2000 network – 23 Special Protection Areas (SPAs) for birds and 101 Special Areas of Conservation (SACs). Altogether, legally protected areas of special nature conservation values account for 22.7% of the province's total area (CRFOP 2016; Hrytsuk 2018).

2.2. Mesic meadows

The research was carried out on semi-natural mesic meadows, which are valuable habitats in terms of nature and very productive permanent grasslands (Kucharski & Perzanowska 2004). These communities of anthropogenic origin, occurring in lowland areas and in lower mountain locations, usually replace felled broad-leaved forests (Kucharski & Perzanowska 2004). They are quite widespread in Poland, however, as indicated by monitoring studies, the state of their preservation is not satisfactory (Stalenga et al. 2016). As in the case of many other types of grasslands, their occurrence is closely associated with traditional farming. Unfortunately, the intensification of farming practices (e.g. an increase in the number of cuts and the level of fertilization) contributes to the disappearance of a characteristic species combination and a considerable floristic simplification of these phytocoenoses in many places, as well as the development of floristically poor subassociations or variants with characteristics of agrocenoses (Grynia 1996; Kucharski 1999; Bator 2005; Kryszak et al. 2006; Kryszak & Kryszak 2007).

According to phytosociological classification, mesic meadows belong to the class of *Molinio-Arrhenatheretea* R. Tx. 1937 and the order of *Arrhenatheretalia* Pawł. 1928 (Wysocki & Sikorski 2002; Kucharski

& Perzanowska 2004; Matuszkiewicz 2008). They develop on the potential habitat of oak-hornbeam forests (*Carpinion betuli*), while in river valleys – on the driest riparian habitats (*Ficario-Ulmetum*) (Kucharski & Perzanowska 2004). Mesic meadows usually develop in flat or low gradient areas with varying exposure, on meso- and eutrophic mineral and mineral-organic soils or on dry mineralized amorphous peat (Matuszkiewicz 2008; Korzeniak 2012). In river valleys, lowland mesic meadows often occur in a mosaic with other types of floristically corresponding meadows and grasslands. The groundwater level in mesic meadows varies, but never reaches the ground surface, while meadows in river valleys may occasionally be inundated (Kucharski & Perzanowska 2004).

Mesic meadows (*Arrhenatherion*) are floristically diverse and their species and quantitative composition as well as the structure and physiognomy change with the increase or decrease in soil fertility and the frequency of mowing and grazing (Kucharski & Perzanowska 2004; Korzeniak 2012; Stalenga et al. 2016). In the surveyed meadows the dominant plant species were sod grasses, mainly tall oat-grass (*Arrhenatherum elatius* (L.) P.Beauv. ex J.Presl & C.Presl.) and orchard grass (*Dactylis glomerata* L.), forming the highest layer of sward (Fig. 1). Grasses were accompanied by a large group of dicotyledon plants. In typically developed vegetation patches, the higher layer was usually formed by plants from the *Apiaceae* family, such as common hogweed (*Heracleum sphondylium* L.) and wild carrot (*Daucus carota* L.), as well as field scabious (*Knautia arvensis* (L.) J.M. Coult.) and goat’s beard (*Tragopogon orientalis* L.). In the lower layer, species from the legume family (*Fabaceae*) occurred: common bird’s-foot trefoil (*Lotus corniculatus* L.), lesser trefoil (*Trifolium dubium* Sibth.), red clover (*T. pratense* L.), white clover (*T. repens* L.) as well as species characteristic of mesic meadows, e.g. common yarrow (*Achillea millefolium* L.), oxeye daisy (*Leucanthemum vulgare* Lam.), spreading bellflower (*Campanula patula* L.). The moss layer was poorly developed.

Fig. 1. Extensively used mesic meadow (*Arrhenatherion*) included in the agri-environment programme – Package 3 (photo by Kamila Brzezińska)

2.3. Study plots

Four groups of meadows (in four management regimes) were selected for the study, with eight study plots in each of them (32 plots in total). Their location is shown in Fig. 2. The spider material was collected in the aforementioned plots in years 2013–2015, but in the case of some plots, not all the years were included into analyses (see explanation in Methods: Collection of spiders).

All the study plots were located in a fragmented, typically agricultural landscape, consisting of a mosaic of meadows, fields and forests, with only a small contribution of such elements as rural development or roads (Table 1; Fig. 3). The contribution of each landscape class and the total number of patches representing each of these class situated near the study plots was similar in all management regimes (Table 1). The area of meadows where the study plots were located was also similar for all the management regimes (Table 1).

The first group of meadows comprises extensively used conventional meadows, which were not included in the agri-environment programme. The remaining groups are meadows contained within different agri-environment packages and their variants under the agri-environment programme for 2007-2013 (Regulation of the Minister of Agriculture and Rural Development 2009, 2013) and later used according to the same rules as those in the programme. All these packages had the following common requirements, e.g.:

- leaving 5–10% of the total area of an agricultural plot unmown, each year it should concern another part of this plot;
- mowing at a height of 5–15 cm;
- no ploughing, rolling or reseeding;
- no harrowing in the period from 1 April to 1 September;
- no plant protection products, except for selective and local weed control using relevant equipment (e.g. herbicide daubers);
- no liming, unless liming does not adversely affect the implemented objective of the scheme;
- no fertilization; in areas other than those fertilized by alluvial deposits, nitrogen fertilization is allowed and the maximum nitrogen dose of 60 kg/ha is not to be exceeded in a given year;
- removal or stacking of the cut biomass within no more than two weeks after mowing or, in justified cases, within a longer period of time, as soon the reasons for the failure to comply with this deadline no longer exist.

Specific groups of meadows differed from each other in the management regime, the mowing system in particular (i.e. the number and the time of cuts made, Figs. 4, 5), as well as other agricultural operations carried out. Detailed differences in the management regimes of particular groups of studied meadows are presented below:

(1) Extensively used conventional meadows (hereinafter referred to as **C-meadows** or **conventional meadows**) were mown once to three times a year. The number of cuts carried out was the highest among all the management types and was 1.8 on average - for the period in which the spider material was collected (Fig. 4). The first cut was made from the third decade of May to the third decade of June (Fig. 5), while the

second cut took place from the third decade of July. The third cut during the material collection was made in only one plot at the end of the second decade of August 2013. The grass was mown over the entire meadow using a rotary mower. Occasionally, small amounts of cattle were grazed in the plots, but this took place outside the period when spiders were caught, i.e. in September or October. A small amount of mineral or organic fertilizers was applied in six plots. During the period of spider collecting, no other agricultural treatments (such as ploughing, reseeding with grass, rolling, liming, harrowing or pulverizing) were carried out in meadows, however, in the period before the beginning of the research, i.e. before 2013, some meadows were harrowed (three plots) or rolled (two plots) once every few years.

(2) Meadows included in Package 3. Extensive permanent grasslands (hereinafter referred to as **E-meadows** or **meadows in extensive package**).

The aim of this package is to protect or preserve the natural values of permanent grasslands. According to the requirements of the package, mowing is allowed here from 1 June to 30 September, with no more than two cuts per year. In the study plots included in this package, one or two cuts were made per year, however, taking into account the cuts made only during the time when the spider material was collected, it was zero to two cuts (Fig. 4). The date of the first cut varied in the study plots. Although one of the plots was mown already in the first decade of June, there were also those where the first cut was made only in September, i.e. after the material was collected (Fig. 5). The second cut was carried out starting from early August. All cuts were made using a rotary mower.

(3) Meadows included in Package 4. Protection of endangered bird species and natural habitats outside Natura 2000 areas or Package 5. Protection of endangered bird species and natural habitats in Natura 2000 areas (variants 4.1 and 5.1 Protection of bird breeding habitats) (hereinafter referred to as **B-meadows** or **meadows in bird variant**).

These two variants are primarily aimed at protecting birds and their habitats, and mowing is allowed from 1 August to 30 September. No agricultural treatments are allowed in the meadows covered by these variants in the period from 1 April to 1 August. In the surveyed plots under these variants, only one cut per year was made, however, taking the cuts made only during spider sampling into account, it was zero or one cut and the average number of cuts was the smallest of all management types (Fig. 4). The first cut at most of the plots took place in August, and at the remaining cases in September, after the spider material was collected (Fig. 5). All cuts were carried out using a rotary mower.

(4) Meadows included in Package 4. Protection of endangered bird species and natural habitats outside Natura 2000 areas or Package 5. Protection of endangered bird species and natural habitats in Natura 2000 areas (variants 4.7 and 5.7 Semi-natural mesic meadows) (hereinafter referred to as **H-meadows** or **meadows in habitat variant**).

The objective of the two aforementioned variants is to preserve the natural values of semi-natural mesic meadows, and mowing can be carried out here from 15 June to 30 September in a non-destructive way to sward and soil cover, with no more than two cuts per year. In the study plots under these variants, one or two cuts per year were made, while during the collection of spiders it was zero to two cuts (Fig. 4). In most cases, the first cut was made in mid-June (Fig. 5). The second cut was carried out from mid-July. All cuts were made using a rotary mower.

Table 1. Area of meadows where the study plots were located and characteristics of their surroundings (in a circle of 1 km^2) in relation to four management regimes. Particular parameters were compared using one-way ANOVA (see Methods). The mean (± standard deviation), *F*-values and *P*-values are presented

	C-meadows	**E-meadows**	**B-meadows**	**H-meadows**	***F***	***P***
Area of studied meadow (ha)	3.7 ± 2.08	2.6 ± 2.91	1.5 ± 0.94	2.1 ± 2.49	1.52	0.232
Meadow cover (%)	35.2 ± 14.09	46.4 ± 24.51	58.0 ± 11.18	48.2 ± 10.64	2.72	0.064
Field cover (%)	33.0 ± 27.05	27.1 ± 11.86	18.8 ± 14.37	25.6 ± 10.69	0.92	0.444
Forest cover (%)	20.2 ± 17.00	16.6 ± 17.40	15.2 ± 8.75	15.1 ± 15.77	0.19	0.900
Urban area cover (%)	2.7 ± 2.10	2.1 ± 2.02	2.9 ± 2.21	2.2 ± 3.02	0.22	0.879
No of patches	77.4 ± 20.85	92.6 ± 46.43	82.0 ± 23.86	99.4 ± 35.71	0.72	0.548

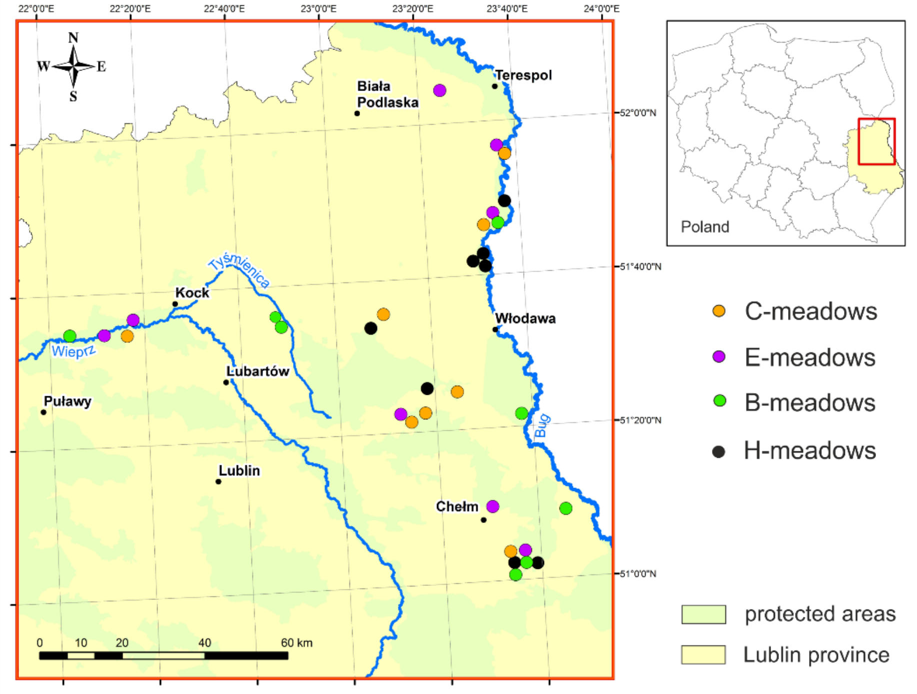

Fig. 2. Location of study plots

Fig. 3. Example of the study plot location; the yellow circle marks the area of 1 km^2 where the landscape structure was compared between meadows under four management regimes, green point marks the middle of three pitfall traps collecting spiders

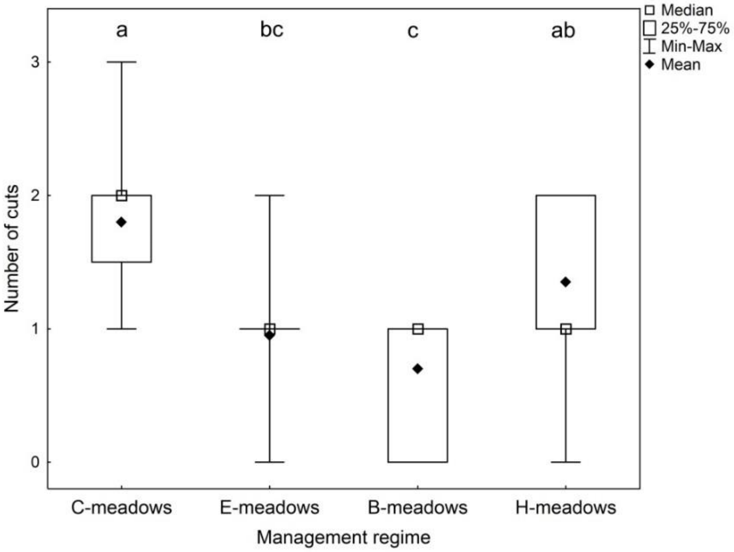

Fig. 4. Number of cuts carried out in the plots during the research season (i.e. when spiders were collected) in relation to meadow management regime. Statistically significant differences between management regimes were found (Kruskal-Wallis test $H_{3,80} = 32.69$, $P < 0.001$). Different letters above the bars indicate significant differences between management regimes (Dunn post hoc test: $P < 0.03$)

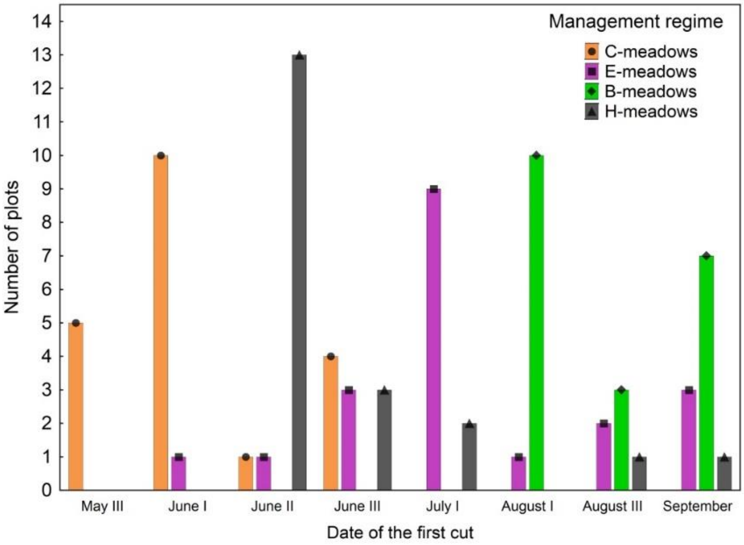

Fig. 5. Date of the first cut in study plots during the research in relation to the management regime. The Roman numerals next to the months' names indicate the decades. Cuts in September were carried out after the spider material collection in a given year

3. METHODS

3.1. Collection of spiders

Epigeic spiders were used as a model in this study. They were collected using pitfall traps. This method is probably the most commonly used trapping method in faunistic and ecological research of active invertebrates living on the soil surface and in low vegetation (Ausden & Drake 2006). It is a quick and easy method of catching a very large number of specimens (Gotelli & Colwell 2001; Brown & Matthews 2016). The resulting catches were used to describe phenology, to estimate abundance and to compare species assemblages (Topping & Sunderland 1992; Gotelli & Colwell 2001). Pitfall traps are a satisfactory method used to compare biodiversity, often focusing on species richness and assemblage distribution patterns (Southwood & Henderson 2000; Gotelli & Colwell 2001; Lange et al. 2011). However, the results obtained with this method should be properly interpreted. As in the case of other active trapping techniques, catches reflect relative activity and susceptibility to trapping, rather than a relative abundance of various species (Topping & Sunderland 1992). Pitfall traps can be used to generate an estimate of "activity-density", which means the abundance of each species as a reflection of its activity during the sampling period and the population density in the sampled habitat (Brown & Matthews 2016). More mobile species can be caught in larger numbers, therefore their contribution in the collected material may exceed their actual contribution in a given assemblage. However, despite some disadvantages, pitfall trapping is the best method to study the fauna of many invertebrate groups, including spiders (Topping & Sunderland 1992; Lange et al. 2011; Brown & Matthews 2016).

Plastic cups (diameter: 84 cm, volume: 330 ml) were used in this study as traps. Each trap was filled to one-third of its volume with a propylene glycol solution as a preservative and a detergent was added to reduce surface tension and to prevent the spiders from escaping (Topping & Luff 1995). The containers were level with the surface of the ground and were covered with rooves approximately 3 cm over the trap to protect from rain and falling of small vertebrates. Three pitfall traps were installed in each study plot along a straight line every 10 m. Pitfall traps were placed at least 20 m from the edge of the meadow in order to avoid "the edge effect" (i.e. to avoid collecting spiders in the ecotone zone) (Stańska et al. 2016).

Every year, samples were collected four times in each study plot from mid-May (the first trap setting on 11 May) until early September (the last trap collection on 2 September). Trap setting dates were similar in each survey year and on each plot. Small differences (of a few days) resulted mainly from unfavourable weather conditions, organizational capacity and pratotechnical treatments (i.e. mowing and hay harvesting). The exposure time of traps during one sampling period was two weeks on each plot (13.6 days on average in every management type). The material collection was organized in such a way to avoid the mowing intervention when traps on particular study plots operated. The first sample was collected from the second decade of May to early June before the meadows were mown for the first time. The second sample was collected from mid-June to the end of the first decade of July when most of the conventional meadows and meadows in the habitat variant were mown (Fig. 5). The third sample was collected between mid-July and the end of July, when the first cut was also carried out in most of the extensive meadows (Fig. 5) and the second cut was already made in some of the conventional meadows and meadows in the habitat variant. The fourth sample was collected in the second decade of August to early September when half of the meadows in the bird variant were also mown (Fig. 5) and the second cut was also made in some of the extensive meadows, in addition to the above-mentioned management regimes. In the next part of this study, periods of the material collection are referred to as the first, second, third and fourth sampling period.

It was not possible to collect the complete material in each plot every year due to the fact that some of the traps were destroyed by animals (mainly wild boars) and weather conditions (rainfall and consequently an inundation of traps). When the destruction was significant, especially when it occurred in the first or second sampling period, i.e. when the number of spiders was large, such plots were not included in the analysis for a given year. This kind of situation occurred four times for each management type. If the destruction occurred only in the third (one case) or fourth (three cases) sampling period, the material from that period was excluded from the analysis but not the entire plot. A total of 316 samples were collected during three years of the survey: 80 samples both in the first and second sampling periods, 79 – in the third period and 77 – in the fourth period.

3.2. Identification and classification of spider species

The material collected by pitfall traps was sorted in the laboratory and the spiders were selected and identified. Spider nomenclature was used according to the World Spider Catalog (2018). Following the identification to the species level, spider species were classified into seven guilds according to Cardoso et al. (2011): ground hunters, ambush hunters, orb web weavers, sheet web weavers, space web weavers, specialists and other hunters. The above division was based mostly on the foraging strategy. The actively hunting spiders living on the ground were included into the guild of ground hunters, whereas to ambush hunters belong spiders waiting for their prey. The guilds of orb web weavers, sheet web weavers and space web weavers were distinguished based on the shape of capture web the spiders produce. The specialists' guild is a cluster of species that specialize in one or very few prey. To the other hunters belong active hunters, which do not construct the capture webs and which were not classified to the other guilds. The affiliation of particular species to the guilds is presented in the Appendix.

In addition, some of the species were identified as rare species (see Appendix). Rare species were defined as those included on the "Red list of threatened animals in Poland" (Staręga et al. 2002) as well as those known from less than 20 localities in the country.

3.3. Data analysis

Due to the fact that some species of spiders are easy to determine on the basis of juveniles, while in the case of others it is very difficult, in all analyses only adult individuals were included. Such attitude allowed to avoid over-representation of species whose juveniles were easily identifiable.

The material collected from three pitfall traps installed in a given plot in one sampling period was pooled and considered as one sample. A different procedure was undertaken in case of rare species analyses where one sample included pooled data from each plot from the whole year. This solution was imposed by the small abundance of rare species in particular sampling periods.

The following parameters characterising the spider assemblages were determined for each sample:

- abundance – the number of adult individuals found in a given sample; this is a resultant of the activity of a specific spider species and its density in the habitat, for the purpose of simplicity hereinafter referred to as "abundance";
- species richness – the number of species found in a sample based on the number of adults;
- species diversity – expressed by the Shannon-Wiener index, calculated according to the formula:
  $H' = - \Sigma p_i \ln p_i$
  where p_i is the proportion of individuals belonging to the *i*th species.
- the number of spider families;
- abundance of the three most numerous families: *Lycosidae*, *Linyphiidae* and *Tetragnathidae*
- species richness of the two largest families: *Lycosidae* and *Linyphiidae*;
- abundance of the four most numerous gilds: ground hunters, sheet web weavers, ambush hunters and other hunters;
- species richness of the two largest species guilds: ground hunters and other hunters;
- abundance of rare species – the pooled number of individuals representing species classified as rare (see Appendix);
- the number of rare species – the pooled number of species classified as rare (see Appendix).

Influence of management regime

Generalized linear mixed models (GLMMs) were used to assess how the management regimes affected spider assemblages in meadows (Bolker et al. 2009). Separate models were built for each of the above parameters, which were considered dependent variables. In each case, the "management regime" (four types of different management regimes) and the "sampling period" (four two-week material collection periods) were treated as fixed categorical explanatory variables. The models also included interactions between “management regime” and “sampling period” to reveal potential differences between management regimes in particular sampling periods. Moreover, in the case of GLMMs assessing the relationship between the variables and species richness, the log-transformed “number of individuals” was included as a continuous explanatory variable to check whether the number of captured species could also be explained by differences in the number of collected individuals. In the case of the number of rare species and number of individuals of rare species, the analyses were done based on pooled data from the whole year and “management regime” was included as only fixed categorical explanatory variable. The year and plot identity were included as random variables because data were collected several times from the same plots (four samples per year and three years of the study) and treated as repeated measures.

Before the analyses, the distribution of dependent variables was checked and the corresponding error distribution and the link function were used in the applied GLMMs (Gaussian error distribution with the identity-link function or Poisson error distribution and log-link function). In all GLMMs with significant results, paired contrasts were calculated to find statistically significant differences between the levels of categorical explanatory variables. The results with $P < 0.05$ were considered as statistically significant. The presented graphs illustrate only statistically significant results, presenting mean values with 95% confidence intervals. The captions for each table with the GLMM results are presented with the applied error distribution and the link function.

Effect of mowing

The GLMMs were also used to test the direct effect of mowing on spiders. These analyses were performed for most of the above-mentioned parameters of spider assemblages (the guild of ambush hunters was excluded from the analysis due to low abundance in the late summer), but separately for each sampling period, except for the first one, as at that time none of the plots had yet been mown.

In each GLMM, the “mowing effect” was treated as a fixed categorical explanatory variable but levels of this variable varied in each of the three sampling periods. In the second sampling period, two categories of meadows were distinguished: meadows not yet mown (“unmown”) and meadows where the first cut was already made (“mown”). In the third sampling period, three categories of meadows were distinguished: meadows not yet mown (“unmown”), meadows mown no more than four weeks before material collection (“S-mown”) and meadows mown more than four weeks before material collection (“L-mown”). During this period, some of the meadows were already mown twice, but they were not distinguished as a separate category, because there were only a few of them. In the fourth period, four groups of meadows were distinguished: meadows not yet mown (“unmown”), meadows mown no more than five weeks before material collection (“S-mown”), meadows mown more than five weeks before material collection (“L-mown”) and meadows mown twice (regardless of when the cut was made; “T-mown”). These categories of meadows were distinguished in particular sampling periods to ensure an appropriate number of individual levels of fixed categorical explanatory variables. In these analyses, the plot identity and year were included as random variables as well.

Most of the GLMMs were performed with the Gaussian error distribution and the identity link function. Before the analysis, some response variables were log-transformed to approach the normal distribution. In the case of rare species, the GLMMs with a binomial error distribution and logit-link function were used. It was due to low abundances of individuals belonging to rare species (many samples contained 0 or only 1 individual). The presence of individuals from rare species was coded as a binary response variable, with 0 indicating no individuals in a sample and 1 indicating at least one individual in a sample.

In all GLMMs with significant results, paired contrasts were calculated to find statistically significant differences between the levels (if more than two) of categorical explanatory variables. The results with $P < 0.05$ were considered as statistically significant. For better clarity, the graphs show all the results, presenting the means with the 95% confidence intervals.

Species composition

To relate the spider species composition to the meadow management and the mowing effect, the redundancy analysis (RDA) was used, which is a constrained linear ordination method. The analyses were performed in CANOCO for Windows 4.5 (ter Braak & Šmilauer 1998). When analysing the relationship between the species composition and the management regime, the material collected in a given plot during one year (pooled data from four sampling periods) was treated as a sample. In the case of studying the influence of mowing effect on species composition, the analyses were performed for three sampling periods: second, third and fourth. The first period was excluded from the analysis because the meadows were not mown at that time. Inter-species correlations were applied, species scores were divided by standard deviation and species were centred (Lepš & Šmilauer 2003). Statistical significance of the ordinations was assessed via the Monte Carlo Permutation tests (999 permutations, full model).

Surrounding of study plots

In addition to farming management, the structural diversity of the surrounding landscape may also have a major impact on the araneofauna of meadows (Batáry et al. 2011; Gallé et al. 2011). Therefore, meadows under different management regimes were compared in terms of the composition of landscape variables in order to check if the landscape structure around the study plots did not differ.

The landscape analysis was carried out based on orthophotomaps generated by mathematical transformation of an aerial image into mapform. The maps based on photos taken in 2012 were received from the Main Geodesic and Cartographic Documentation Centre in Warsaw. Such vector-based GIS maps were used to perform landscape analyses using ArcGIS 10.4.1 (ESRI Inc.). A circle of 1 km^2 (100 ha; the radius of approx. 564 m) was created for each study plot, placing the middle of three pitfall traps in its centre. Previous studies indicate that a radius of 500 m is large enough to describe the landscape relevant to spider dispersal (e.g. Clough et al. 2005; Schmidt & Tscharntke 2005; Concepción et al. 2012). The percentage contribution of each landscape element (class) – 1) meadows, 2) fields, 3) forests, and 4) urban elements (buildings, roads etc.) – was calculated for each circle designated around the study plots. In addition, the total number of patches per each class was calculated, which reflects the degree of landscape fragmentation. The area of meadows with the study plots was also calculated. Meadows under each management regime where compared with each other in terms of the above variables using one-way ANOVA.

IBM SPSS Statistics ver. 21.0 for Windows was used for all generalized linear mixed models. The average percentage of families, guilds and species in spider assemblages, as well as differences in landscape variables and the number of cuts between plots under different management regimes, were calculated in Statistica ver. 12.

4. RESULTS

4.1. Effect of the management regime on spider assemblages

4.1.1. Abundance, species richness and species diversity

A total of 31,945 adult individuals of spiders belonging to 161 species were collected during the three years of the research (see the taxonomic list in Appendix): 9,109 individuals representing 113 species in the first year; 9,726 individuals and 113 species in the second year; 13,110 individuals and 122 species in the third year. The number of individuals and species of spiders captured in the subsequent years of the study per meadows under different management regimes is presented in Table 2.

Table 2. Number of spider individuals and spider species collected during three years of the study in meadows of four management regimes

Management regime	**Years of study**			
	2013	**2014**	**2015**	**2013–2015**
Number of individuals				
C-meadows	2,933	2,304	4,010	9,247
E-meadows	2,031	2,642	2,393	7,066
B-meadows	2,313	1,761	3,170	7,244
H-meadows	1,832	3,019	3,537	8,388
Total	9,109	9,726	13,110	31,945
Number of species				
C-meadows	57	60	64	92
E-meadows	72	66	76	107
B-meadows	76	75	90	122
H-meadows	49	64	73	92
Total	113	113	122	161

The mean spider abundance was 85.8 for C-meadows, 56.5 for E-meadows, 59.4 for B-meadows and 76.6 for H-meadows (means were estimated from the statistical model presented in Table 3). In general, the effect of the management regime on spider abundance was not significant, but the interaction between this variable and the sampling period was significant (Table 3). The abundance of spiders varied between meadows in different management regimes in periods 3 and 4. In these two periods, more spider individuals were collected in C- and H-meadows than on B- and E-meadows (Fig. 6). Moreover, spider abundance was affected by the sampling period (Table 3). The largest number of individuals was collected in the first sampling period and their number significantly decreased in the following periods (Fig. 9).

Species richness was significantly influenced by the management regime (Table 4) and the difference was found between H-meadows, where the mean number of collected spider species was the lowest, and C- and B-meadows (Fig. 7). Species richness was also affected by the sampling period (Table 4). The average number of species found in a sample in the first two periods was similar (ca. 15–16 species), while it decreased significantly in the next two periods, reaching the lowest value in the last period (Fig. 9). Moreover, the number of collected spider species positively correlated with the number of spider individuals, i.e. the sample size (Fig. 8).

Table 3. Results of the generalized linear mixed model with Poisson error distribution and log-link function, assessing the effect of the management regime and the sampling period on spider abundance in meadows. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Management regime	1.945	3,300	0.122
Sampling period	4977.260	3,300	**<0.001**
Management regime x sampling period	44.209	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.162 ± 0.044	3.711	**<0.001**
Year	0.019 ± 0.019	0.995	0.320

The mean Shannon diversity index was: 1.80 for C-meadows, 1.81 for E-meadows, 1.78 for B-meadows and 1.64 for H-meadows (means were estimated from the statistical model presented in Table 5). Species diversity was affected by the sampling period, but not by the management regime and the interaction between these two variables was not significant (Table 5). The highest species diversity was observed in the second sampling period, while the lowest in the fourth period (Fig. 9).

Significant differences were found between the plots (in the case of abundance and species diversity) but not between the years (Tables 3, 4, 5).

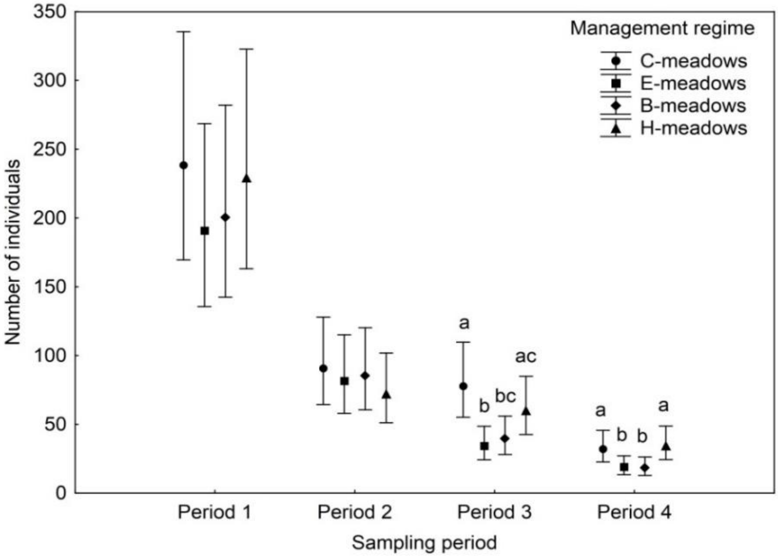

Fig. 6. Abundance of spiders (mean with 95% confidence limits) in four sampling periods in relation to meadow management regimes. The means are estimated from GLMM presented in Table 3. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods (Period 3: *P* < 0.017; Period 4: *P* < 0.027)

Table 4. Results of the generalized linear mixed model with Gaussian error distribution and identity-link function assessing the effect of the management regime, the sampling period and the number of individuals on the spider species richness in meadows. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Management regime	3.697	3,299	**0.012**
Sampling period	16.005	3,299	**<0.001**
Management regime x sampling period	0.526	9,299	0.855
Number of individuals	179.028	1,299	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	1.172 ± 0.599	1.958	0.050
Year	0.161 ± 0.248	0.647	0.517

Table 5. Results of the generalized linear mixed model with Gaussian error distribution and identity-link function assessing the effect of the management regime and the sampling period on the species diversity of spiders in meadows. Significant results are shown in bold

Variable	***F***	***df*1; *df*2**	***P***
Management regime	1.509	3,300	0.212
Sampling period	41.858	3,300	**<0.001**
Management regime x sampling period	1.593	9,300	0.116
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.020 ± 0.009	2.117	**0.034**
Year	0.005 ± 0.006	0.781	0.061

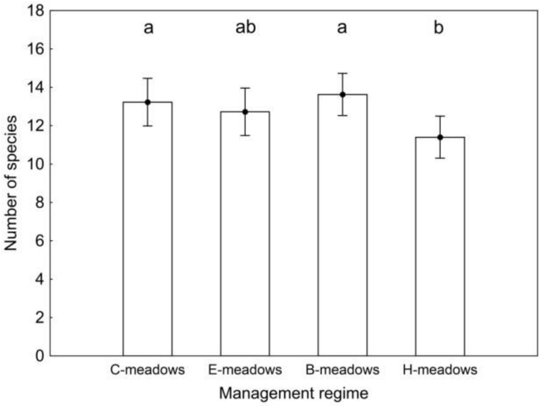

Fig. 7. Species richness of spiders (mean with 95% confidence limits) in four management regimes. The means are estimated from GLMM presented in Table 4. Different letters above the bars indicate significant differences between management regimes (*P* < 0.040)

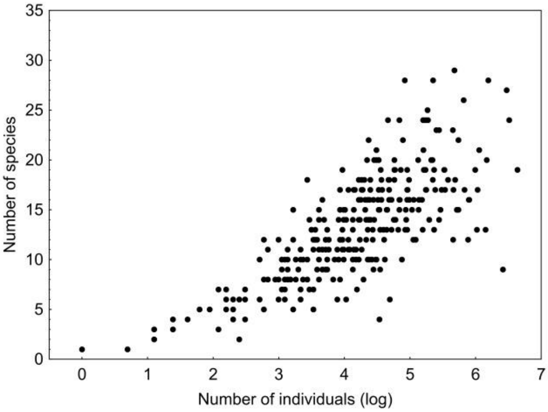

Fig. 8. Relationship between the number of spider species and the log-transformed number of individuals collected in meadows during the study period

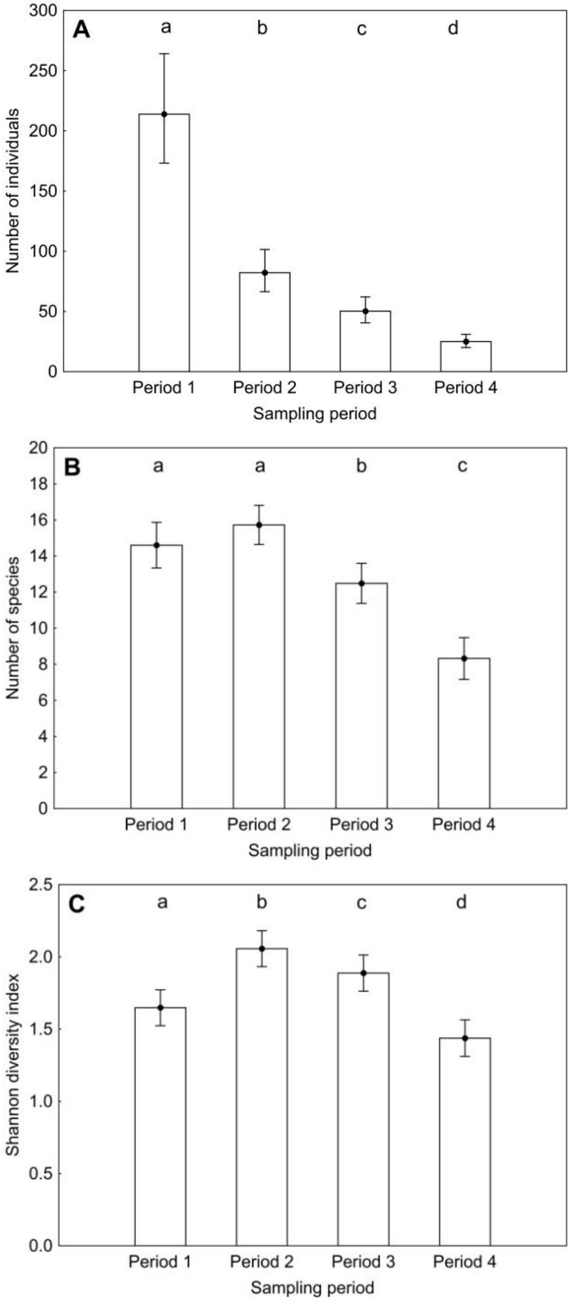

Fig. 9. Spider abundance (A), species richness (B) and species diversity (C) (mean with 95% confidence limits) in four sampling periods. The means are estimated from GLMMs presented in Tables 3-5. Different letters above the bars indicate significant differences between sampling periods (abundance: $P < 0.001$; species richness: $P < 0.003$; species diversity: $P < 0.005$)

4.1.2. Families

The spiders captured during the three years of the research belonged to 18 families. A total of 18 families were identified in the meadows in bird variant, 17 families in the meadows in extensive package, 16 families in the habitat variant meadows and 14 families in the conventional meadows (Table 6). *Lycosidae* (19,944 individuals in total) was the largest family in all four management regimes, on average accounting for about 60% of the spiders collected. In the B-meadows *Tetragnathidae* was the second largest family and *Linyphiidae* (only slightly less numerous) was the third one. In meadows under other management regimes, *Linyphiidae* constituted the second and *Tetragnathidae* the third largest family. *Thomisidae* was the fourth largest family in all surveyed meadows, regardless of their management regime. The contribution of each of the other families did not exceed 2% (Table 6).

The species-richest family was *Linyphiidae* (60 species in total), followed by *Lycosidae* (25 species), *Gnaphosidae* and *Thomisidae* (14 species each) (Table 7).

Table 6. Contribution of families (mean with 95% confidence limits) in spider assemblages in meadows in relation to the management regime (data pooled from all years and sampling periods)

Family	C-meadows	E-meadows	B-meadows	H-meadows
Araneidae	0.02 (–0.02 – 0.05)	0.09 (–0.02 – 0.20)	0.03 (–0.01 – 0.07)	0.06 (–0.04 – 0.15)
Clubionidae	–	0.12 (–0.01 – 0.23)	0.09 (0.02 – 0.16)	0.05 (–0.03 – 0.13)
Dictynidae	0.09 (0.02 – 0.15)	0.34 (–0.04 – 0.72)	0.38 (0.16 – 0.59)	0.24 (–0.02 – 0.50)
Eutichuridae	–	–	0.06 (–0.07 – 0.19)	–
Gnaphosidae	0.64 (0.29 – 0.10)	1.26 (0.55 – 1.96)	1.98 (1.31 – 2.65)	1.49 (0.82 – 2.16)
Hahnidae	0.19 (0.03 – 0.35)	0.65 (0.17 – 1.13)	0.51 (0.23 – 0.79)	0.48 (0.16 – 0.80)
Linyphiidae	27.8 (19.75 – 35.91)	18.58 (11.57 – 25.59)	13.55 (9.08 – 18.03)	22.73 (15.30 – 30.15)
Liocranidae	0.01 (–0.01 – 0.03)	0.12 (–0.01 – 0.25)	0.13 (–0.01 – 0.27)	0.03 (–0.01 – 0.07)
Lycosidae	57.63 (50.35 – 64.92)	61.23 (54.91 – 67.55)	62.55 (58.22 – 66.89)	58.78 (52.11 – 65.45)
Mimetidae	–	0.02 (–0.02 – 0.06)	0.04 (–0.03 – 0.11)	–
Miturgidae	0.04 (–0.01 – 0.10)	0.18 (0.00 – 0.36)	0.43 (0.16 – 0.71)	0.07 (0.01 – 0.15)
Philodromidae	0.56 (–0.29 – 1.41)	1.24 (0.35 – 2.13)	0.84 (0.34 – 1.33)	0.33 (0.07 – 0.60)

Phrurolithidae	0.16 (–0.01 – 0.32)	0.25 (0.06 – 0.44)	0.48 (0.03 – 0.92)	0.09 (0.00 – 0.18)
Pisauridae	–	0.06 (–0.03 – 0.14)	0.04 (–0.01 – 0.08)	0.01 (–0.01 – 0.03)
Salticidae	0.08 (–0.03 – 0.19)	0.15 (–0.02 – 0.32)	0.07 (0.00 – 0.15)	0.05 (–0.01 – 0.12)
Tetragnathidae	10.77 (8.40 – 13.13)	11.54 (7.27 – 15.80)	15.46 (11.03 – 19.88)	12.49 (7.49 – 17.50)
Theridiidae	0.15 (–0.03 – 0.33)	0.10 (–0.01 – 0.21)	0.15 (0.01 – 0.29)	0.30 (0.13 – 0.46)
Thomisidae	1.83 (1.14 – 2.52)	4.08 (2.20 – 5.96)	3.21 (2.12 – 4.30)	2.79 (1.49 – 4.09)

Table 7. Total number of spider species belonging to particular families collected during the study period in relation to the management regime

Family	C-meadows	E-meadows	B-meadows	H-meadows	Total
Araneidae	1	4	1	2	6
Clubionidae	0	3	4	2	5
Dictynidae	1	1	2	1	2
Eutichuridae	0	0	1	0	1
Gnaphosidae	10	9	12	9	14
Hahnidae	1	3	1	1	3
Linyphiidae	37	36	43	31	60
Liocranidae	1	1	3	1	3
Lycosidae	19	21	21	22	25
Mimetidae	0	1	1	0	1
Miturgidae	1	2	2	2	2
Philodromidae	2	3	3	1	3
Phrurolithidae	1	1	1	1	1
Pisauridae	0	2	2	1	2
Salticidae	3	4	4	2	8
Tetragnathidae	2	2	2	2	2
Theridiidae	6	4	6	7	9
Thomisidae	7	10	13	7	14

The number of collected spider families was affected by the management regime and the sampling period (Table 8). The number of families identified in the bird variant meadows was significantly higher compared to meadows under other management regimes (Fig. 10). The largest number of spider families was determined in the first sampling period (mean 6.5) and their number was decreasing in the subsequent periods (Fig. 11).

Table 8. Results of the generalized linear mixed model with Gaussian error distribution and identity-link function, assessing the effect of the management regime and the sampling period on the number of spider families in meadows. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Management regime	3.089	3,300	**0.027**
Sampling period	76.838	3,300	**<0.001**
Management regime x sampling period	1.448	9,300	0.167
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.561 ± 0.198	2.829	**0.005**
Year	0.375 ± 0.392	0.955	0.339

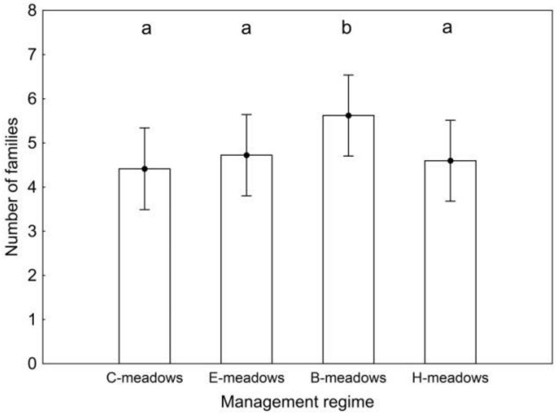

Fig. 10. Number of spider families (mean with 95% confidence limits) in four management regimes. The means are estimated from GLMM presented in Table 8. Different letters above the bars indicate significant differences between management regimes ($P < 0.038$)

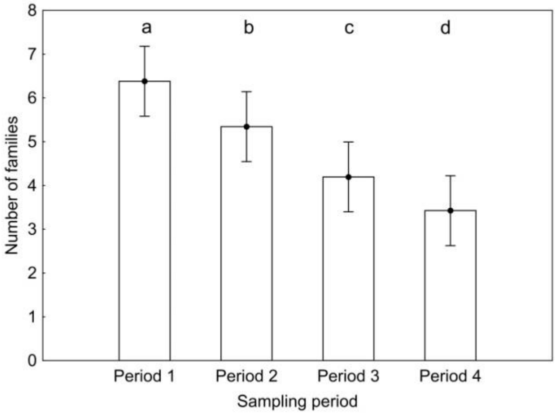

Fig. 11. Number of spider families (mean with 95% confidence limits) in four sampling periods. The means are estimated from GLMM presented in Table 8. Different letters above the bars indicate significant differences between sampling periods ($P < 0.001$)

The effect of the management regime on the number of individuals was significant in the case of *Linyphiidae*, but not in the case of families *Lycosidae* and *Tetragnathiidae* (Table 9). In general, linyphiids were the most abundant in conventionally used meadows and the least abundant in meadows in the bird variant (Fig. 12). Considering specific sampling periods, no differences in the abundance between particular management regimes were observed in the first and second periods, as opposed to the third and fourth periods. In the two latter periods, spiders of the family *Linyphiidae* reached greater abundance in C- and H-meadows compared to the two other management types, especially B-meadows (Fig. 13).

Although no effect of the management regime on the abundance of the family *Lycosidae* was found (due to the lack of differences in the first period, when these spiders were most abundant), some differences between management regimes were observed in the second, third and fourth sampling periods (Fig. 14). Differences between H-meadows (the lowest mean abundance) and E- and B-meadows (the highest abundance) were observed in the second sampling period. In the third period the differences between E-meadows where the smallest number of spiders of the family *Lycosidae* was caught, and C-meadows with the largest number of individuals, were noticed. In the last sampling period, the number of individuals captured in the extensive package meadows was significantly lower compared to meadows in the other management regimes (Fig. 14).

In the case of the *Tetragnathidae* family, despite the statistically significant interaction between the management regimes and the sampling periods (Table 9), no differences were found in any of the analysed sampling periods between meadows under different management regimes in terms of the abundance of collected spiders.

The effect of the sampling period on the abundance of spiders was significant for all analysed families (Table 9). The number of individuals of the family *Lycosidae* decreased with the progress of the season (Fig. 15). The number of individuals of the family *Linyphiidae* was increasing from the first to the third sampling period and decreased again in the fourth sampling period (Fig. 15). The number of individuals representing the *Tetragnathidae* family was decreasing until the third sampling period and increased in the last period compared to the two preceding periods (Fig. 15).

Significant differences were found between plots but not between years of the study, both in the case of the number of families as well as the abundance of spiders from three analysed families (Tables 8, 9).

Table 9. Results of the generalized linear mixed models with Poisson error distribution and log-link function, assessing the effect of the management regime and the sampling period on the abundance of spiders of the families *Lycosidae*, *Linyphiidae* and *Tetraganthidae*. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Lycosidae			
Management regime	0.905	3,300	0.439
Sampling period	4,824.926	3,300	**<0.001**
Management regime x sampling period	40.611	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.234 ± 0.063	3.711	**<0.001**
Year	0.033 ± 0.033	0.995	0.320
Linyphiidae			
Management regime	3.017	3,300	**0.030**
Sampling period	414.290	3,300	**<0.001**
Management regime x sampling period	9.418	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.366 ± 0.102	3.585	**<0.001**
Year	0.109 ± 0.110	0.994	0.320
Tetragnathidae			
Management regime	0.633	3,300	0.594
Sampling period	289.325	3,300	**<0.001**
Management regime x sampling period	19.635	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.436 ± 0.122	3.566	**<0.001**
Year	0.176 ± 0.177	0.995	0.320

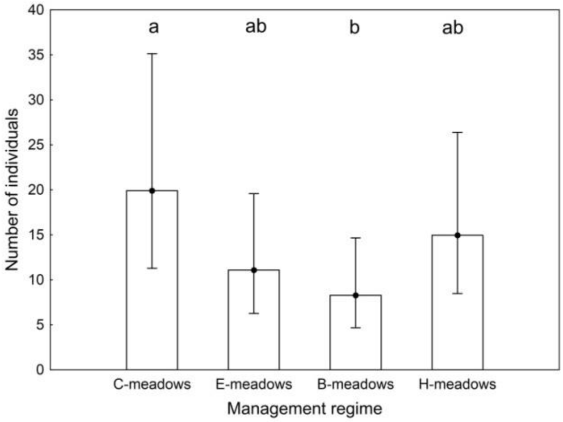

Fig. 12. Abundance of spiders (mean with 95% confidence limits) of the family *Linyphiidae* in four management regimes. The means are estimated from GLMM presented in Table 9. Different letters above the bars indicate significant differences between management regimes (*P* = 0.026)

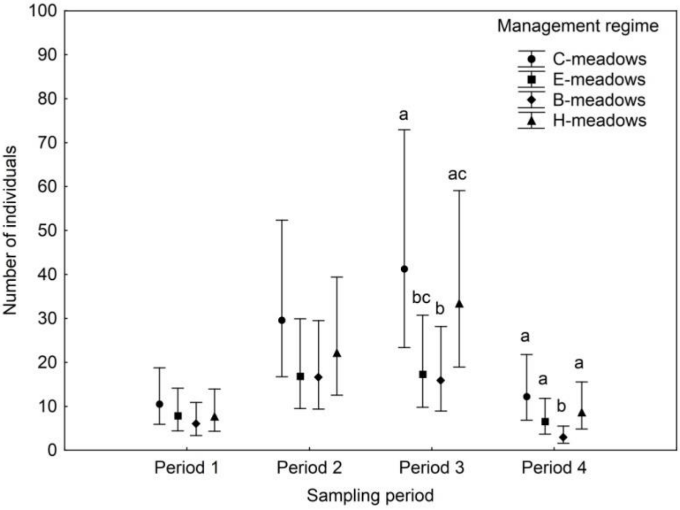

Fig. 13. Abundance of spiders (mean with 95% confidence limits) of the family *Linyphiidae* in four sampling periods in relation to management regime in meadows. The means are estimated from GLMM presented in Table 9. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods (Period 3: $P < 0.045$; Period 4: $P < 0.048$)

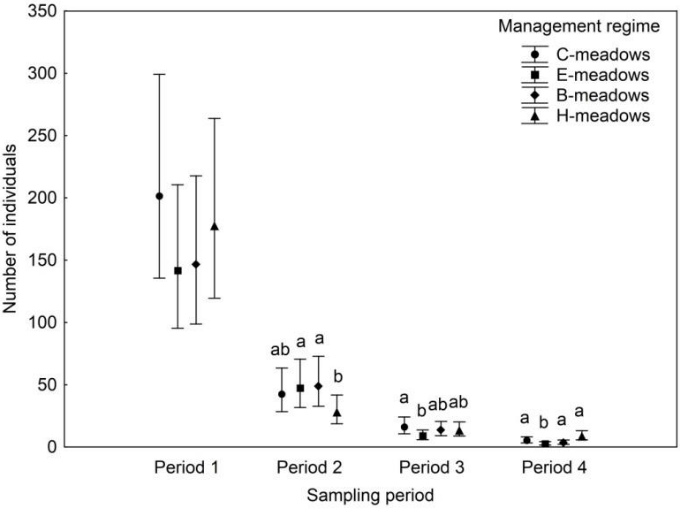

Fig. 14. Abundance of spiders (mean with 95% confidence limits) of the family *Lycosidae* in four sampling periods in relation to the management regime in meadows. The means are estimated from GLMM presented in Table 9. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods (Period 2: $P < 0.049$; Period 3: $P < 0.041$; Period 4: $P < 0.033$)

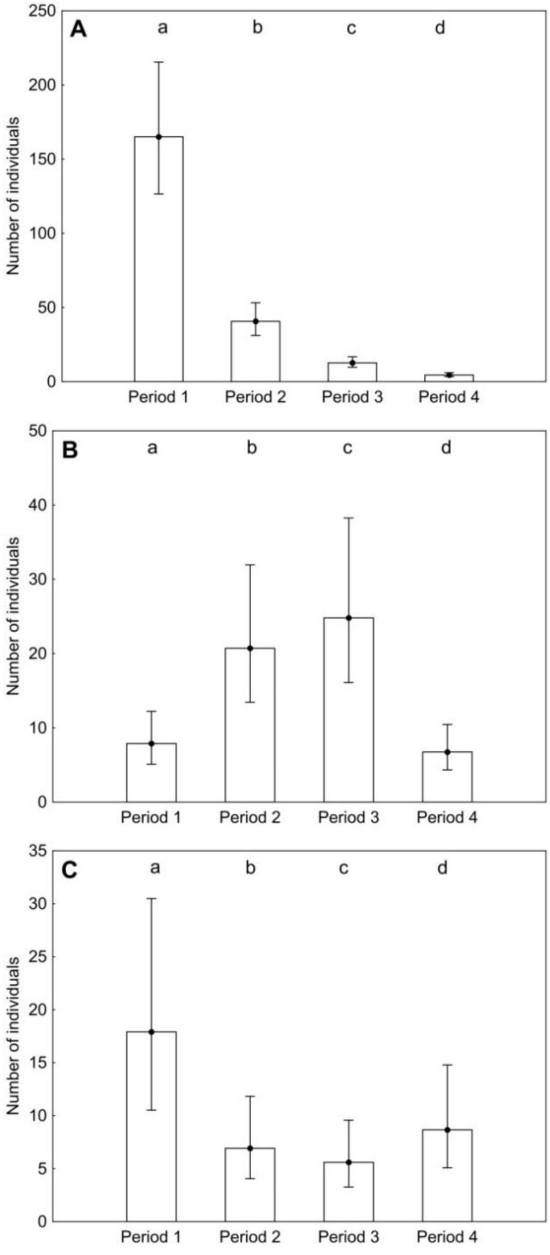

Fig. 15. Abundance of spiders (mean with 95% confidence limits) of the families: A) *Lycosidae*, B) *Linyphiidae*, and C) *Tetragnathidae* in four sampling periods. The means are estimated from GLMM presented in Table 9. Different letters above the bars indicate significant differences between sampling periods (*Lycosidae*: $P < 0.001$; *Linyphiidae*: $P < 0.018$; *Tetragnathidae*: $P < 0.009$)

The effect of the management regime on species richness was statistically not significant for both families *Lycosidae* and *Linyphiide* (Table 10). However, in the case of the family *Lycosidae* the interaction between management regime and sampling period was significant (Table 10) and the differences in the number of species between management regimes were observed in the second sampling period when significantly more species were found in E-meadows compared to C- and H-meadows and B-meadows compared to H-meadows (Fig. 16).

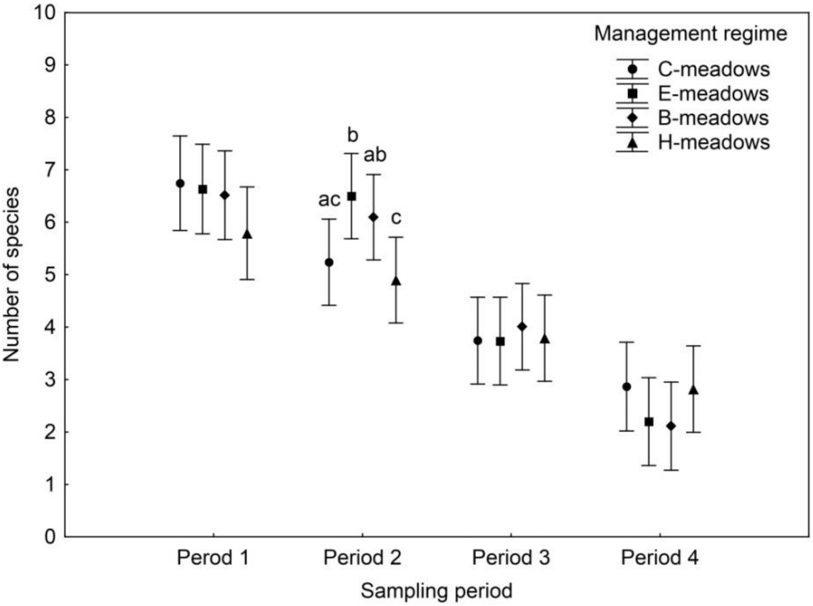

Fig. 16. Species richness of spiders (mean with 95% confidence limits) of the family *Lycosidae* in four sampling periods in relation to the management regime in meadows. The means are estimated from GLMM presented in Table 10. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods ($P < 0.041$)

Moreover, the number of spider species of both families was positively correlated with the number of collected spider individuals (Figs. 17, 18) and influenced by the sampling period (Table 10). The largest number of species of the family *Lycosidae* was identified in the first sampling period and their number was decreasing in the subsequent periods, whereas the largest number of species of the family *Linyphiidae* was recorded in the second and the third period (Fig. 19).

Moreover, significant differences were found between the plots, but not between the years of the study (Table 10).

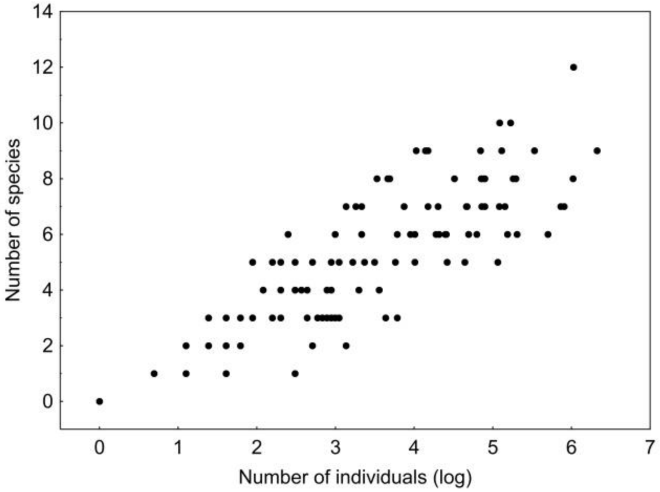

Fig. 17. Relationship between the log-transformed number of individuals and the number of spider species of the family *Lycosidae* collected in meadows during the study period

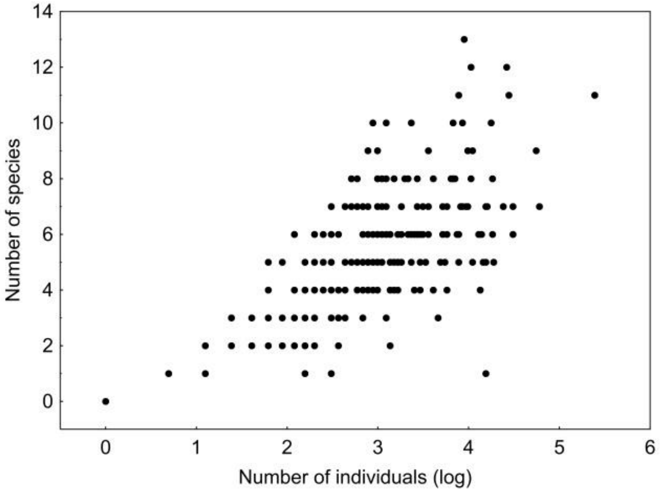

Fig. 18. Relationship between the log-transformed number of individuals and the number of spider species of the family *Linyphiidae* collected in meadows during the study period

Table 10. Results of the generalized linear mixed models with Gaussian error distribution and identity-link function, assessing the effect of the management regime, the sampling period and the number of individuals on the species richness of spiders of the families *Lycosidae* and *Linyphiidae*. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Lycosidae			
Management regime	0.417	3,299	0.741
Sampling period	73.656	3,299	**<0.001**
Management regime x sampling period	2.311	9,299	**0.016**
Number of individuals	20.176	1,299	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.497 ± 0.193	2.571	**0.010**
Year	Not estimated	–	–
Linyphiidae			
Management regime	1.190	3,299	0.314
Sampling period	12.980	3,299	**<0.001**
Management regime x sampling period	0.922	9,299	0.507
Number of individuals	97.046	1,299	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.681 ± 0.286	2.379	**0.017**
Year	0.173 ± 0.208	0.833	0.405

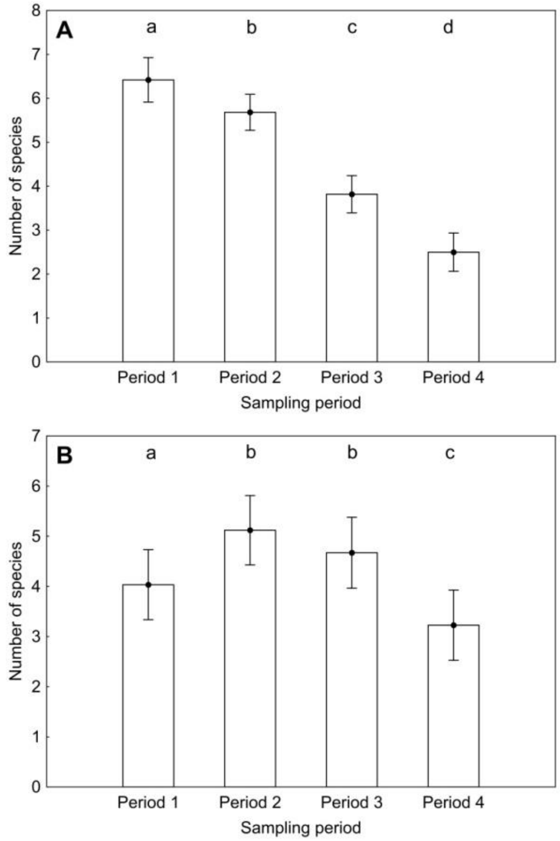

Fig. 19. Species richness of spiders (mean with 95% confidence limits) of the families: A) *Lycosidae* and B) *Linyphiidae* in four sampling periods. The means are estimated from GLMMs presented in Table 10. Different letters above the bars indicate significant differences between sampling periods (*Lycosidae*: $P < 0.011$; *Linyphiidae*: $P < 0.049$)

4.1.3. Guilds

Altogether, spiders captured during the three years of the research belonged to 7 guilds. The ground hunters were the largest guild (20,512 individuals in total), whose average contribution on a plot ranged from almost 58.6% in C-meadows to 65.9% on B-meadows. The second largest guild were other hunters (9,149 individuals), reaching on average from 26.6% (B-meadows) to 34.5% (C-meadows). The next two largest guilds – sheet web weavers and ambush hunters (1,373 and 847 individuals, respectively) accounted on average for 1.8% to 8.1% (Table 11). Spiders from three other guilds: orb web weavers, space web weavers and specialists were collected sporadically (9, 39 and 16 individuals, respectively, caught during the study period).

The species-richest guild were other hunters (58 species in total), followed by ground hunters (46 species), sheet web weavers (27 species) and ambush hunters (14 species) (Table 12).

Table 11. Contribution of guilds (mean with 95% confidence limits) in spider assemblages in meadows in relation to the management regime (data pooled from all years and sampling periods)

Guild	C-meadows	E-meadows	B-meadows	H-meadows
Ground hunters	58.57 (51.13 – 66.02)	63.34 (57.18 – 69.50)	65.91 (61.63 – 70.18)	60.69 (53.94 – 67.44)
Other hunters	34.49 (27.11 – 41.87)	29.34 (23.09 – 35.60)	26.60 (22.20 – 30.99)	28.04 (22.04 – 34.05)
Sheet web weavers	4.94 (2.16 – 7.72)	3.03 (2.24 – 3.82)	4.07 (3.09 – 5.04)	8.12 (4.62 – 11.62)
Ambush hunters	1.83 (1.14 – 2.52)	4.08 (2.20 – 5.96)	3.21 (2.16 – 4.30)	2.79 (1.49 – 4.09)
Space web weavers	0.14 (–0.03 – 0.30)	0.08 (–0.01 – 0.17)	0.08 (0.01 – 0.15)	0.30 (0.13 – 0.46)
Orb web weavers	0.02 (–0.02 – 0.05)	0.09 (–0.02 – 0.20)	0.03 (–0.01 – 0.07)	0.06 (–0.04 – 0.15)
Specialists	0.02 (–0.02 – 0.05)	0.04 (–0.02 – 0.09)	0.11 (–0.02 – 0.25)	-

Table 12. Total number of species from particular guilds collected during the whole study period in relation to the management regime

Guild	C-meadows	E-meadows	B-meadows	H-meadows	Total
Ground hunters	33	34	40	35	46
Other hunters	31	39	47	28	58
Sheet web weavers	14	15	14	13	27
Ambush hunters	7	10	13	7	14
Space web weavers	5	3	5	7	8
Orb web weavers	1	4	1	2	6
Specialists	1	2	2	0	2

The effect of the management regime on the abundance of the four analysed guilds was not significant (Table 13). However, in the case of ground hunters, other hunters and sheet web weavers, differences between management regimes were observed in certain sampling periods. In the case of ground hunters, differences occurred in the last three sampling periods. In the second sampling period, this guild was significantly more abundant in B- and E-meadows compared to H-meadows. In the two consecutive periods, the smallest number of spiders was caught in E-meadows, which differed significantly from C-meadows (in the third period) and C- and H-meadows (in the fourth period) (Fig. 20). Other hunters in the last two sampling periods were most abundant on conventionally used meadows and meadows in the habitat variant, and the least abundant in meadows in the bird variant (Fig. 21). In the case of the sheet web guild, statistically significant differences in the number of spiders were observed in the third sampling period between H-meadows (the most abundant) and E-meadows (the least abundant) (Fig. 22).

The sampling period significantly affected the number of spiders in all analysed guilds (Table 13). The total abundance of all guilds, except the sheet web guild decreased with the progress of the season. In the case of the latter guild, the largest number of spiders was recorded in the third sampling period, while the lowest in the fourth period (Fig. 23).

In two the most numerous guilds, it was found that the effect of the management regime on the species richness was significant both for ground hunters and other hunters (Table 14). The number of ground hunters' species identified in meadows in the bird variant was significantly higher compared to meadows under other management systems (Fig. 24). In the case of other hunters, statistically significant differences were found between H-meadows (the least number of species) as well as C- and E-meadows (the largest number of species; Fig. 24).

Furthermore, the interaction between the management regime and the sampling period was significant in the case of the ground hunters (Table 14) and differences between the management regimes were found in the first and the second sampling periods. In both these periods, the highest species richness was observed in B-meadows (Fig. 25).

Moreover, the number of spider species was influenced by the sampling period and positively affected by the number of spider individuals belonging to both guilds (Table 14; Figs. 26, 27). The largest number of species representing the guild of ground hunters was found in the first sampling period and their number decreased in the subsequent periods, whereas the largest number of species belonging to the guild of other hunters was recorded in the second sampling period (Fig. 28).

In the case of all analysed guilds, significant differences in the abundance and the number of species were found between plots, but not between years of the study (Tables 13, 14).

Table 13. Results of the generalized linear mixed models with Poisson error distribution and log-link function, assessing the effect of the management regime and the sampling period on the abundance of spiders belonging to the four most abundant guilds in meadows. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Ground hunters			
Management regime	0.832	3,300	0.477
Sampling period	4,938.634	3,300	**<0.001**
Management regime x sampling period	43.845	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.224 ± 0.060	3.710	**<0.001**
Year	0.033 ± 0.033	0.995	0.319
Other hunters			
Management regime	1.134	3,300	0.336
Sampling period	119.396	3,300	**<0.001**
Management regime x sampling period	52.206	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.275 ± 0.076	3.632	**<0.001**
Year	0.012 ± 0.012	0.970	0.332
Sheet web weavers			
Management regime	1.530	3,300	0.207
Sampling period	116.372	3,300	**<0.001**
Management regime x sampling period	5.696	9,300	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.455 ± 0.136	3.351	**0.001**
Year	0.108 ± 0.111	0.975	0.330
Ambush hunters			
Management regime	0.306	3,300	0.821
Sampling period	96.422	3,300	**<0.001**
Management regime x sampling period	1.425	9,300	0.177
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.322 ± 0.100	3.234	**0.001**
Year	0.231 ± 0.236	0.236	0.328

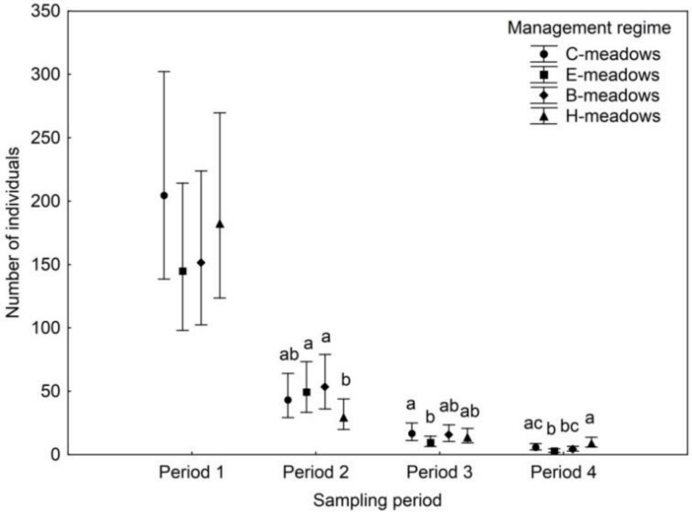

Fig. 20. Abundance of spiders (mean with 95% confidence limits) belonging to the guild of ground hunters in four sampling periods in relation to the management regime in meadows. The means are estimated from GLMM presented in Table 13. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods (Period 2: $P < 0.048$; Period 3: $P < 0.046$; Period 4: $P < 0.033$)

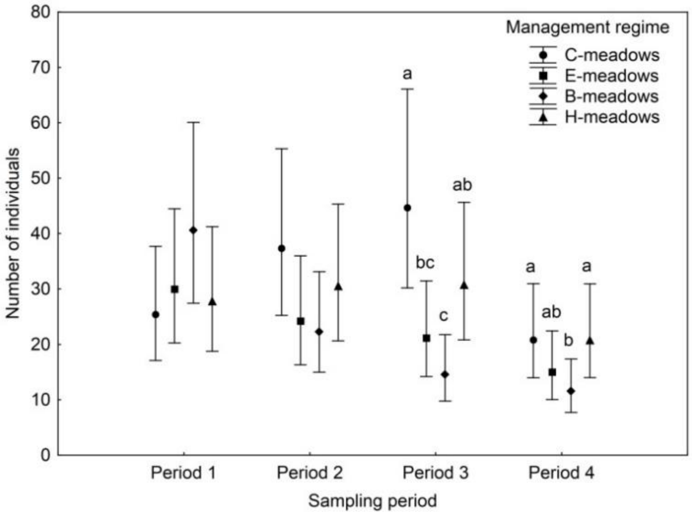

Fig. 21. Abundance of spiders (mean with 95% confidence limits) belonging to the guild of other hunters in four sampling periods in relation to the management regime in meadows. The means are estimated from GLMM presented in Table 13. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods (Period 3: $P < 0.014$; Period 4: $P < 0.047$)

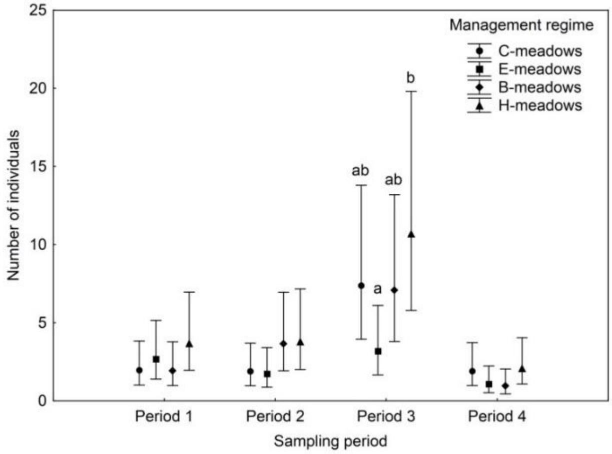

Fig. 22. Abundance of spiders (mean with 95% confidence limits) belonging to the guild of sheet web weavers in four sampling periods in relation to the management regime in meadows. The means are estimated from GLMM presented in Table 13. Different letters above the whiskers indicate significant differences between management regimes in a given sampling period (*P* = 0.017)

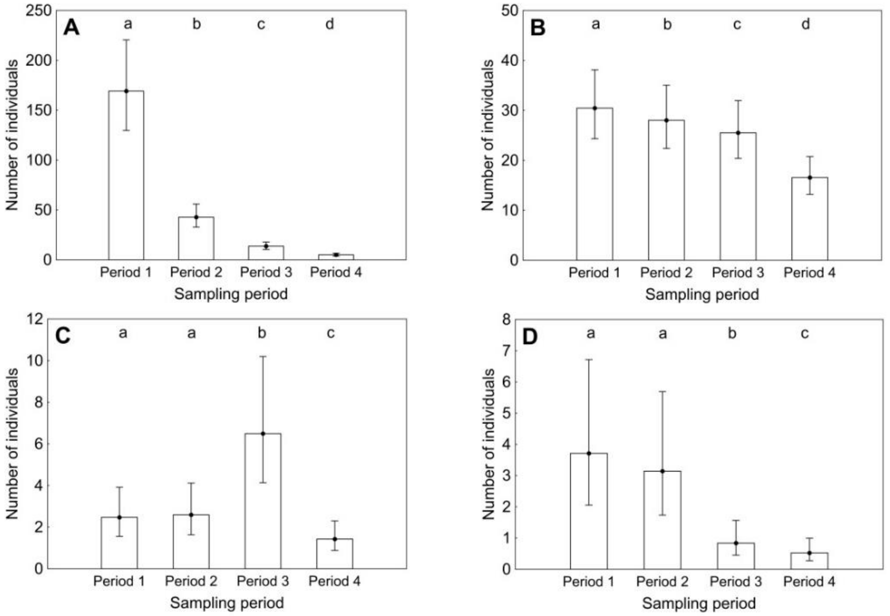

Fig. 23. Abundance of spiders (mean with 95% confidence limits) belonging to the guilds of: A) ground hunters, B) other hunters, C) sheet web weavers and D) ambush hunters in four sampling periods. The means are estimated from GLMMs presented in Table 13. Different letters above the whiskers indicate significant differences between sampling periods (ground hunters: *P* < 0.001; other hunters: *P* < 0.005; sheet web weavers: *P* < 0.002; ambush hunters: *P* < 0.037)

Table 14. Results of the generalized linear mixed models with Gaussian error distribution and the identity-link function assessing the effect of the management regime, the sampling period and the number of individuals on the species richness of spiders belonging to the guilds of ground hunters and other hunters in meadows. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Ground hunters			
Management regime	3.267	3,299	**0.022**
Sampling period	72.476	3,299	**<0.001**
Management regime x sampling period	2.748	9,299	**0.004**
Number of individuals	25.462	1,299	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.515 ± 0.233	2.212	**0.027**
Year	0.071 ± 0.107	0.661	0.508
Other hunters			
Management regime	5.282	3,299	**0.001**
Sampling period	13.260	3,299	**<0.001**
Management regime x sampling period	0.311	9,299	0.971
Number of individuals	130.353	1,299	**<0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.656 ± 0.252	2.599	**0.009**
Year	0.019 ± 0.044	0.439	0.661

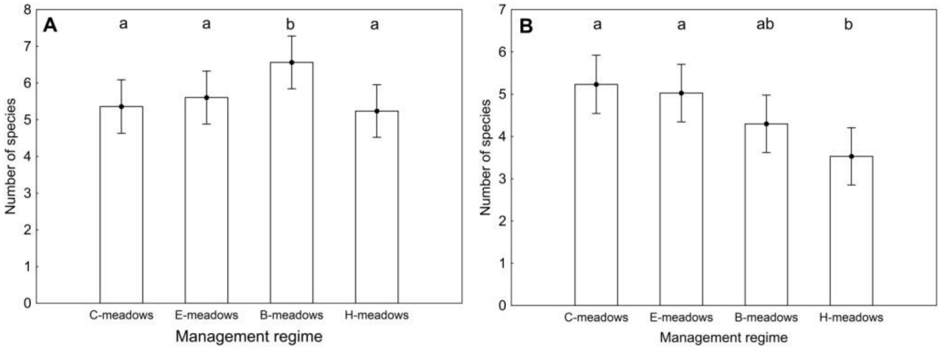

Fig. 24. Species richness (mean with 95% confidence limits) of the guilds of: A) ground hunters and B) other hunters in four management regimes. The means are estimated from GLMMs presented in Table 14. Different letters above the whiskers indicate significant differences between management regimes (ground hunters: $P < 0.043$; other hunters: $P < 0.002$)

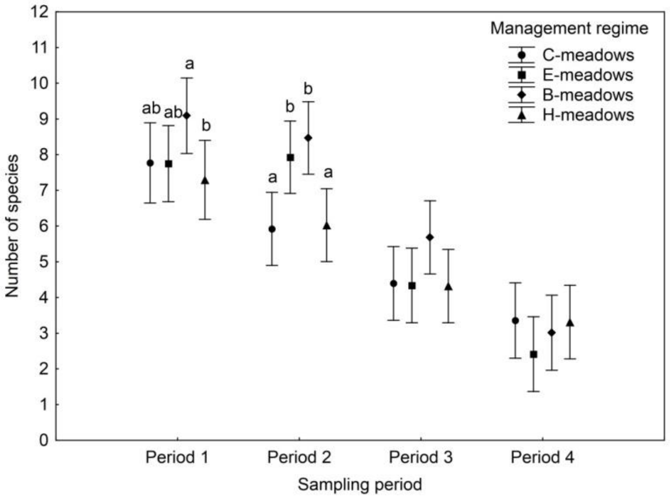

Fig. 25. Species richness of spiders (mean with 95% confidence limits) belonging to the guild of ground hunters in four sampling periods in relation to the management regime in meadows. The means are estimated from GLMM presented in Table 14. Different letters above the whiskers indicate significant differences between management regimes in particular sampling periods (Period 1: *P* = 0.011; Period 2: *P* < 0.007)

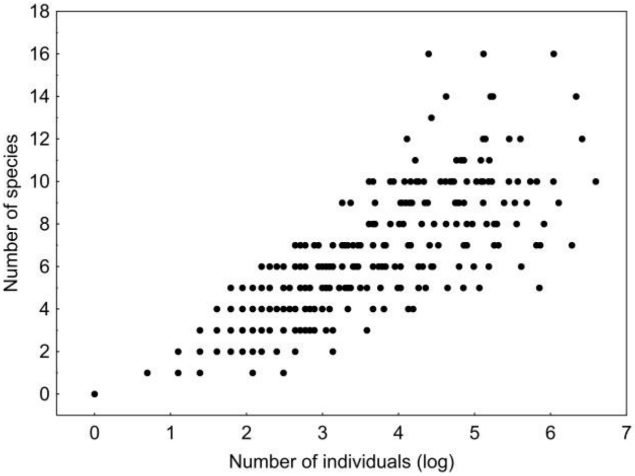

Fig. 26. Relationship between the log-transformed number of individuals and the number of spider species belonging to the guild of ground hunters collected in meadows during the study period

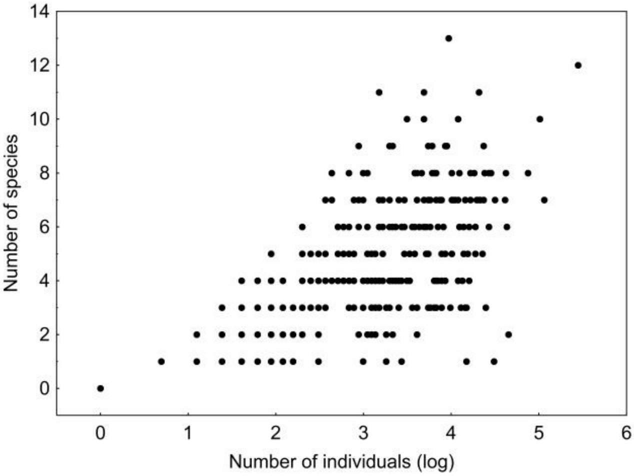

Fig. 27. Relationship between the log-transformed number of individuals and the number of spider species belonging to the guild of other hunters collected in meadows during the study period

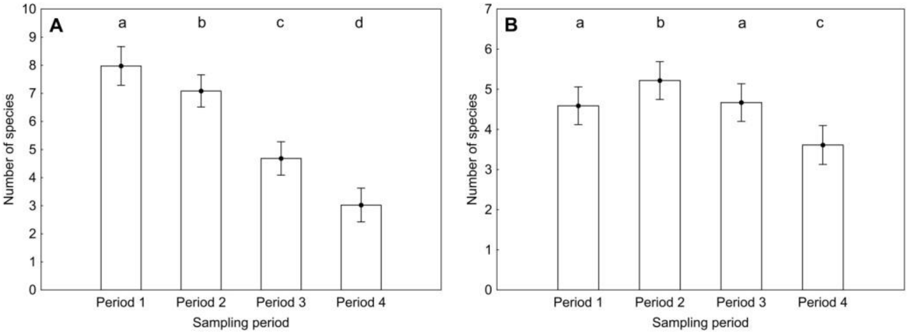

Fig. 28. Species richness of spiders (mean with 95% confidence limits) belonging to the guilds of A) ground hunters and B) other hunters in four sampling periods. The means are estimated from GLMMs presented in Table 14. Different letters above the whiskers indicate significant differences between sampling periods (ground hunters: $P < 0.017$; other hunters: $P < 0.025$)

4.1.4. Species composition in different management regimes

The most abundant species

Meadows in all four management regimes were dominated by a few abundant spider species, which are widely distributed residents of open habitats. Of the 161 species of spiders revealed, the most numerous was

Pardosa palustris – 10,462 individuals caught in total (32.8% of all spiders collected). Other most abundant species include: *Pardosa pullata* (2,512 collected individuals), *Pachygnatcha degeeri* (3,538), *Pardosa prativaga* (2,512), *Erigone dentipalpis* (1,459) and *Erigone atra* (1,138). Among the species caught, as many as 42 (26% of all species) were represented by one individual and 90 (56%) by no more than 10 individuals (see Appendix). Mean percentage contribution of the most numerous species were presented in Figs. 29, 30, 31, 32. Six the most numerous species which abundance exceeded 1,000 individuals during the study period (pooled data from all study plots) were marked by different colours.

In the C-meadows and the meadows under the habitat variant, *P. palustris* reached the highest mean percentage contribution (35.7% and 29.3% respectively; Figs. 29, 32), whereas in meadows under the extensive package and the bird variant, *P. pullata* reached the highest mean contribution (22.8% and 21.3%, respectively; Figs. 30, 31).

In the conventionally used meadows, only four species (in addition to *P. palustris*) reached the contribution above 5%: *P. pullata* (7.9%), *E. dentipalpis* (7.8%), *P. degeeri* (7.7%), *P. prativaga* (5.7%) (Fig. 29). It is worth to note that in these meadows, contrary to meadows included in the agri-environment packages, *Oedothorax fuscus* – a species often found in agricultural areas, occurred in large numbers reaching the contribution of 5% while its contribution in other meadows did not exceed 1% (Figs. 29, 30, 31, 32). In E-meadows, *P. pullata* was followed by *P. palustris* with the contribution of 20.3%. Other abundant species in this system of use include *P. degeeri* (8.8%), *P. prativaga* (6.2%) and *E. atra* (5.8%) (Fig. 30). In the meadows under the bird variant, as many as four species reached the contribution above 10%. In addition to the most abundant *P. pullata*, those were: *P. palustris* (19.7%), *P. degeeri* (14.4%) and *P. prativaga* (11.9%). None of the other species exceeded 4% (Fig. 31). It should be noted that the contribution of *E. dentipalpis* was low (1%) comparing to the meadows included in the other management regimes (Figs. 29, 30, 31, 32). In the meadows under the habitat variant, three species reached the contribution above 10%: *P. palustris* (29.3%), *P. degeeri* (11.8%) and *P. prativaga* (11.7%). Other abundant species included: *P. pullata* (8.3%), *E. dentipalpis* (8.0%) and *Agyneta affinis* (5.4%; Fig. 32).

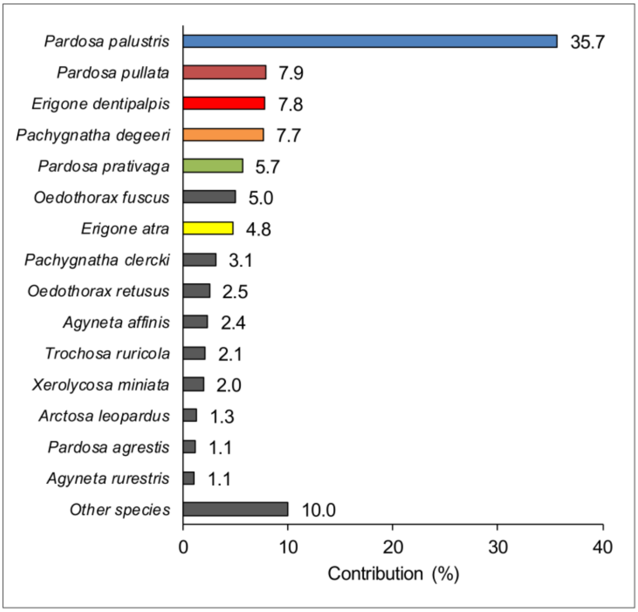

Fig. 29. Mean contribution of spider species in meadows under conventional management (pooled data from all years and sampling periods). Only species with at least 1% contribution are presented

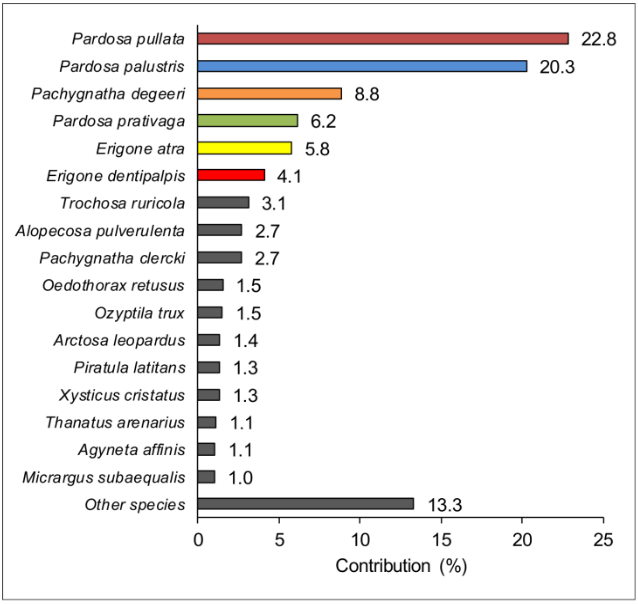

Fig. 30. Mean contribution of spider species in meadows under extensive package (pooled data from all years and sampling periods). Only species with at least 1% contribution are presented

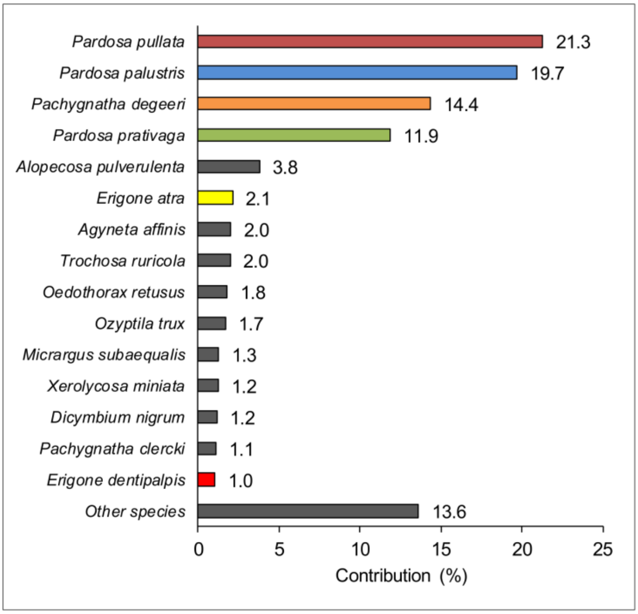

Fig. 31. Mean contribution of spider species in meadows under bird variant (pooled data from all years and sampling periods). Only species with at least 1% contribution are presented

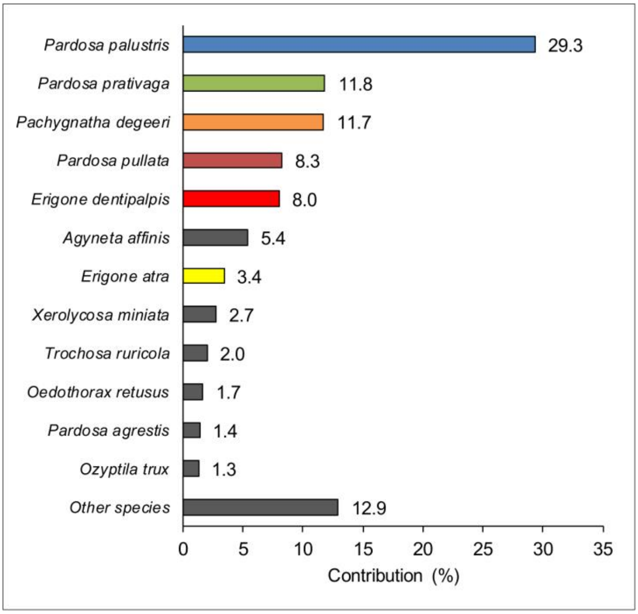

Fig. 32. Mean contribution of spider species in meadows under habitat variant (pooled data from all years and sampling periods). Only species with at least 1% contribution are presented

Exclusive species

The most of exclusive spider species (recorded only in one type of management regime) were found on the meadows under the bird variant (26 species; see Appendix). In the remaining types of meadows, the number of such species was lower: E-meadows – 11, C-meadows – 9 species, H-meadows – 8 (see Appendix). Among the exclusive species of B-meadows, as many as 9 species were classified as rare, and four of them belonged to the EN category (endangered): *Haplodrassus moderatus*, *Ceratinella major*, *Trichopternoides thorelli*, *Xysticus lineatus*. Definitely less rare species in the group of exclusive ones were found in the other types of use: H-meadows – 4 species, C-meadows – 3 and E-meadow – 1. Only one species from the EN category was recorded in the conventional meadow – *Larinia jeskovi*.

Rare species

A total of 469 individuals of spiders belonging to the rare species (including species from the "Red list of threatened animals in Poland" and those known from less than 20 localities in the country) were found in this study (see Appendix). The abundance of rare species in meadows included in the agri-environment programme was similar (E-meadows – 140 individuals; B-meadows – 144; H-meadows – 138). In conventional meadows, the number of individuals was three times lower compared to meadows in the programme (47 individuals). The abundance of rare species was affected by the management regime (Table 15), but the significant difference was observed only between the C-meadows and the B-meadows (Fig. 33).

During the three years of research, a total of 29 species were collected which were classified as rare. The most of rare species were found in meadows under the bird variant (20 species), the same number of species (12 each) was recorded in the extensive package and the habitat variant, and the smallest number of species (9) was found in the conventional meadows (see Appendix). The management regime affected the number of rare species (Table 16) and the statistically significant differences, as in the case of the number of individuals, were determined only between the C-meadows and the B-meadows (Fig. 34). In both cases, random variable "plot" was statistically significant.

Table 15. Results of the generalized linear mixed model with Gaussian error distribution and the identity-link function assessing the effect of the management regime on spider abundance of rare species in meadows. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Management regime	3.438	3,76	**0.021**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.632 ± 0.208	3.040	**0.002**
Year	0.017 ± 0.029	0.573	0.567

Table 16. Results of the generalized linear mixed model with Gaussian error distribution and the identity-link function assessing the effect of the management regime on the number of rare spider species in meadows. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Management regime	3.470	3,76	**0.020**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	1.057 ± 0.437	2.419	**0.016**
Year	0.012 ± 0.064	0.186	0.852

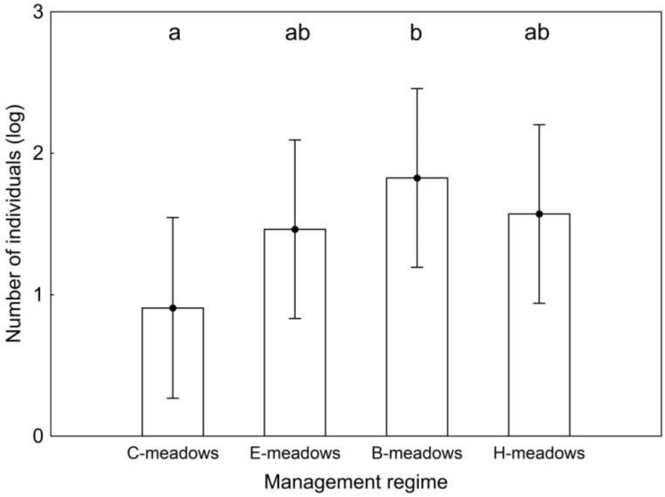

Fig. 33. Abundance of rare spider species (mean with 95% confidence limits) in four management regimes. The means are estimated from the GLMM presented in Table 15. Different letters above the bars indicate significant differences between management regimes ($P = 0.039$)

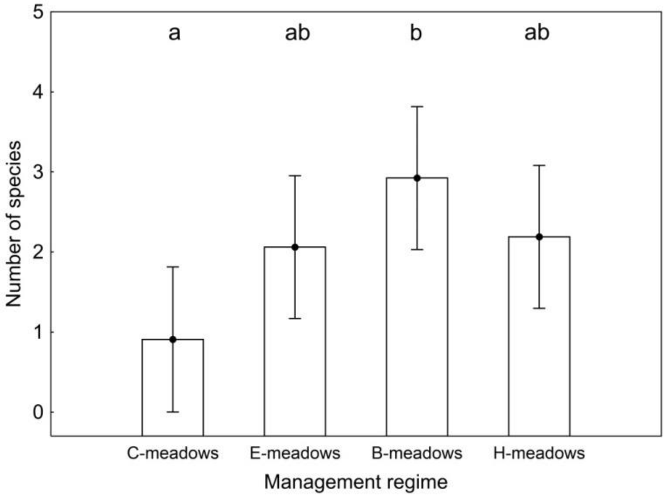

Fig. 34. Number of rare spider species (mean with 95% confidence limits) in four management regimes. The means are estimated from GLMM presented in Table 16. Different letters above the bars indicate significant differences between management regimes (*P* = 0.002)

Comparison of spider species composition

The RDA analysis showed that the spider species composition was not affected by management regime in meadows (sum of all eigenvalues = 0.07; Monte Carlo Permutation Test *F* = 1.58; *P* = 0.197). All canonical axes explained only 7% of the total variation (Table 17). Despite the fact that the model was not significant, the ordination diagram indicates that some management regimes may favour certain species (Fig. 35). B-meadows were suitable for spider species like *Walckenaeria atrotibialis*, *Zora armillata*, *Ozyptila brevipes*, whereas the conventional meadows were preferred by *Oedothorax apicatus, O. fuscus*, *Araeoncus humilis, Pachygnatha clercki*. Meadows under habitat variant were favoured by *Agyneta affinis* and *Ozyptila westringi*.

Table 17. Results of the redundancy analysis (RDA) of the impact of management regimes on spider species composition

Axes	1	2	3	4	Total variance
Eigenvalues	0.061	0.006	0.002	0.729	1.000
Sum of all canonical eigenvalues					0.070

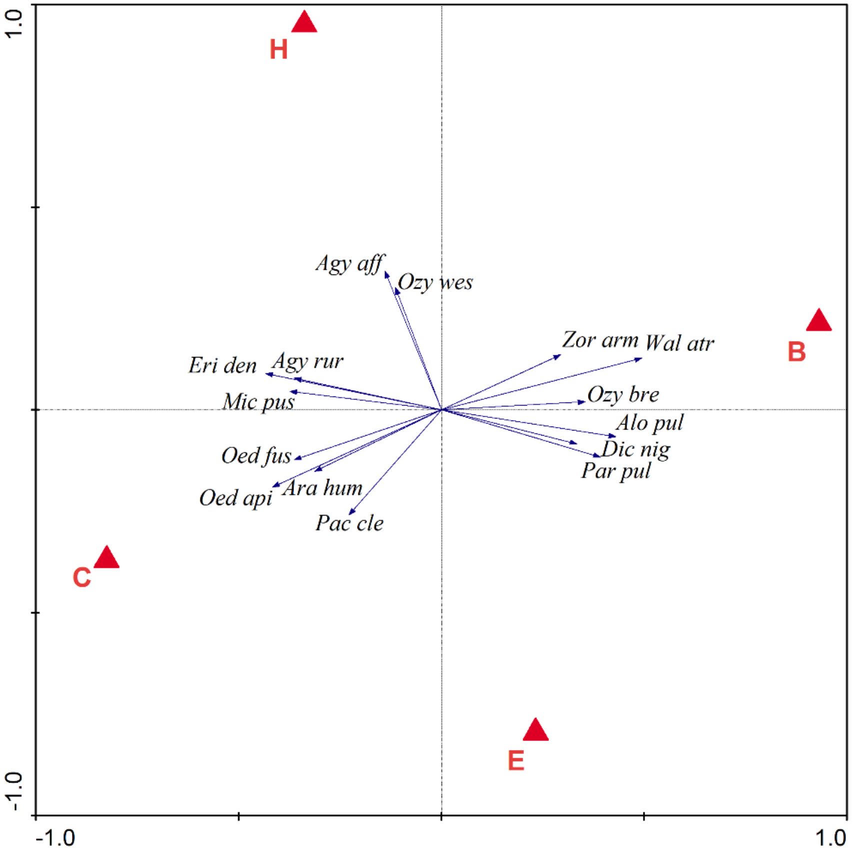

Fig. 35. Ordination diagram (RDA) showing the association of spider species with the four management regimes: C – conventional meadows, E – meadows in extensive package, B – meadows in bird variant, H – meadows in habitat variant. Only spider species with a fit-range above 10% are shown. Abbreviations of spider names: *Agy aff – Agyneta affinis, Agy rur – Agyneta rurestris, Alo pul – Alopecosa pulverulenta, Ara hum – Araeoncus humilis, Dic nig – Dicymbium nigrum, Eri den – Erigone dentipalpis, Mic pus – Microlinyphia pusilla, Oed api – Oedothorax apicatus, Oed fus – Oedothorax fuscus, Ozy bre – Ozyptila brevipes, Ozy wes – Ozyptila westringi, Pac cle – Pachygnatha clercki, Par pul – Pardosa pullata, Wal atr – Walckenaeria atrotibialis, Zor arm – Zora armillata*

4.2. Effect of mowing

4.2.1. Abundance, species richness and species diversity

Mowing had a significant effect on the abundance of spiders only in the third sampling period, whereas no effect was observed in the two other analysed periods (Table 18). In the third sampling period, significantly more individuals were found in the plots where mowing was carried out at least four weeks before material collection (L-mown meadows) compared to unmown plots (Fig. 36). Neither the species richness nor the species diversity was affected by mowing in any of the analysed sampling periods (Tables 19, 20; Figs. 37, 38). No significant differences were found in any of the analysed cases, neither between plots or between years (Tables 18, 19, 20).

Table 18. Results of the generalized linear mixed models assessing the effect of mowing on the abundance of spiders in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	0.001	1,78	0.975
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.082 ± 0.050	1.651	0.099
Year	0.069 ± 0.078	0.887	0.375
Third sampling period			
Mowing effect	4.316	2,76	**0.017**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.089 ± 0.066	1.349	0.177
Year	0.020 ± 0.035	0.564	0.573
Fourth sampling period			
Mowing effect	1.202	3,73	0.315
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.158 ± 0.153	1.034	0.301
Year	Not estimated		

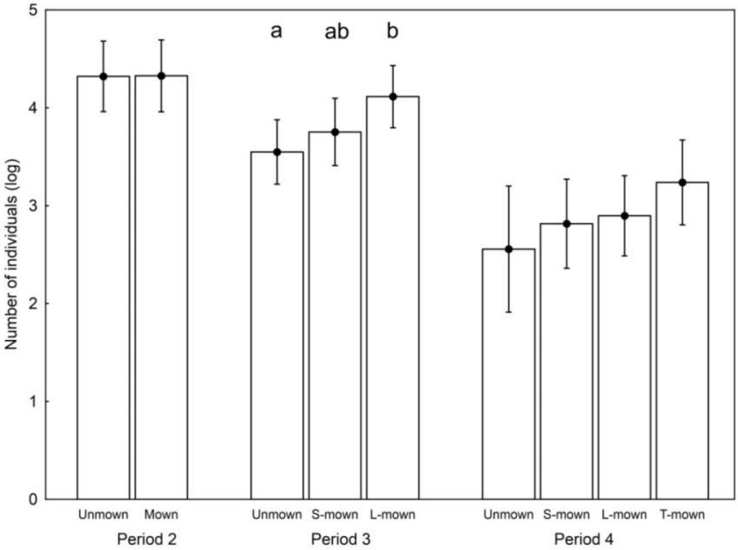

Fig. 36. Abundance of spiders (mean with 95% confidence limits) in different groups of meadows in three sampling periods. Legend: Unmown – meadows that have not yet been mown; Mown – mown meadows; S-mown – meadows that were mown not earlier than four weeks (in the case of the third sampling period) or five weeks (in the case of the fourth sampling period) before material collection; L-mown – meadows that were mown more than four weeks (the third period) or five weeks (the fourth period) before material collection; T-mown – meadows that were mown twice. The means are estimated from GLMM presented in Table 18. Different letters above the bars indicate significant differences between the meadows (*P* = 0.005)

Table 19. Results of the generalized linear mixed models assessing the effect of mowing on the species richness of spiders in the second, third and fourth sampling periods

Variable	***F***	***df*1,*df*2**	***P***
Second sampling period			
Mowing effect	2.659	1,78	0.107
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	2.567 ± 2.909	0.882	0.378
Year	2.226 ± 2.792	0.797	0.425
Third sampling period			
Mowing effect	0.118	2,76	0.889
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	2.725 ± 1.875	1.453	0.146
Year	0.678 ± 1.104	0.614	0.539
Fourth sampling period			
Mowing effect	1.478	3,73	0.228
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.129 ± 1.115	0.115	0.908
Year	0.617 ± 0.961	0.642	0.521

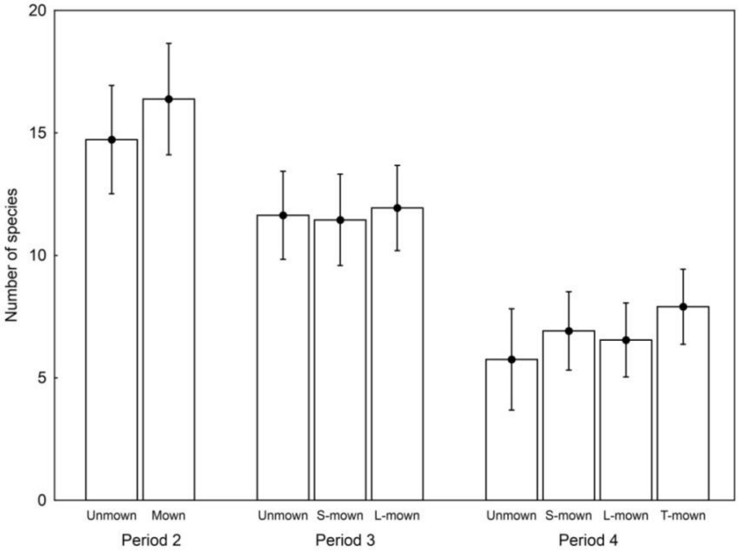

Fig. 37. Species richness of spiders (mean with 95% confidence limits) in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 19

Table 20. Results of generalized linear mixed models assessing the effect of mowing on the species diversity of spiders in the second, third and fourth sampling periods

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	1.248	1,78	0.267
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.028 ± 0.019	1.501	0.133
Year	Not estimated		
Third sampling period			
Mowing effect	0.140	2,76	0.870
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.026 ± 0.020	1.280	0.201
Year	0.012 ± 0.016	0.719	0.472
Fourth sampling period			
Mowing effect	0.282	3,73	0.838
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.039 ± 0.039	0.982	0.326
Year	0.010 ± 0.019	0.517	0.605

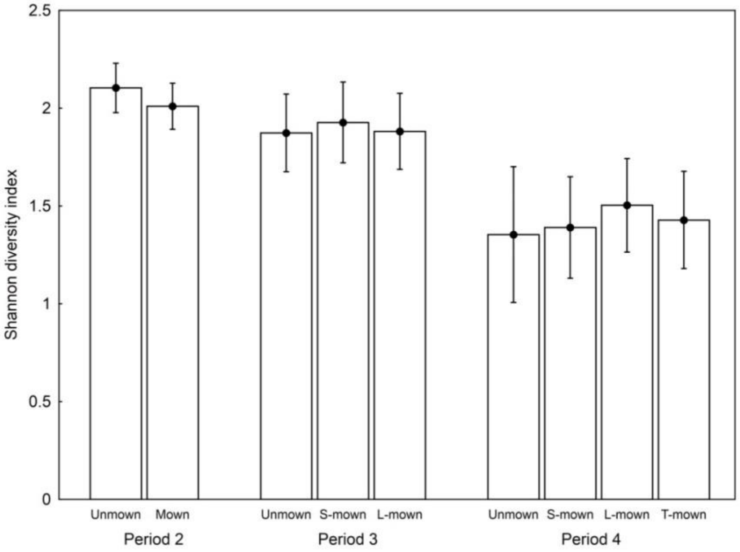

Fig. 38. Species diversity of spiders (mean with 95% confidence limits) in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 20

4.2.2. Families

The effect of mowing on the number of families was significant only in the third sampling period (Table 21). In this period, the number of families found in the mown (both S-mown and L-mown) meadows was statistically significantly smaller than in the meadows that had not yet been mown (Fig. 39).

Of the three analysed families, the effect of mowing on the number of captured individuals was found only in the case of the family *Linyphiidae* (Table 22; Fig. 40), whereas no such effect was found for the families *Lycosidae* and *Tetragnathidae* (Tables 23, 24; Figs. 41, 42). In the second and third research period, the number of linyphiids captured on the meadows that were already mown was larger compared to those that had not yet been mown. In the fourth research period, statistically significant differences were found between unmown and S-mown meadows on the one hand and between L-mown and T-mown meadows on the other hand. In the two latter groups of meadows, the number of individuals belonging to the family *Linyphiidae* was almost twice as high as in the two former groups (Fig. 40).

No effect of mowing on the number of captured spider species, representing the two families analysed in this respect, i.e. *Lycosidae* and *Linyphiidae*, was observed in any of the analysed sampling periods (Tables 25, 26; Figs. 43, 44).

Moreover, significant differences were found between plots (in a few cases), but not between years of the study (Tables 21, 22, 23, 24, 25, 26).

Table 21. Results of generalized linear mixed models assessing the effect of mowing on the number of spider families in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	3.640	1,78	0.060
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	1.666 ± 0.599	2.783	**0.005**
Year	0.790 ± 0.845	0.935	0.350
Third sampling period			
Mowing effect	5.636	2,76	**0.005**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.100 ± 0.185	0.538	0.590
Year	0.254 ± 0.308	0.824	0.410
Fourth sampling period			
Mowing effect	1.848	3,73	0.146
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	Not estimated		
Year	0.148 ± 0.206	0.717	0.473

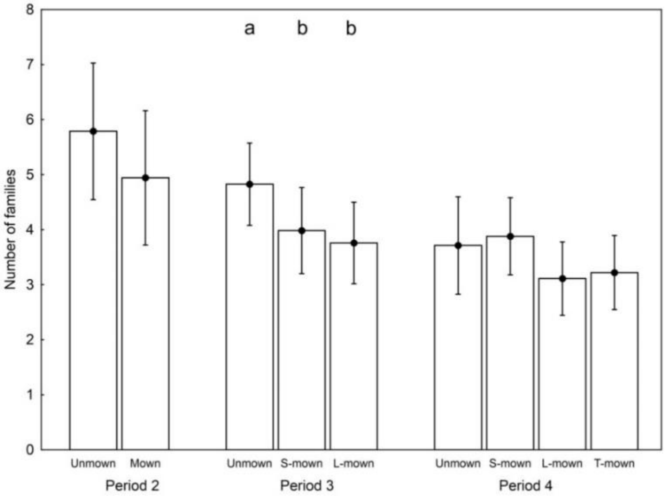

Fig. 39. Number of spider families (mean with 95% confidence limits) in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 21. Different letters above the bars indicate significant differences between the meadows ($P < 0.020$)

Table 22. Results of generalized linear mixed models assessing the effect of mowing on the abundance of spiders of the family *Linyphiidae* in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	4.967	1,78	**0.029**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.637 ± 0.525	1.213	0.225
Year	0.211 ± 0.321	0.707	0.512
Third sampling period			
Mowing effect	6.891	2,76	**0.002**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.310 ± 0.159	1.943	0.052
Year	0.118 ± 0.148	0.797	0.425
Fourth sampling period			
Mowing effect	3.267	3,73	**0.026**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.298 ± 0.164	1.823	0.068
Year	0.619 ± 0.647	0.956	0.339

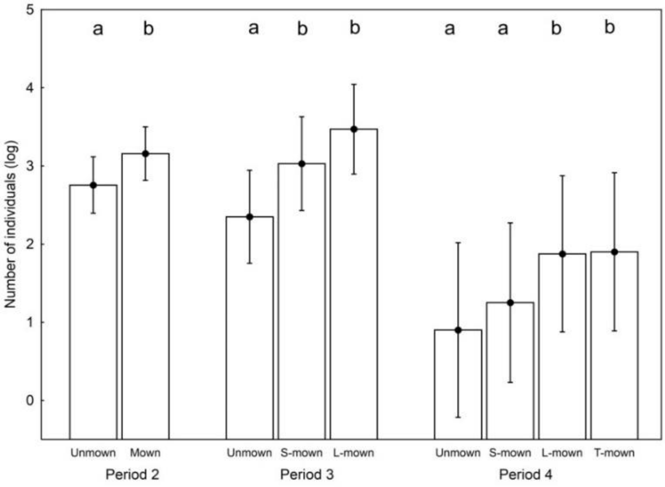

Fig. 40. Abundance of spiders (mean with 95% confidence limits) of the family *Linyphiidae* in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 22. Different letters above the bars indicate significant differences between groups of plots (Period 2: $P = 0.012$, Period 3: $P < 0.030$, Period 4: $P < 0.045$)

Table 23. Results of generalized linear mixed models assessing the effect of mowing on the abundance of spiders of the family *Lycosidae* in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Second sampling period			
Mowing effect	2.870	1,78	0.094
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.161 ± 0.098	1.642	0.101
Year	0.223 ± 0.241	0.923	0.356
Third sampling period			
Mowing effect	0.998	2,76	0.373
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.214 ± 0.100	2.133	**0.033**
Year	0.055 ± 0.073	0.747	0.455
Fourth sampling period			
Mowing effect	0.696	3,73	0.558
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.161 ± 0.128	1.259	0.208
Year	0.027 ± 0.054	0.504	0.614

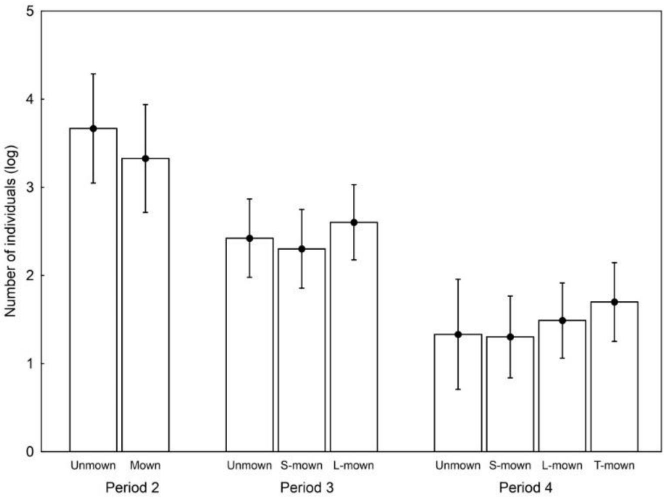

Fig. 41. Abundance of spiders (mean with 95% confidence limits) of the family *Lycosidae* in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 23

Table 24. Results of generalized linear mixed models assessing the effect of mowing on the abundance of spiders of the family *Tetragnathidae* in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	***F***	***df*1,*df*2**	***P***
Second sampling period			
Mowing effect	0.704	1,78	0.404
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.486 ± 0.179	2.719	**0.007**
Year	0.220 ± 0.238	0.923	0.356
Third sampling period			
Mowing effect	0.384	2,76	0.682
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.413 ± 0.165	2.499	**0.012**
Year	0.240 ± 0.261	0.918	0.359
Fourth sampling period			
Mowing effect	2.642	3,73	0.056
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.201 ± 0.200	1.002	0.316
Year	0.172 ± 0.214	0.803	0.422

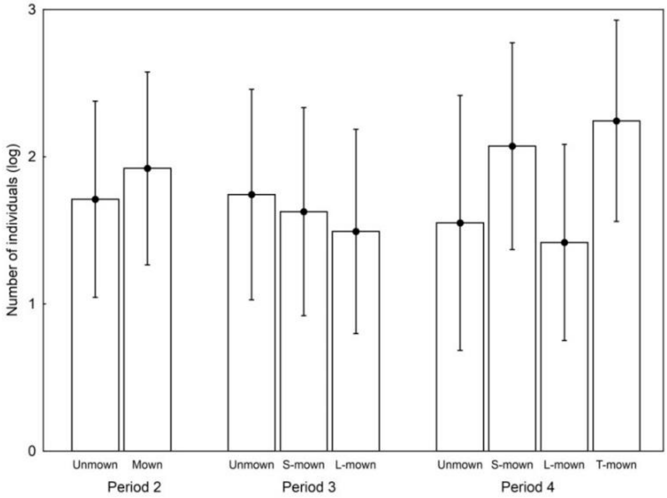

Fig. 42. Abundance of spiders (mean with 95% confidence limits) of the family *Tetragnathidae* in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 24

Table 25. Results of generalized linear mixed models assessing the effect of mowing on the species richness of spiders of the family *Lycosidae* in the second, third and fourth sampling periods

Variable	***F***	***df*1,*df*2**	***P***
Second sampling period			
Mowing effect	3.098	1,78	0.082
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.404 ± 0.519	0.779	0.436
Year	0.086 ± 0.218	0.393	0.695
Third sampling period			
Mowing effect	0.885	2,76	0.417
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.697 ± 0.384	1.815	0.070
Year	Not estimated		
Fourth sampling period			
Mowing effect	1.727	3,73	0.169
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.147 ± 0.282	0.521	0.603
Year	Not estimated		

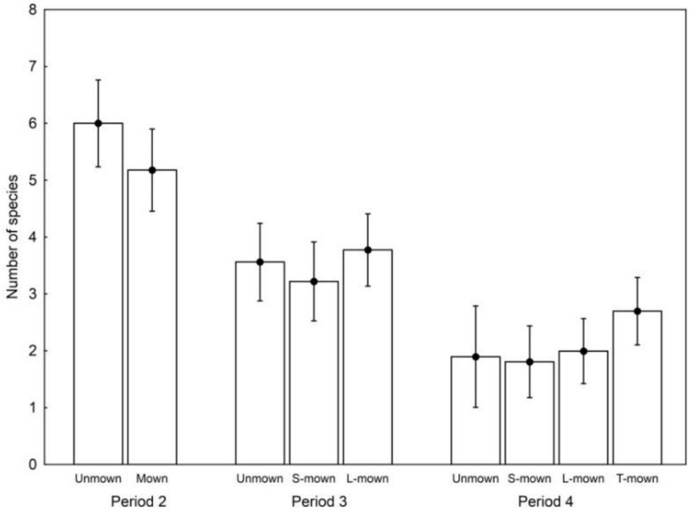

Fig. 43. Species richness of spiders (mean with 95% confidence limits) of the family *Lycosidae* in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 25

Table 26. Results of generalized linear mixed models assessing the effect of mowing on the species richness of spiders of the family *Linyphiidae* in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	0.219	1,78	0.641
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	2.228 ± 1.075	2.073	**0.038**
Year	0.449 ± 0.609	0.738	0.460
Third sampling period			
Mowing effect	1.508	2,76	0.228
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	1.765 ± 0.963	1.833	0.067
Year	0.214 ± 0.404	0.531	0.596
Fourth sampling period			
Mowing effect	1.937	3,73	0.131
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.796 ± 0.564	1.413	0.158
Year	1.787 ± 1.894	0.943	0.345

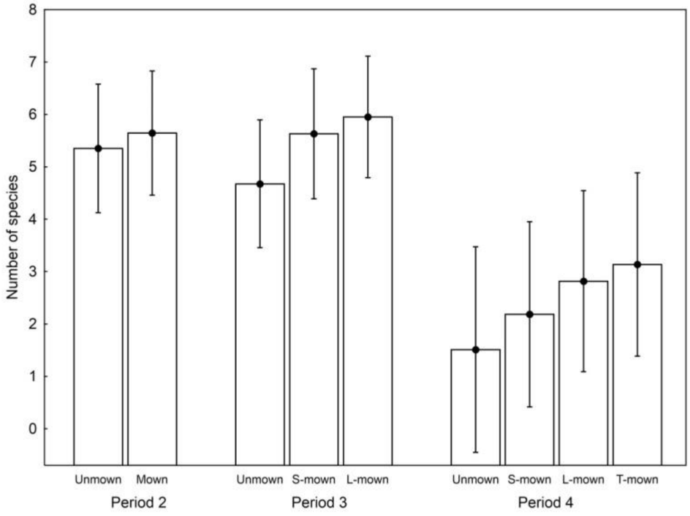

Fig. 44. Species richness of spiders (mean with 95% confidence limits) of the family *Linyphiidae* in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 26

4.2.3. Guilds

The effect of mowing on the number of spiders belonging to the guilds of ground hunters and sheet web weavers was not revealed in any of the study periods (Tables 27, 28; Figs. 45, 46). In the case of other hunters, the effect of mowing on the abundance of spiders was significant in the last two sampling periods (Table 29). In the third sampling period, significantly more individuals belonging to this guild were captured on L-mown meadows compared to meadows that had not yet been mown. Whereas in the fourth sampling period, the largest number of individuals belonging to other hunters was found on T-mown meadows compared to unmown plots (Fig. 47).

Species richness of ground hunters was significantly affected by mowing in the second sampling period (Table 30) and more species from this guild were revealed on unmown plots than on mown ones (Fig. 48). In the case of other hunters, species richness was not affected by mowing in any of the sampling periods (Table 31; Fig. 49).

Moreover, significant differences were found between plots (in a few cases), but not between years of the study (Tables 27, 28, 29, 30, 31).

Table 27. Results of generalized linear mixed models assessing the effect of mowing on the abundance of spiders belonging to the guild of ground hunters in the second, third and fourth sampling periods

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	3.692	1,78	0.058
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.166 ± 0.096	1.734	0.083
Year	0.234 ± 0.251	0.930	0.352
Third sampling period			
Mowing effect	0.778	2,76	0.463
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.175 ± 0.090	1.940	0.052
Year	0.063 ± 0.080	0.778	0.436
Fourth sampling period			
Mowing effect	0.430	3,73	0.732
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.124 ± 0.118	1.054	0.292
Year	Not estimated	-	-

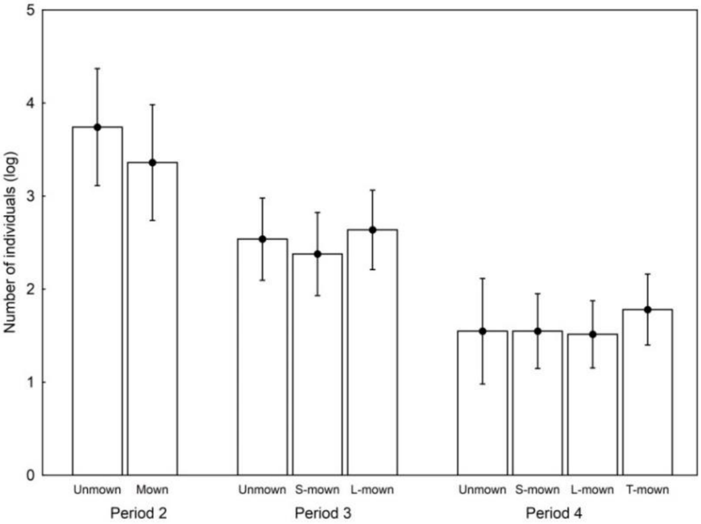

Fig. 45. Abundance of spiders (mean with 95% confidence limits) belonging to the guild of ground hunters in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 27

Table 28. Results of generalized linear mixed models assessing the effect of mowing on the abundance of spiders belonging to the guild of sheet web weavers in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	0.028	1,78	0.866
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.191 ± 0.095	2.014	**0.044**
Year	0.003 ± 0.020	0.140	0.889
Third sampling period			
Mowing effect	1.121	2,76	0.331
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.462 ± 0.188	2.458	**0.014**
Year	0.047 ± 0.071	0.654	0.513
Fourth sampling period			
Mowing effect	1.824	3,73	0.150
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.072 ± 0.069	1.038	0.299
Year	0.244 ± 0.257	0.947	0.343

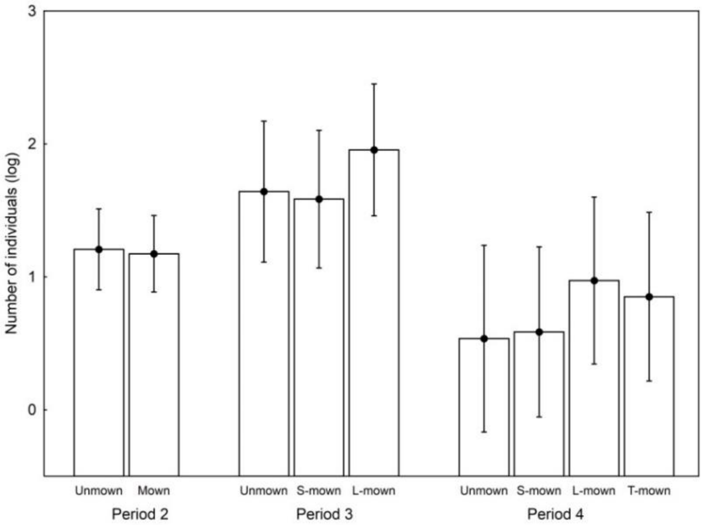

Fig. 46. Abundance of spiders (mean with 95% confidence limits) belonging to the guild of sheet web weavers in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 28

Table 29. Results of generalized linear mixed models assessing the effect of mowing on the abundance of spiders belonging to the guild of other hunters in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	2.523	1,78	0.116
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.131 ± 0.104	1.257	0.209
Year	0.029 ± 0.050	0.585	0.559
Third sampling period			
Mowing effect	3.698	2,76	**0.029**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.320 ± 0.160	1.997	**0.046**
Year	0.110 ± 0.138	0.798	0.425
Fourth sampling period			
Mowing effect	2.730	3,73	**0.049**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.733 ± 0.429	1.707	0.088
Year	1.464 ± 1.541	0.950	0.342

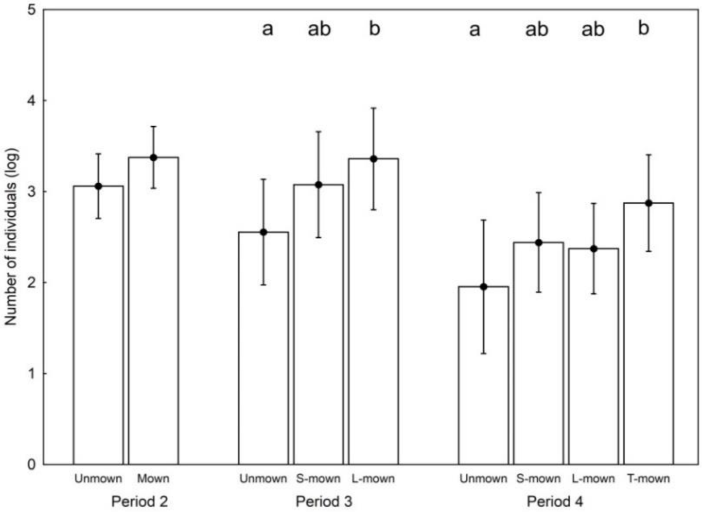

Fig. 47. Abundance of spiders (mean with 95% confidence limits) belonging to the guild of other hunters in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 29. Different letters above whiskers indicate significant differences between groups of plots (Period 3: $P < 0.009$, Period 4: $P < 0.035$)

Table 30. Results of generalized linear mixed models assessing the effect of mowing on the species richness of spiders belonging to the guild of ground hunters in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	***df*1,*df*2**	*P*
Second sampling period			
Mowing effect	11.070	1,78	**0.001**
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.944 ± 0.898	1.051	0.293
Year	0.884 ± 1.096	0.806	0.420
Third sampling period			
Mowing effect	1.780	2,76	0.176
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.584 ± 0.492	1.185	0.236
Year	Not estimated		
Fourth sampling period			
Mowing effect	1.159	3,73	0.331
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.173 ± 0.340	0.510	0.610
Year	Not estimated		

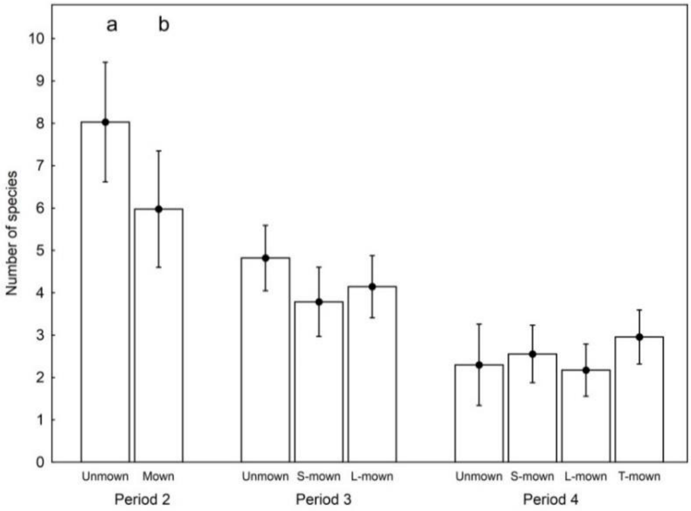

Fig. 48. Species richness of spiders (mean with 95% confidence limits) belonging to the guild of ground hunters in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 30. Different letters above the bars indicate significant differences between groups of plots ($P < 0.001$)

Table 31. Results of generalized linear mixed models assessing the effect of mowing on the species richness of spiders belonging to the guild of other hunters in the second, third and fourth sampling periods. Significant results are shown in bold

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	0.719	1,78	0.399
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	2.830 ± 1.069	2.646	**0.008**
Year	0.486 ± 0.589	0.825	0.409
Third sampling period			
Mowing effect	1.295	2,76	0.280
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	2.837 ± 1.058	2.682	**0.007**
Year	0.253 ± 0.374	0.678	0.497
Fourth sampling period			
Mowing effect	0.942	3,73	0.425
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.090 ± 0.461	1.972	**0.049**
Year	0.422 ± 0.498	0.847	0.397

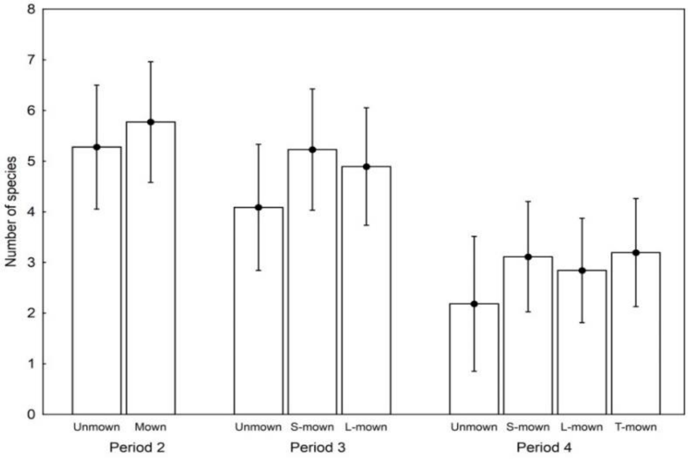

Fig. 49. Species richness of spiders (mean with 95% confidence limits) belonging to the guild of other hunters in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 31

4.2.4. Species composition and rare species occurrence

Rare species

The mowing did not influence the probability of occurrence in a sample of individuals belonging to the rare species in the three sampling periods (Table 32; Fig. 50).

Table 32. Results of generalized linear mixed models assessing the effect of mowing for the probability of occurrence of spider individuals belonging to the rare species in the second, third and fourth sampling periods

Variable	*F*	*df*1,*df*2	*P*
Second sampling period			
Mowing effect	2.154	1,78	0.146
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	1.003 ± 0.738	1.358	0.174
Year	0.191 ± 0.381	0.502	0.616
Third sampling period			
Mowing effect	2.307	2,76	0.107
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.023 ± 0.505	0.046	0.964
Year	Not estimated		

Fourth sampling period			
Mowing effect	0.569	3,73	0.637
Random variable	Estimate ± *SE*	*Z*	*P*
Plot	0.072 ± 0.803	0.090	0.929
Year	0.144 ± 0.452	0.318	0.750

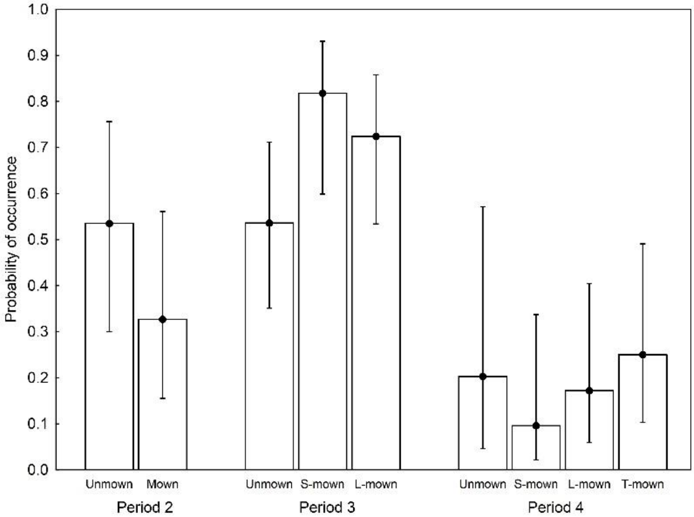

Fig. 50. Probability of occurrence (with 95% confidence limits) of spider individuals belonging to the rare species in different groups of meadows in three sampling periods. Legend as in Fig. 36. The means are estimated from GLMMs presented in Table 32

Spider species composition in relation to mowing

The RDA analysis performed for the data collected in the second period showed that mowing regime crucially affects the composition of spider assemblages in studied meadows (sum of all eigenvalues = 0.228; Monte Carlo Permutation Test $F = 5.14$; $P = 0.001$). The all canonical axes explained 22.8% of the total variation, of which 19.5% was explained by the Axis 1 (Table 33). The ordination diagram clearly demonstrated that mown meadows were suitable for *E. dentipalpis* whereas unmown plots were preferred by *Walckenaeria atrotibialis, Alopecosa pulverulenta, Piratula hygrophila, Pardosa pullata* (Fig. 51). *Pardosa palustris, Pardosa prativaga, Haplodrassus signifer, Bathyphanthes gracilis* and *Drassyllus pusillus* were located intermediate between mown and unmown plots.

In the third sampling period, similarly to the second one, the mowing regime influenced the composition of local spider assemblages. Although the model was significant (Monte Carlo Permutation Test *F* = 5.34; *P* = 0.001), the all canonical axes explained only 7.6% of the total variation (Axis 1 explained 7.2%) (Table 34). The ordination diagram showed that *Walckenaeria atrotibialis*, *Piratula hygrophila* and *Drassyllus praeficus* clearly preferred unmown plots, whereas *Mermessus trilobatus* and *Agyneta rurestris* favoured L-mown meadows, but the last relationship was not significant (Fig. 52).

In the fourth sampling period, the mowing regime affected the composition of spider assemblages, as in the other two research periods. Though, the model was significant (Monte Carlo Permutation Test *F* = 5.03; *P* = 0.013), the all canonical axes explained only 8.4% of the total variation (Axis 1 explained 6.9%) (Table 35). The ordination diagram showed that twice mown meadows (T-meadows) were preferred by *Pardosa palustris, Agyneta rurestris, Erigone dentipalpis, Xerolycosa miniata, Microlinyphia pusilla*, while *Agyneta affinis* favoured L-mown meadows whereas *Diplostyla concolor* and *Zelotes latreillei* preferred unmown or S-mown meadows, but the two last relationships were not significant (Fig. 53).

Table 33. Results of the redundancy analysis (RDA) of the impact of mowing regime on spider assemblages in the second sampling period

Axes	**1**	**2**	**3**	**4**	**Total variance**
Eigenvalues	0.195	0.033	0.335	0.168	1.000
Sum of all canonical eigenvalues					0.228

Table 34. Results of the redundancy analysis (RDA) of the impact of mowing regime on spider assemblages in the third sampling period

Axes	**1**	**2**	**3**	**4**	**Total variance**
Eigenvalues	0.072	0.004	0.332	0.167	1.000
Sum of all canonical eigenvalues					0.076

Table 35. Results of the redundancy analysis (RDA) of the impact of mowing regime on spider assemblages in the fourth sampling period

Axes	**1**	**2**	**3**	**4**	**Total variance**
Eigenvalues	0.069	0.014	0.001	0.605	1.000
Sum of all canonical eigenvalues					0.084

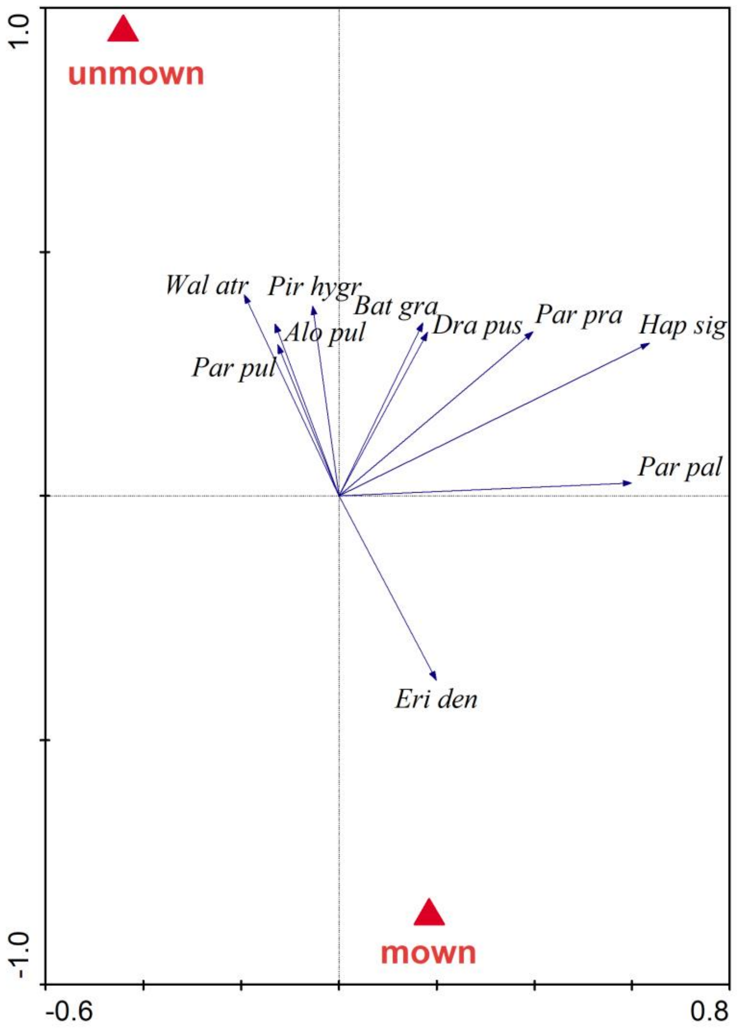

Fig. 51. Ordination diagram (RDA) showing the association of spider species to mown and unmown meadows in the second sampling period (Monte Carlo Permutation Test: mown – *F* = 16.53, *P* = 0.019; unmown – *F* = 5.14, *P* = 0.001). Only spider species with a fit-range above 10% are shown. Legend: unmown – meadows that have not yet been mown; mown – mown meadows. Abbreviations of spider names: *Alo pul – Alopecosa pulverulenta, Bat gra – Bathyphantes gracilis, Dra pus – Drassyllus pusillus, Eri den – Erigone dentipalpis, Hap sig – Haplodrassus signifier, Par pal – Pardosa palustris, Par pra – Pardosa prativaga, Par pul – Pardosa pullata, Pir hyg – Piratula hygrophila, Wal atr – Walckenaeria atrotibialis*

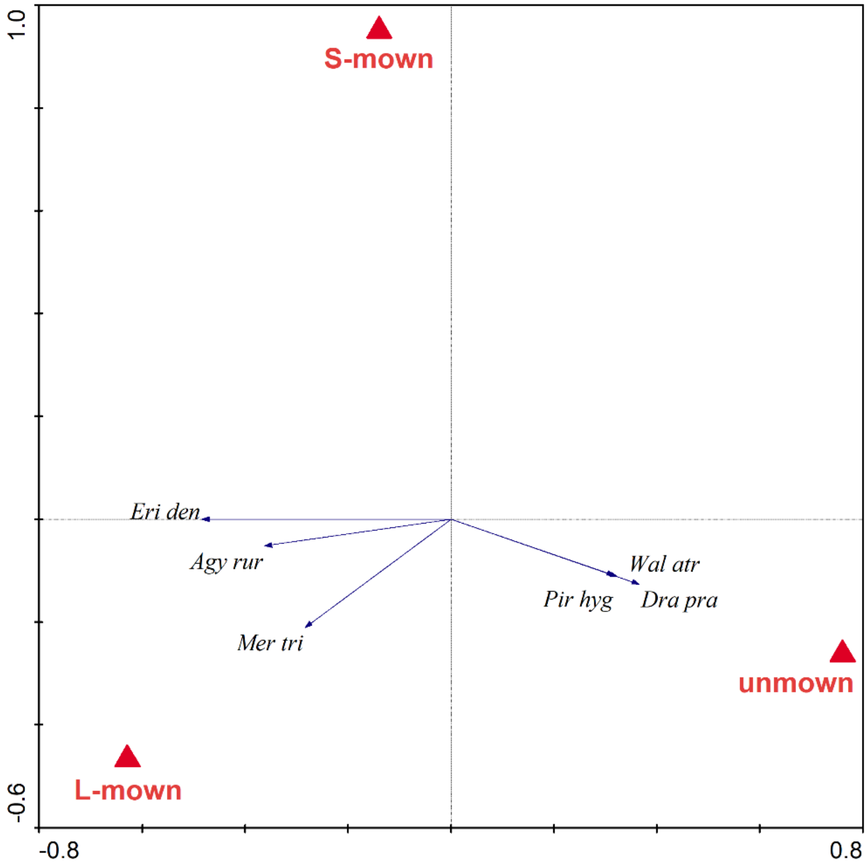

Fig. 52. Ordination diagram (RDA) showing the association of spider species to unmown, S-mown and L-mown meadows in the third sampling period (Monte Carlo Permutation Test: unmown – *F* = 5.34, *P* = 0.001; S-mown and L-mown – *P* > 0.05). Only spider species with a fit-range above 10% are shown. Legend: unmown – meadows that have not yet been mown; S-mown – meadows that were mown not earlier than four weeks before material collection; L-mown – meadows that were mown more than four weeks before material collection. Abbreviations of spider names: *Agt rur – Agyneta rurestris*, *Dra pra – Drassyllus praeficus*, *Eri den – Erigone dentipalpis*, *Mer tri – Mermessus trilobatus*, *Pir hyg – Piratula hygrophila*, *Wal atr – Walckenaeria atrotibialis*

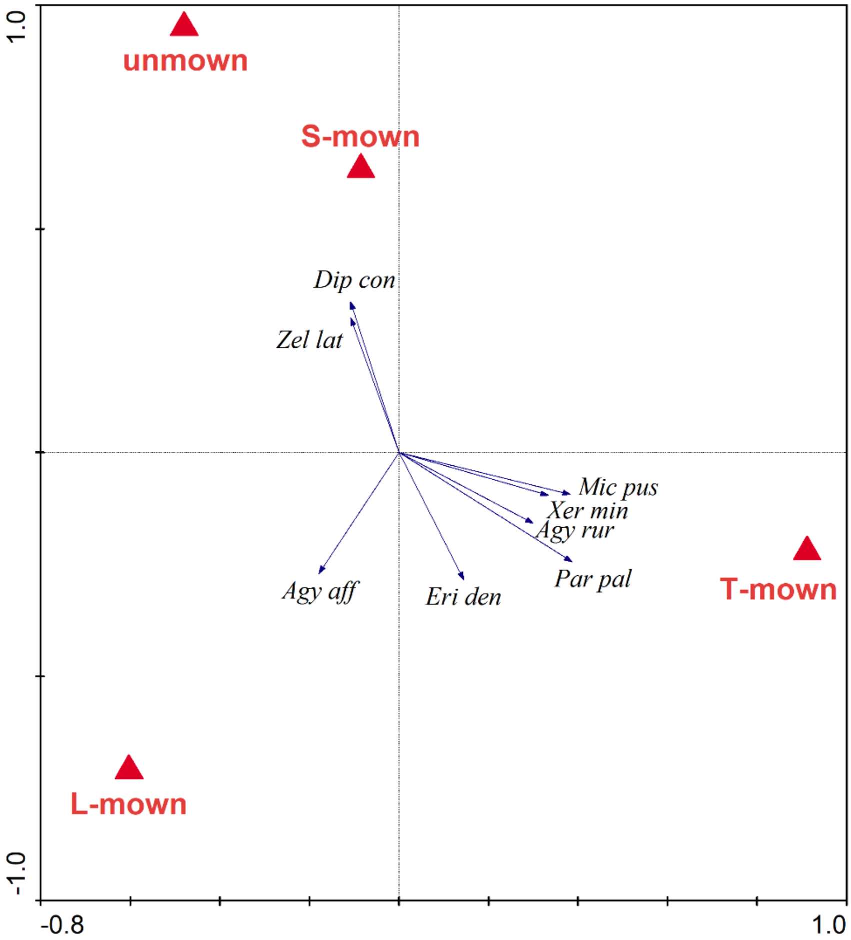

Fig. 53. Ordination diagram (RDA) showing the association of spider species to unmown, S-mown, L-mown and T-mown meadows in the fourth sampling period (Monte Carlo Permutation Test: T-mown – $F = 5.03$, $P = 0.013$; unmown, S-mown and L-mown – $P > 0.05$). Only spider species with a fit-range above 10% are shown. Legend: unmown – meadows that have not yet been mown; S-mown – meadows that were mown not earlier than five weeks before material collection; L-mown – meadows that were mown more than five weeks before material collection; T-mown – meadows that were mown twice. Abbreviations of spider names: *Agy aff* – *Agyneta affinis, Agy rur* – *Agyneta rurestris, Dip con* – *Diplostyla concolor, Eri den* – *Erigone dentipalpis, Mic pus* – *Microlinyphia pusilla, Par pal* – *Pardosa palustris, Zel lat* – *Zelotes latreillei, Xer min* – *Xerolycosa miniata*

5. DISCUSSION

5.1. Impact of management regimes on spider assemblages

The obtained results only partially confirmed the hypothesis that the management regime affects the epigeic spider assemblages in meadows. Although there were some differences between meadows under different management regimes, they were rather small and there were not many of them. The differences found were related to the total number of spider species, the number of species belonging to two guilds: ground hunters and other hunters, the number of families, the abundance of the family *Linyphiidae* as well as the abundance and the number of rare species. In addition, some of the parameters characterising the spider assemblages were found to be different only in some of the sampling periods.

The hypothesis tested in this study that the management regime affects the spider assemblages was based on the fact that the analysed meadows differed in terms of the date of the first cut (and subsequent ones, if any), the number of cuts, leaving (or not) unmown fragments in a meadow and performing such management practices as fertilization or grazing. All of these factors play a key role in the shaping of invertebrate assemblages inhabiting hay meadows, including spiders (e.g. Knop et al. 2006; Buri et al. 2013; Buri et al. 2014; Birkhofer et al. 2015). Unfortunately, it is very difficult to assess the impact of each of these factors separately based on the research carried out in real agricultural conditions, as was the case in this study. Therefore, all the factors mentioned above that differentiate meadows and affect spider assemblages make up what we call the management regime. This type of approach is quite often found in studies comparing the impact of agriculture management regimes of different intensity on organisms as well as those investigating the effectiveness of AES (e.g. Schwab et al. 2002; Knop et al. 2006). An alternative to this type of research is to carry out an experiment in which, for example, the number and timing of cuts are strictly planned, specific doses of fertilizers are applied, etc. (Thorbek & Blide 2004). Such studies obviously provide valuable information on the impact of individual agricultural treatments on invertebrate assemblages inhabiting meadows, but they do not provide an answer to the question of how these organisms are affected by the actual farming where treatments performed are not determined by a researcher.

The previous research assessing the impact of management regimes on spider communities living in meadows showed mixed effects. The majority of authors proved that more intensive farming (usually a more intensive mowing regime) has a negative effect on spider species richness, diversity and abundance (Birkhofer et al. 2015; Buri et al. 2016; Řezáč & Heneberg 2018). However, in some studies, the difference between more and less intensive management regimes has not been demonstrated at all (Knop et al. 2006; Pech et al. 2015).

One of the factors which have a huge impact on organisms occurring in meadows is the mowing regime, i.e. the number and timing of cuts and the method of mowing. In general, delaying the first cut has a significant positive effect on invertebrate species richness, species diversity and abundance (Humbert et al. 2012; Buri et al. 2013; Buri et al. 2016). In some cases, this effect may be extremely strong, e.g. orthopteran densities in meadows of Switzerland, where mowing was delayed by a month, were up to five times higher compared to reference sites (Buri et al. 2013). Spiders may also be positively affected by delayed mowing, e.g. Buri et al. (2016) showed that their density was about 80% higher in meadows where mowing was delayed (carried out after 15 July) compared to reference meadows (mown after 15 June). On the other hand, Knop et al. (2006) did not observe any changes in the species richness and species evenness of spiders in meadows where mowing was delayed in relation to control meadows.

In this study, the management regimes differed significantly in the timing of mowing. Most of the C-meadows were mown for the first time at the end of May and early June, while meadows under the bird variant (the most restrictive variant in terms of mowing deadlines) were mown in August and September. In the case of E-meadows, the first cut was carried out from June to September, whereas the most of H-meadows were mown for the first time around mid-June. It is the concentration of mowing on multiple plots at the same time can be the cause of the difference between the management regimes in species richness (calculated per sample), which was significantly lower on H-meadows compared to C-and B-meadows. Time-synchronized cuts, especially over large areas, considerably reduce both the species diversity and abundance of common arthropods (Cizek et al. 2012). The difference in the number of species may also partly result from the fact that mowing carried out in mid-summer has a much greater negative impact on species diversity and abundance of spiders than mowing carried out in spring and late summer or autumn (Baines et al. 1998).

The analysed management regimes also differed in the number of species belonging to two guilds: ground hunters and other hunters. In the case of the former, statistically significant differences were found between B-meadows (where the largest number of species was found) and the other types of meadows, which may indicate that the delay in the first cut is an important factor positively affecting the number of species belonging to this guild. However, in the case of the guild of other hunters, the smallest number of species was found on H-meadows, which (as in the case of the total number of species) may result from the fact that most of the cuts in this management regime were carried out in the same period of the growing season.

Surprisingly, the studied spider assemblages generally did not differ significantly in terms of the species diversity and abundance, however, in the case of the latter parameter, the differences between management regimes were found in the third and fourth sampling period. At that time, more spiders were caught on C- and H-meadows compared to meadows with the two other management regimes, which was mainly due to the presence of a larger number of individuals of the family *Linyphiidae*, which clearly preferred mown areas (all C-meadows and most H-meadows were mown before the third sampling period). *Linyphiidae* was the only analysed family that was noticeably affected by the management regime and significantly more linyphiid individuals were collected on C-meadows (mown first) than on B-meadows (mown last). This is mainly due to the fact that the family *Linyphiidae* comprises many pioneer species that colonize both the intensively mown areas (Nentwig 1988) and heavily grazed pastures (de Keer & Maelfait 1988). This may be the reason for some differences in the species composition of spider assemblages in particular management regimes.

Generally, meadows under different management regimes were characterised by similar species composition, although the average contribution of particular species was slightly different. In C- and H-meadows a higher contribution of *Pardosa palustris* (35% and 30%, respectively) compared to E- and B-meadows (c. 20%) was observed. This may indicate that this species prefers meadows with a more intensive management regime, which was confirmed by the results of the research conducted by Batáry et al. (2012), who showed the higher abundance of *P. palustris* on conventionally used meadows (mown more often) compared to organic meadows. The situation was similar for *Oedothorax fuscus*, the contribution of which was on average 5% on C-meadows and did not exceed 1% on other types of meadows. It is a pioneer species that occurs on intensively cut grasslands (Nentwig 1988) and grazed pastures (de Keer & Maelfait 1987). It is worth to emphasise that *Erigone dentipalpis* reached the lowest contribution in the latest and least frequently mown meadows in bird variant compared to other meadows where its contribution was several times higher. This spider is considered to be a typical agrobiont – an abundant species in disturbed, predictably ephemeral habitats (Samu & Szinetár 2002).

The assessment of the impact of management regimes on spiders is to some extent hampered by their phenology. It is a group of invertebrates, whose abundance changes drastically during the season and individual families reach their abundance peaks in different periods of the growing season. It is very likely that some changes in the abundance or species richness caused e.g. by mowing coincide with changes caused by natural causes, and most likely this kind of situation took place in the presented research. In the second and third research period, the abundance of the family *Linyphiidae* increased more than twice compared to the first period. This change may have been partly caused by their phenology, but also by the first cuts carried out on the surveyed meadows. This could be indicated by the increased abundance of linyphiids in meadows under the management regimes with the earliest mowing, i.e. C- and H-meadows. This is also evidenced by the analysis of abundance on the mown and unmown plots, which showed that the increase occurred on mown plots. It is also possible that the increase in the abundance caused by the phenology of this family and the increase caused by mowing coincided in time.

One of the reasons for the lack of major differences between the management regimes may have been the large variation in timing of the first cut within each of them. Consequently, some of the C-meadows were mown at the same time as E- or H-meadows. Although there were other differentiating factors such as e.g. leaving (or not) unmown refugia or a varying number of cuts, it could still happen that in a particular year one plot under a given management regime did not differ (in terms of timing and the number of cuts) from a plot under another management regime. Nevertheless, this study was intended to compare different management regimes and to check the effectiveness of agri-environment programme under actual farming conditions. The timing and the number of cuts were not agreed with farmers – they were carried out at farmers' discretion and the only regulations followed by the meadow owners were those imposed by the implemented agri-environment packages.

Another reason for the relatively small differences in spider assemblages inhabiting meadows under different management regimes may be the inclusion in the analysis of the period when meadows were not yet mown and spiders were then most abundant (the first sampling period). During this period, there were hardly any statistically significant differences in the analysed parameters (except species richness of ground hunters guild). In the other sampling periods, there were many more differences between the analysed management regimes, but then mowing was the factor contributing to these differences. The first sampling period, however, could not be excluded from the analyses, because their assumption was to check how the management regime affects the spider assemblages, not only at the time of mowing (i.e. from the second to the fourth sampling period). The lack of huge differences in spider assemblages in the first sampling period proved that such differences occur only during that period when pratotechnical treatments are applied in meadows. When this factor is absent, the spider communities show significant similarity.

5.2. Effect of mowing

Mowing has a significant effect on many groups of organisms. It is a necessary treatment preventing the encroachment of bushes and trees in meadows, and consequently secondary succession; one or two cuts per year are beneficial for meadow plant diversity (Antonsen & Olsson 2005; Pech et al. 2015; Smith et al. 2018). The problem is more complicated in the case of invertebrates. On the one hand, part of the study showed an increase in the abundance and diversity of some groups of these animals after mowing or lack of any changes (Knop et al. 2006; Birkhofer et al. 2015). On the other hand, many other studies provided evidence for the negative impact of mowing on many groups of invertebrates, including spiders (Nyffeler & Breene 1990; Baines et al. 1998; Polchaninova 2003; Thorbek & Bilde 2004; Cizek et al. 2012). Spiders, as less mobile compared to invertebrates equipped with wings, can suffer much more from mowing within a short period of time compared to those capable of flying and thus quickly escaping butterflies or beetles (Mazalová et al. 2015).

The decline in the abundance and biodiversity of spiders during and after mowing is a result of several factors. Firstly, spiders die as a result of a direct impact, i.e. killed during mowing, and secondly, some of those who managed to survive, migrate from a mown habitat immediately after plants are cut. Thorbek & Blide (2004) showed that the abundance of spiders can decrease by up to 50%, as a result of these two factors, one week after cutting the grass. The habitat structure changes as a result of mowing, both due to vegetation cutting and soil destruction by equipment used for mowing and haymaking. The vegetation structure which directly influenced web spiders (Uetz 1991) preventing many species from constructing webs and getting food, greatly impacts ground-dwelling spiders as well (Lafage & Pétillon 2014). Plants are used by spiders as places of mating, laying eggs, shelter, wintering and as platforms from where they can move through gossamer threads (Robinson 1981; Uetz 1991; Wise 1995). Reducing the height of vegetation in a short period of time causes major changes in microclimate conditions, like humidity, shade, temperature (Guido & Gianelle 2001; Gardiner & Hassall 2009). In order to avoid dehydration, spiders move to places with higher vegetation, where humidity is higher and the temperature is lower (de Keer et al. 1989). Furthermore, in an exposed habitat, devoid of complex vegetation, they are also more likely to fall prey to predators, mainly birds (Gunnarsson 1996). The food resources of spiders, including the abundance of springtails, also decline as a result of mowing (Purvis & Curry 1981). The cumulative effect of mortality, emigration and the above-mentioned changes in the habitat resulting from mowing can be much greater than direct mortality, which suggests delayed effects of habitat disruption, lasting at least a few weeks (Thorbek & Blide 2004).

Considering the above negative factors acting on spiders, it was expected that parameters such abundance, species richness and species diversity would be significantly lower on the mown plots compared to unmown plots. Surprisingly, the presented study has not shown any major negative impact of mowing on epigeic spider assemblages. The negative impact was observed only in the case of the number of families, which was significantly lower on the mown plots in the third sampling period, and the number of species belonging to the guild of ground hunters, which was also lower on the mown plots in the second sampling period. Mowing had no significant effect on species richness and species diversity in any of the sampling periods, while in the case of spider abundance – a positive effect was observed in the third period. Other authors have also reported results that do not confirm the negative impact of mowing on spider assemblages. For example, Pech et al. (2015) collected more individuals of spiders on mown plots but did not find any differences in species richness and species composition. On the other hand, Buri et al. (2016) found significantly fewer spiders at mown sites compared to unmown sites. Therefore, it seems that the results may largely depend on the analysed group of spiders. Individual families, functional groups (e.g. guilds) or even species of spiders can respond differently to changes that occur during mowing. The research conducted by Cattin et al. (2003) on waterlogged grasslands in western Switzerland showed that the abundance of certain less mobile families such as *Clubiondae* and *Hahniidae* was reduced as a result of mowing. In the case of *Clubionidae*, this could be associated with the mowing of reed beds, because dry stems of reeds are used by spiders from this family as overwintering shelters. The negative impact on *Hahniidae*, on the other hand, may be due to changes in the structure of litter and soil surface. For example, one of the species of this family, *Antistea elegans*, builds webs in small ground depressions, which are destroyed by mowing equipment. Thorbek & Blide (2004) showed that *Erigone atra* suffers most from the process of cutting (being killed during mowing), while *Bathyphantes gracilis* emigrates immediately after mowing. *Oedothorax apicatus*, on the other hand, suffers from these two factors. In general, spiders inhabiting vegetation and less mobile epigeic spiders tend to reach higher abundance on unmown plots, whereas wandering species show preferences for mown grasslands (Nyffeler & Breene 1990; Cattin et al. 2003; Polhaninova 2003).

The presented study also has shown that various groups of spiders respond differently to mowing. The abundance of the families *Lycosidae* and *Tetragnathidae* did not differ between unmown and mown plots (regardless of when the mowing was carried out). On the other hand, mowing enhanced the abundance of linyphiids and spiders belonging to the guild of other hunters, which consisted mainly of members of this family. Larger numbers of spiders from these groups on mown meadows may indicate that such areas are an excellent habitat for colonisation by these organisms. Linyphiids are characterised by a great ability to spread, e.g. through ballooning, which may be a cause of their increased number after mowing (e.g. Dean & Sterling 1985; Greenstone et al. 1987; Blandenier & Fürst 1998). The increase in the abundance of these spiders after mowing may result from recolonisation by spiders migrating from adjacent mown areas or refugia (e.g. field margins, wasteland), where they could hide to survive agricultural treatments carried out in meadows.

5.3. Assessment of the agri-environment programme's role

There is no doubt that agri-environment programmes by imposing certain rules in the meadow management regimes, such as a delay in the first cut or the obligation to leave unmown places as refugia, play a major role in promoting the biodiversity of many groups of organisms, including spiders (e.g. Buri et al. 2013; Buri et al. 2014; Buri et al. 2016). On the other hand, some studies do not confirm the positive impact of AES on spider assemblages or the results obtained are not conclusive. For example, Knop et al. (2006) showed that the species richness and species evenness of spiders did not differ between control meadows and meadows under the agri-environment scheme. Řezáč & Heneberg (2018) found that the abundance of spiders was three times higher in meadows covered by AES compared to meadows under standard management, but only common vegetation-dwelling farmland spiders reached higher abundance, while epigeic spiders declined or were insensitive to AES.

The results obtained in this study did not confirm the hypothesis that spider assemblages are more abundant, more rich in species and have higher species diversity in meadows covered by agri-environment programme compared to conventionally managed meadows. The formulating of such a hypothesis was supported first of all by the smaller number of cuts carried out in meadows covered by the programme (C-meadows are significantly different in this respect from E- and B-meadows) and the delay of the first cut (up to 2-3 months) compared to conventionally used meadows. Secondly, conventionally used meadows were mown completely, i.e. without leaving any unmown fragments, which was obligatory in meadows included in packages. This is a very important factor because such refugia play a major function in preserving the biodiversity (Buri et al. 2013; Buri et al. 2014). Individuals that emigrated from mown meadows gather in such places, and consequently, the latter can be recolonised, which mitigates the negative effects of mowing (Mazalová et al. 2015). The third aspect that distinguished the meadows in agri-environment packages from the conventionally used meadows was the use of small doses of fertilizers and grazing of small herds of cows in September and October after the sampling. Both these factors may have some influence on spider assemblages (Bell et al. 2001), but they were applied only occasionally and their impact was probably insignificant. However, it cannot be entirely excluded.

Nevertheless, some findings may indicate a positive role of certain management regimes in AES in promoting the biodiversity of spiders. First of all, most of the species – 122 – identified during the three years of the study were found on B-meadows, while only 92 species were found on C-meadows and H-meadows. In addition, a larger number of rare species and individuals of these species was captured in meadows covered by the agri-environment packages, although statistically significant differences were found only between C- and B-meadows. The largest number of families was also found in meadows in the bird variant. This was probably due to the fact that meadows covered by this variant were mown the latest and the smallest number of times (at least during sampling). Such a combination of these two factors seems to be the most favourable for spiders, which is also recommended by other authors (Cizek et al. 2012; Lafage & Pétillon 2014). However, these findings are not sufficient to prove the important role of the agri-environment programme in preserving the biodiversity of spiders.

Several potential causes may explain the lack of significant differences between meadows in the agri-environment programme and conventionally used meadows. First of all, the effectiveness of AES depends on the analysed group of organisms. For example, Knop et al. (2006), in their research in meadows in Switzerland, found that species richness of vascular plants, grasshoppers and wild bees was significantly higher on hay meadows covered by agri-environment scheme compared to conventionally used meadows, whereas no such regularity was observed in the case of spiders. Secondly, the effectiveness of AES largely depends on landscape complexity (Batáry et al. 2011; Concepción et al. 2012). The species richness increases from simple to complex landscapes, because in this gradient the number of habitats that are sources of biodiversity also increases. In this study, the landscape within a 500 m radius from a given plot did not differ in the number of patches of particular habitats and their percentage contribution. All studied plots were located in the landscape typical of the Lublin region, consisting of a mosaic of fields, meadows, forests, clumps of trees and small watercourses. This could largely contribute to the lack of significant differences between spider assemblages in different management regimes. It can, therefore, be assumed that leaving unmown refugia did not bring the expected effects, because the fragmented landscape of the Lublin region provides many natural refugia (e.g. field margins, wasteland, clumps of trees). Furthermore, the high fragmentation of meadows also meant that mowing was carried out at different times in different places instead of synchronised mowing over a large area, which can negatively affect the spider assemblages (Thorbek & Blide 2004). According to the literature, the effectiveness of AES is much greater in simplified landscapes compared to the complex ones (Batáry et al. 2011) and in the case of the Lublin region, we had to deal with the latter one.

6. CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The study revealed a relatively moderate difference between the analysed meadow management regimes in terms of their impact on epigeic spider assemblages. Furthermore, no significant differences were found between conventionally used meadows and meadows included in the agri-environment programme in terms of the analysed parameters, especially those under the extensive package and the habitat variant. On the other hand, a positive effect on spider assemblages was observed in the case of the bird variant. The highest number of species was found on the meadows under this variant, both per sample (in this case together with C-meadows) and in total captured during three years of the research. These meadows were also characterised by the largest number of rare species and individuals belonging to these species, the largest number of exclusive species and the largest number of spider families. The management regime there was characterised by the most restrictive limitations regarding the date of mowing (mowing was not permitted here until the first of August) as well as the smallest number of cuts carried out during the sampling periods.

The lack of clear differences between the conventionally used meadows versus meadows under the extensive package and the habitat variant may indirectly indicate that leaving unmown sites in meadows as refugia and delaying the first cut by about a month do not have a positive effect on epigeic spider assemblages. On the other hand, some results show that spider assemblages are positively affected (at least in terms of the total number of species and the number of rare species and individuals belonging to these species) by a considerable delay in mowing (until August, when spiders are already much less abundant) as well as the diversification of cutting over time. The latter finding may be supported by the fact that the smallest number of spider species was found on the meadows under the habitat variant, both in total and on average per sample, which probably resulted mainly from the fact that most cuts were carried out at the same time in growing season (i.e. in the second decade of June, i.e. immediately after the date when mowing was allowed on these meadows).

Although the mere execution of mowing did not cause a decline in the abundance, species richness and species diversity of spiders, it affected the composition of spider assemblages. The higher abundance of spiders of the family *Linyphiidae* (and the guild of other hunters, which consists mostly of spiders of this family) was observed at mown sites of the meadows, which indicates that mostly these spiders colonise meadows after cutting.

The conducted research proves that the implementation of the agri-environment programme in areas where extensive farming is carried out, in a highly fragmented landscape, as in the case of the Lublin region, brings moderate effects in promoting the biodiversity of epigeic spiders. This may be due to the existence of many natural refugia (e.g. field margins, clumps of trees), where spiders can hide after mowing and from where they migrate to recolonise the mown areas. Secondly, the strong fragmentation of the landscape makes mowing synchronised in time and space much less likely (many individual meadow owners acting independently), which also gives spiders the opportunity to escape to unmown areas. Thirdly, in addition to mowing, agricultural activity in meadows is carried out in a moderate manner (small doses of fertilizers, occasional, not very intensive grazing), which probably results in a less destructive effect of the mowing operation on spiders.

Obviously, the findings of the presented study refer to epigeic spiders in the specific area, while in other areas, with more intensive farming and less fragmented landscapes, differences between management regimes may be much larger and agri-environment programme more effective. In the case of the surveyed area, maintaining the current form of agriculture, with possible delays in mowing, seems to be a sufficient measure to preserve the biodiversity of epigeic spiders. Nonetheless, based on the results of the conducted research, it is possible to formulate several recommendations for agriculture, the implementation of which, both in the study area and other areas, may contribute to the preservation of high biodiversity of epigeic spiders in meadows. They include:

1) delaying the first cut until August
2) ensuring the existence of refugia – both natural, e.g. in the form of field margins, or created by leaving unmown fragments of meadows
3) performing no more than 1–2 cuts during the growing season
4) differentiation of cuts in time and space.

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8. APPENDIX

List of spider species recorded in mesic meadows in different management regimes.

Legend:
C – conventional meadows, E – meadows in extensive package, B – meadows in bird variant, H – meadows in habitat variant; Guilds of spiders (based on Cardoso et al. 2011): ground hunters (GH), other hunters (OH), ambush hunters (AH), sheet web weavers (SW), space web weavers (SPW), orb web weavers (OW), specialists (S); Categories of threatened species (based on the "Red list of threatened animals in Poland"): endangered (EN), vulnerable (VU), data deficient (DD); R – rare species known from less than 20 localities in Poland.

Species	Guild	Threat	C	E	B	H	Total
Araneidae							
Araneus quadratus Clerck, 1757	OW		0	1	0	0	1
Argiope bruennichi (Scopoli, 1772)	OW		0	1	0	0	1
Cercidia prominens (Westring, 1851)	OW		0	0	2	0	2
Hypsosinga pygmaea (Sundevall, 1831)	OW		0	1	0	1	2
Larinia jeskovi Marusik, 1986	OW	EN	1	0	0	0	1
Mangora acalypha (Walckenaer, 1802)	OW		0	1	0	1	2
Clubionidae							
Clubiona diversa O. P.-Cambridge, 1862	OH	VU	0	1	2	0	3
Clubiona neglecta O. P.-Cambridge, 1862	OH		0	0	2	2	4
Clubiona reclusa O. P.-Cambridge, 1863	OH		0	2	4	1	7
Clubiona stagnatilis Kulczyński, 1897	OH		0	4	0	0	4
Clubiona subtilis L. Koch, 1867	OH		0	0	1	0	1

Species	**Guild**	**Threat**	**C**	**E**	**B**	**H**	**Total**
Dictynidae							
Argenna patula (Simon, 1874)	GH	R	0	0	1	0	1
Argenna subnigra (O. P.-Cambridge, 1861)	GH		9	19	26	18	72
Eutichuridae							
Cheiracanthium erraticum (Walckenaer, 1802)	OH		0	0	4	0	4
Gnaphosidae							
Drassodes pubescens (Thorell, 1856)	GH		0	1	2	3	6
Drassyllus lutetianus (L. Koch, 1866)	GH		5	11	11	16	43
Drassyllus praeficus (L. Koch, 1866)	GH	VU	1	12	31	13	57
Drassyllus pusillus (C. L. Koch, 1833)	GH		34	36	58	54	182
Haplodrassus moderatus (Kulczyński, 1897)	GH	EN	0	0	2	0	2
Haplodrassus signifier (C. L. Koch, 1839)	GH		0	1	3	0	4
Haplodrassus silvestris (Blackwall, 1833)	GH		0	1	2	0	3
Micaria formicaria (Sundevall, 1831)	GH		1	0	0	0	1
Micaria pulicaria (Sundevall, 1831)	GH		4	4	10	9	27
Zelotes aeneus (Simon, 1878)	GH		3	0	1	1	5
Zelotes apricorum (L. Koch, 1876)	GH		1	0	0	0	1
Zelotes electus (C. L. Koch, 1839)	GH		2	1	10	1	14
Zelotes latreillei (Simon, 1878)	GH		1	7	9	3	20
Zelotes longipes (L. Koch, 1866)	GH		3	0	3	4	10

Species	Guild	Threat	C	E	B	H	Total
Hahniidae							
Antistea elegans (Blackwall, 1841)	SW		0	1	0	0	1
Hahnia nava (Blackwall, 1841)	SW		18	37	33	32	120
Hahnia pusilla C. L. Koch, 1841	SW		0	4	0	0	4
Linyphiidae							
Abacoproeces saltuum (L. Koch, 1872)	OH		0	0	1	0	1
Agyneta affinis (Kulczyński, 1898)	SW		164	73	147	344	728
Agyneta fuscipalpa (C. L. Koch, 1836)	SW		2	0	0	1	3
Agyneta mollis (O. P.-Cambridge, 1871)	SW		39	11	28	28	106
Agyneta mossica (Schikora, 1993)	SW	DD	0	0	1	0	1
Agyneta rurestris (C. L. Koch, 1836)	SW		77	19	9	60	165
Agyneta saxatilis (Blackwall, 1844)	SW		0	0	0	1	1
Allomengea vidua (L. Koch, 1879)	SW		0	0	1	0	1
Araeoncus humilis (Blackwall, 1841)	OH		40	15	4	12	71
Bathyphantes gracilis (Blackwall, 1841)	SW		34	36	22	33	125
Bathyphantes nigrinus (Westring, 1851)	SW		0	0	1	0	1
Bathyphantes parvulus (Westring, 1851)	SW		0	2	15	0	17
Centromerita bicolor (Blackwall, 1833)	SW		1	0	0	0	1
Ceratinella brevipes (Westring, 1851)	OH		18	18	6	0	42
Ceratinella brevis (Wider, 1834)	OH		0	4	1	3	8
Ceratinella major Kulczyński, 1894	OH	EN	0	0	1	0	1

Species	**Guild**	**Threat**	**C**	**E**	**B**	**H**	**Total**
Dicymbium nigrum (Blackwall, 1834)	OH		34	54	92	21	201
Diplocephalus cristatus (Blackwall, 1833)	OH		2	1	0	0	3
Diplostyla concolor (Wider, 1834)	SW		2	6	22	22	52
Erigone atra Blackwall, 1833	OH		438	351	127	222	1138
Erigone dentipalpis (Wider, 1834)	OH		588	262	45	564	1459
Erigone longipalpis (Sundevall, 1830)	OH	R	1	0	0	0	1
Gnathonarium dentatum (Wider, 1834)	OH		1	15	2	0	18
Gongylidiellum latebricola (O. P.-Cambridge, 1871)	OH		0	1	0	0	1
Gongylidiellum murcidum Simon, 1884	OH		1	1	3	2	7
Kaestneria pullata (O. P.-Cambridge, 1863)	SW		0	0	2	0	2
Lophomma punctatum (Blackwall, 1841)	OH		0	1	0	0	1
Mermessus trilobatus (Emerton, 1882)	OH		4	4	0	7	15
Metopobactrus prominulus (O. P.-Cambridge, 1873)	OH		1	9	22	1	33
Micrargus herbigradus (Blackwall, 1854)	OH		1	0	3	1	5
Micrargus subaequalis (Westring, 1851)	OH		52	60	104	48	264
Microlinyphia pusilla (Sundevall, 1830)	SW		8	1	0	5	14
Neriene clathrata (Sundevall, 1830)	SW		1	0	0	0	1
Oedothorax apicatus (Blackwall, 1850)	OH		84	4	1	3	92
Oedothorax fuscus (Blackwall, 1834)	OH		504	40	13	77	634
Oedothorax gibbosus (Blackwall, 1841)	OH		0	0	3	1	4
Oedothorax retusus (Westring, 1851)	OH		223	74	122	153	572
Palliduphantes alutacius (Simon, 1884)	SW		0	0	0	1	1

Species	Guild	Threat	C	E	B	H	Total
Palliduphantes insignis (O. P.-Cambridge, 1913)	SW		1	0	0	0	1
Pelecopsis parallela (Wider, 1834)	OH		3	12	5	0	20
Pocadicnemis juncea Locket & Millidge, 1953	OH		2	3	10	3	18
Pocadicnemis pumila (Blackwall, 1841)	OH		2	1	1	1	5
Porrhomma campbelli F. O. P.-Cambridge, 1894	SW	DD	0	0	0	1	1
Porrhomma microphthalmum (O. P.-Cambridge, 1871)	SW	VU	4	1	4	5	14
Porrhomma pygmaeum (Blackwall, 1834)	SW		2	1	0	0	3
Savignia frontata Blackwall, 1833	OH		3	13	4	0	20
Silometopus elegans (O. P.-Cambridge, 1873)	OH	VU	0	0	0	1	1
Stemonyphantes lineatus (Linnaeus, 1758)	SW		0	1	0	0	1
Styloctetor compar (Westring, 1861)	OH		3	15	10	1	29
Tallusia expert (O. P.-Cambridge, 1871)	SW		1	0	0	0	1
Tapinocyba insecta (L. Koch, 1869)	OH		0	0	2	0	2
Tapinocyboides pygmaeus (Menge, 1869)	OH	R	0	0	1	0	1
Tenuiphantes mengei (Kulczyński, 1887)	SW		0	1	1	0	2
Tiso vagans (Blackwall, 1834)	OH		8	9	19	2	38
Trichopternoides thorelli (Westring, 1861)	OH	EN	0	0	1	0	1
Walckenaeria antica (Wider, 1834)	OH		0	0	2	0	2
Walckenaeria atrotibialis (O. P.-Cambridge, 1878)	OH		1	5	69	6	81
Walckenaeria dysderoides (Wider, 1834)	OH		0	0	1	0	1
Walckenaeria nudipalpis (Westring, 1851)	OH		0	0	1	0	1
Walckenaeria vigilax (Blackwall, 1853)	OH		1	1	2	0	4

Species	Guild	Threat	C	E	B	H	Total
Liocranidae							
Agroeca brunnea (Blackwall, 1833)	GH		0	0	1	0	1
Agroeca cuprea Menge, 1873	GH		0	0	1	0	1
Liocranoeca striata (Kulczyński, 1882)	GH		2	5	7	2	16
Lycosidae							
Alopecosa cuneata (Clerck, 1757)	GH		18	18	24	13	73
Alopecosa pulverulenta (Clerck, 1757)	GH		73	152	306	47	578
Arctosa leopardus (Sundevall, 1833)	GH		116	72	5	86	279
Arctosa lutetiana (Simon, 1876)	GH	VU	1	2	2	7	12
Aulonia albimana (Walckenaer, 1805)	GH		0	2	3	1	6
Hygrolycosa rubrofasciata (Ohlert, 1865)	GH	VU	0	0	2	0	2
Pardosa agrestis (Westring, 1861)	GH		115	60	21	115	311
Pardosa amentata (Clerck, 1757)	GH		8	0	1	5	14
Pardosa lugubris (Walckenaer, 1802)	GH		7	1	2	3	13
Pardosa maisa Hippa & Mannila, 1982	GH	VU	0	1	0	0	1
Pardosa monticola (Clerck, 1757)	GH		0	0	0	1	1
Pardosa paludicola (Clerck, 1757)	GH		19	12	19	6	56
Pardosa palustris (Linnaeus, 1758)	GH		3607	2321	1536	2998	10462
Pardosa prativaga (L. Koch, 1870)	GH		534	486	790	702	2512
Pardosa pullata (Clerck, 1757)	GH		712	1155	1451	664	3982
Pirata piraticus (Clerck, 1757)	GH		9	60	28	24	121
Pirata piscatorius (Clerck, 1757)	GH		2	5	0	3	10

Species	Guild	Threat	C	E	B	H	Total
Pirata tenuitarsis Simon, 1876	GH		0	1	5	1	7
Piratula hygrophila (Thorell, 1872)	GH		6	35	23	19	83
Piratula latitans (Blackwall, 1841)	GH		28	64	58	67	217
Trochosa robusta (Simon, 1876)	GH	VU	0	0	0	1	1
Trochosa ruricola (De Geer, 1778)	GH		218	175	144	197	734
Trochosa spinipalpis (F. O. P.-Cambridge, 1895)	GH		1	8	10	5	24
Trochosa terricola Thorell, 1856	GH		1	2	1	0	4
Xerolycosa miniata (C. L. Koch, 1834)	GH		118	22	77	224	441
Mimetidae							
Ero furcata (Villers, 1789)	S		0	1	3	0	4
Miturgidae							
Zora armillata Simon, 1878	GH	EN	0	3	13	5	21
Zora spinimana (Sundevall, 1833)	GH		3	6	17	1	27
Philodromidae							
Thanatus arenarius L. Koch, 1872	OH	VU	29	63	50	25	167
Thanatus striatus C. L. Koch, 1845	OH	VU	0	6	5	0	11
Tibellus oblongus (Walckenaer, 1802)	OH		1	2	1	0	4
Phrurolithidae							
Phrurolithus festivus (C. L. Koch, 1835)	GH		9	15	29	7	60
Pisauridae							
Dolomedes fimbriatus (Clerck, 1757)	OH		0	1	1	1	3
Pisaura mirabilis (Clerck, 1757)	OH		0	2	2	0	4

Species	Guild	Threat	C	E	B	H	Total
Salticidae							
Calositticus caricis (Westring, 1861)	OH	R	0	0	0	1	1
Calositticus floricola (C. L. Koch, 1837)	OH		0	2	0	0	2
Calositticus inexpectus (Logunov & Kronestedt, 1997)	OH		3	6	1	2	12
Euophrys frontalis (Walckenaer, 1802)	OH		0	0	1	0	1
Heliophanus flavipes (Hahn, 1832)	OH		0	1	0	0	1
Marpissa radiata (Grube, 1859)	OH	VU	1	0	0	0	1
Phlegra fasciata (Hahn, 1826)	OH		0	0	1	0	1
Talavera aequipes (O. P.-Cambridge, 1871)	OH		1	1	2	0	4
Tetragnathidae							
Pachygnatha clercki Sundevall, 1823	OH		292	163	74	52	581
Pachygnatha degeeri Sundevall, 1830	OH		711	620	1149	1058	3538
Theridiidae							
Asagena phalerata (Panzer, 1801)	SPW		2	0	0	4	6
Cryptachaea riparia (Blackwall, 1834)	SPW		0	0	0	1	1
Enoplognatha caricis (Fickert, 1876)	SPW	DD	0	0	1	0	1
Enoplognatha mordax (Thorell, 1875)	SPW	VU	1	1	0	3	5
Enoplognatha thoracica (Hahn, 1833)	SPW		0	3	1	8	12
Euryopis flavomaculata (C. L. Koch, 1836)	S		1	1	10	0	12
Neottiura bimaculata (Linnaeus, 1767)	SPW		1	0	1	2	4
Robertus arundineti (O. P.-Cambridge, 1871)	SPW		2	1	1	2	6
Robertus lividus (Blackwall, 1836)	SPW		1	0	1	2	4

Species	**Guild**	**Threat**	**C**	**E**	**B**	**H**	**Total**
Thomisidae							
Ozyptila brevipes (Hahn, 1826)	AH		0	1	5	0	6
Ozyptila pullata (Thorell, 1875)	AH	VU	0	19	10	0	29
Ozyptila rauda Simon, 1875	AH	EN	0	20	6	0	26
Ozyptila scabricula (Westring, 1851)	AH	VU	0	0	1	3	4
Ozyptila trux (Blackwall, 1846)	AH		66	85	110	98	359
Ozyptila westringi (Thorell, 1873)	AH	R	8	11	7	73	99
Xysticus acerbus Thorell, 1872	AH		1	1	0	0	2
Xysticus bifasciatus C. L. Koch, 1837	AH		0	14	1	0	15
Xysticus cristatus (Clerck, 1757)	AH		46	74	40	24	184
Xysticus erraticus (Blackwall, 1834)	AH		0	0	1	0	1
Xysticus kochi Thorell, 1872	AH		30	9	14	22	75
Xysticus lineatus (Westring, 1851)	AH	EN	0	0	3	0	3
Xysticus striatipes L. Koch, 1870	AH		4	0	14	10	28
Xysticus ulmi (Hahn, 1831)	AH		5	4	3	4	16
Total			9247	7066	7244	8388	31945

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