Czech University of Life Sciences Prague

Faculty of Environmental Sciences
Department of Ecology

Effects of habitat structure on breeding success of Grey Partridges (*Perdix perdix*)

Diploma Thesis

Author: Sarah Sophia Mayer

Supervisor: Prof. Dr. Miroslav Šálek

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DIPLOMA THESIS ASSIGNMENT

Sarah Sophia Mayer

Nature Conservation

Thesis title

Effects of habitat structure on breeding success of Grey Partridges (Perdix perdix)

Objectives of thesis

I set out to undertake a thorough literature review on the factors influencing not only the breeding success, but also the occurrence of Grey Partridges, as well as on protective management strategies aimed at reversing the trend of their declining population. Subsequently, I analysed habitat variables influencing the breeding success of Grey Partridges in their areas of occurrence during the pre-breeding/breeding and post-breeding period (further on home ranges; HRs) in the Czech Republic using publicly available data. Therefore, the overall objective of the thesis is the identification of the impacts of habitat structures on the breeding success of Grey Partridges prior and during the breeding period as well as after the breeding period. I hypothesized that 1) breeding success of Grey Partridges depends on unmanaged, herbaceous habitats and diverse landscapes rather than cultivated, uniform areas, 2) supporting habitat structures for Grey Partridges differ between the HRs, and 3) favourable habitats for predators, such as forests, have negative influence on the breeding success of Grey Partridges. Based on my results I will give management recommendations for conservationists working on reversing the decline of this disappearing farmland bird species.

Methodology

Observations of Grey Partridges within the Czech Republic were downloaded from the public database "Avif" and filtered according to specified criteria for pre-breeding and post-breeding periods. Additionally, the conditions for successful breeding were determined on the basis of the closest distance between an observed pair and the family covey of the same year. Two home range scales (200 m and 1000 m) were buffered around the observed pre-breeding pairs in QGIS and the selected habitat variables within were calculated based on the freely available Geodatabase CORINE Land Cover 2018. Those selected habitat variables are the proportion of each land cover class, forest as well as non-forest edge lengths, and habitat diversity as the dominance index of the Simpson's Diversity Index. Afterwards, Generalized Linear Mixed-Effects Models were fitted in R to test which habitat variables influence the breeding success of Grey Partridges.

The proposed extent of the thesis

30-40 pp

Keywords

Perdix peridx, breeding success, habitat structure, farmland, home range, unmanaged area, diversity, conservation

Recommended information sources

Bro, E., Reitz, F., Clobert, J., Mayot, P., 2000. Nesting success of grey partridges (Perdix perdix) on agricultural land in North-Central France: relation to nesting cover and predator abundance. Game & Wildlife Science 17, 199–218.

Černý, M., Rymešová, D., Šálek, M., 2020. Habitat scarcity forms an ecological trap for the grey partridge (Perdix perdix) within a central European agricultural landscape. Eur J Wildl Res 66, 83. https://doi.org/10.1007/s10344-020-01422-w

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prof. Dr. Mgr. Miroslav Šálek

Supervising department

Department of Ecology

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prof. Mgr. Bohumil Mandák, Ph.D.

Head of department

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prof. RNDr. Vladimír Bejček, CSc.

Dean

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Declaration

hereby declare that I have independently elaborated the diploma/final thesis with the topic of "Effects of habitat structure on breeding success of Grey Partridges (*Perdix perdix*)" and that I have cited all the information sources that I used in the thesis and that are also listed at the end of the thesis in the list of used information sources.

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In Prague on 29.03.2023

S. Mayer
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Effects of habitat structure on breeding success of Grey Partridges (*Perdix perdix*)

Abstract

The loss of suitable habitats due to agricultural intensification is one of the main reasons why populations of farmland birds, including Grey Partridges (*Perdix perdix*), have been declining rapidly over the last 50 years. Therefore, this thesis analyses the supporting and hindering effects of habitat structures on the breeding success of Grey Partridges in their areas of occurrence during the pre-breeding/breeding and post-breeding period. Ornithological observation data from 01/2012 to 12/2021 within the Czech Republic were downloaded from the public database “Avif”, and land cover data from the geodatabase “CORINE Land Cover 2018”. Grey Partridge pairs as well as corresponding family coveys were filtered from the data based on date and group size. Next, two buffer scales (200 m and 1000 m) representing the two examined areas of occurrence (further on home ranges) were drawn around the location of the pairs in QGIS, and habitat variables (habitat proportions, diversity, length of linear features) within these home ranges were calculated. Then, the breeding success (0/1 – family covey was max. 1000 m from an observed pair earlier) was set as the response variable in two generalized linear mixed-effect models whose predictors were the habitat variables, except for the dominant category (arable land). In the pre-breeding/breeding home range (200 m buffer radius), both natural and managed grasslands, as well as linear, herbaceous structures along non-forest edges and settlements have a positive effect on the probability of a successful breeding of Grey Partridges, reflecting the importance of a concealed nesting site. The breeding success in the post-breeding home range (1000 m buffer radius) is promoted by a diverse landscape with natural grassland patches, offering good foraging grounds with a variety of insects which is essential for the chick’s survival. Simultaneously, habitat structures that represent important habitats for predators of Grey Partridges (forest edges, other productive areas (= vineyards and orchards)) decrease the probability of breeding success. The negative effect of habitat diversity in the pre-breeding/breeding home range as well as the one of other productive areas implies an ecological trap in the remaining unmanaged areas and potential alternative habitats. Therefore, the overall breeding success of Grey Partridges depends on a heterogeneous landscape with a network of natural grassland patches as well as broadly based linear, herbaceous structures.

Keywords: *Perdix perdix,* breeding success, habitat structure, home range, farmland, unmanaged area, diversity, conservation

Vlivy biotopové struktury na hnízdní úspěšnost koroptve polní (*Perdix perdix*)

Abstrakt

Ztráta vhodných stanovišť zapříčiněná zemědělskou intenzifikací je jedním z hlavních důvodů, proč počty ptáků žijících v zemědělské krajině, včetně koroptve polní (*Perdix perdix*), za posledních 50 let rapidně klesají. Z tohoto důvodu se předkládaná diplomová práce zabývá pozitivními a negativními vlivy biotopových struktur na vyvedení snůšky koroptve polní v oblastech výskytu během předhnízdního/hnízdního a pohnízdního období. Ornitologická data získaná z pozorování v rámci České republiky z období od ledna 2021 do prosince 2021 byla stažena z veřejné databáze "Avif" a data o pokryvnosti biotopů z geodatabáze "CORINE Land Cover 2018". Ze získaných dat byly vyfiltrovány páry a příslušná hejna koroptve polní na základě data a velikosti skupiny, a v QGIS byla použita dvě měřítka funkce „buffer"" (200 m a 1000 m) simulující dvě zkoumané oblasti výskytu (dále domovské okrsky) i, nakreslené okolo polohy párů a následně byly spočítány biotopové proměnné (velikost biotopů, diverzita, plochy či délky lineárních prvků) v rámci těchto kruhů. Dále, hnízdní úspěšnost (0/1 - hejno bylo max. 1000 m od dříve pozorovaného páru) byla nastavena jako vysvětlovaná proměnná ve dvou zobecněných lineárních smíšených modelech, jejichž prediktory byly biotopové proměnné, vyjma převládající kategorie (obdělávaná půda). V předhnízdním/hnízdním okrsku (rádius funkce „buffer" 200 m) mají pozitivní vliv na pravděpodobnost vyvedení snůšky koroptve polní přírodní i obhospodařované travní porosty, stejně jako lineární bylinné struktury podél nelesních okrajů a sídel. To dokazuje důležitost ukrytého místa k hnízdění. Úspěšnost vyvedení snůšky v pohnízdním domovském okrsku (rádius funkce „buffer" 1000 m) je zvyšováno diverzifikovanou krajinou s přírodními travnatými porosty, která nabízí vyhovující místa ke sběru potravy s množstvím hmyzu, který je zásadní pro přežití mláďat. Současně, stanovištní struktury, které představují dobrý životní prostor pro predátory lovící koroptve (lesní okraje a další vhodná místa jako vinice či sady) snižují pravděpodobnost vyvedení snůšky. Negativní vliv biotopové diverzity v předhnízdním/hnízdním okrsku stejně jako efekt jiných produktivních ploch naznačuje ekologickou past skrytou ve zbylých neobhospodařovaných oblastech a potenciálních alternativních biotopech. Celková hnízdní úspěšnost koroptve polní tedy závisí na heterogenní krajině se sítí přírodních travnatých ploch a široce zakládaných lineárních bylinných porostů.

Klíčová slova: *Perdix perdix*, hnízdní úspěšnost, biotopová struktura, domovský okrsek, zemědělská půda, neobhospodařované územ, diverzita, ochrana

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Lift of abbreviations

- CLC: Corine Land cover Class
- GLMM: Generalized Linear Mixed-Effects Models
- HR: Home range
- 200 HR: 200 m buffer radius home range
- 1000 HR: 1000 m buffer radius home range

1. Introduction

Farmland birds have declined rapidly since the latter half of the 20th century (Donald et al., 2001; Aebischer and Ewald, 2010; Reif and Vermouzek, 2019; Traba and Morales, 2019). One major reason for these declines is said to be the loss of habitat through the conversion of semi-natural habitats to agricultural areas (Gaston et al., 2003). Field margins and other unmanaged patches within the agricultural landscape are turned into arable land, while smaller fields are merged to large ones (Robinson and Sutherland, 2002). Thereby, the utilised agricultural area dominates the European landscape, accounting for 39,5% of the EU's land area in 2020 (Eurostat, 2022). In the Czech Republic the share of agricultural land is even higher (53,25% in 2020; Ministerstvo zemědělství, 2021). Additionally, modern agricultural practices, such as lower crop diversity, fewer crop rotations, increased usage of chemicals as fertilisers and pesticides, and intensive grassland management, are impacting bird populations negatively (Fuller et al., 1995; Newton, 2004; Frenzel et al., 2016; Reif and Vermouzek, 2019). This agricultural intensification led to a homogenization of the landscape. However, habitat heterogeneity is the key for farmland biodiversity because without it, suitable habitats for foraging, nesting, sheltering and rearing the chicks are lost (Benton et al., 2003). Furthermore, the loss of suitable habitat results in a higher risk of predation of farmland birds in agricultural landscapes (Whittingham and Evans, 2004). Together, it causes the evident declines of farmland birds (Evans, 2004), demonstrating that they are highly sensitive to agricultural intensification and, as a result, are useful bioindicators in illustrating the influence of factors on biodiversity at landscape scale (Gregory et al., 2005; Billeter et al., 2008). For example, farmland bird populations in the Czech Republic have significantly decreased since the country's accession to the EU, which followed an agricultural intensification away from the more traditional management (Reif and Vermouzek, 2019).

Thus, unmanaged patches within agricultural landscapes, such as fallow land or field margins, are very important for farmland bird species (Traba and Morales, 2019). One species that is especially dependent on a network of uncultivated habitats within the agricultural landscape is the Grey Partridge (*Perdix perdix*; Šálek et al., 2004). Specifically, field boundaries, weedy patches, ruderals, and managed hedgerows are important habitats for nesting, sheltering, rearing of the young, and foraging (Rands, 1987a; Šálek et al., 2004; Vickery et al., 2004; Černý et al., 2020). The possibility of nest concealment against predation is an important factor of nest site selection, which is why Grey Partridges choose breeding sites with abundant permanent vegetation and a high amount of dead grass and leaf litter (Panek, 1997; Rands, 1988). However, these suitable habitats are scarce in a modern agricultural landscape, forcing Grey Partridges to shift their habitat usages toward riskier or unsuitable habitat types (Harmange et al., 2019; Černý et al., 2020; Hille et al., 2021). At the same time, the remaining suitable habitats probably act as ecological traps, as the predators also select these habitats rich in prey (Bro et al., 2004; Rantanen et al., 2010; Černý et al., 2020). Therefore, the Grey Partridge experienced one of the greatest population declines of all farmland birds (Kuijper et al., 2009), comprising 99% in the Czech Republic between 1933 and 2017 (Šálek and Zámečník, 2020). Considering all of these contradictory factors, management measures aimed at stabilising Grey Partridge populations must be applied at habitat and landscape scale, with an emphasis on habitat improvement (Kuijper et al., 2009). Therefore, this thesis seeks to discover habitat structures that have an impact on Grey Partridge's breeding success in order to support these conservation measures, as breeding success is primarily what regulates population dynamics (Panek, 1997).

2. Aims and Hypothesis

I set out to undertake a thorough literature review on the factors influencing not only the breeding success, but also the occurrence of Grey Partridges, as well as to determine protective management strategies aimed at reversing the trend of their declining population. Subsequently, I analysed habitat variables influencing the breeding success of Grey Partridges in their areas of occurrence during the pre-breeding/breeding and post-breeding period (further on home ranges; HRs) in the Czech Republic using publicly available data. Therefore, the overall objective of the thesis is the identification of the impacts of habitat structures on the breeding success of Grey Partridges prior and during the breeding period as well as after the breeding period. I hypothesised that 1) breeding success of Grey Partridges depends on unmanaged, herbaceous habitats and diverse landscapes rather than cultivated, uniform areas, 2) effects of habitat structures differ between the HRs, as the requirements of Grey Partridges change from nesting to chick rearing, and 3) favourable habitats for predators, such as forests, have negative influence on the breeding success of Grey Partridges. Based on my results I will advise management recommendations for conservationists working on reversing the decline of this disappearing farmland bird species.

3. Literature Review

3.1. Ecology of Grey Partridge *Perdix perdix*

The monogamous and resident Grey Partridge (*Perdix perdix*) is originally a steppe bird, although nowadays it mainly occurs in steppe-like agricultural landscapes, such as grasslands or shrublands, across most of Europe and middle-western Asia. (IUCN, 2020a; Hille et al., 2021). During the non-breeding period the species forms coveys that break up into pairs in late February or March for the breeding period, which lasts to July or August in the Czech Republic (Šálek and Marhoul, 2008). Adults mainly feed on grains, weed seeds, cereals, clover and grass leaves for most of the year (Potts, 1970; Pulliainen, 1984; IUCN, 2020a). However, Grey Partridges also need invertebrates in their diet, especially during the breeding period for egg production and successful chick development, but also for facilitating the moult (Aebischer and Ewald, 2012; Hille et al., 2021). Naturally, species population dynamic is mainly regulated by the nesting success (Blank et al., 1967; Panek, 1997; Aebischer and Ewald, 2004) which depends on good weather conditions, population densities and predation pressure (Panek, 1992; Panek 1997). Predation is known to be the main reason for the nest failure of Grey Partridges (Bro et al., 2000a; Rymešová et al., 2013; Černý et al., 2020). Over the last decades, Grey Partridge populations have been rapidly declining in several countries (Kuijper et al., 2009; EBCC, 2023; PECBMS, 2023). However, it is still listed as a 'least concern' species in Europe on the IUCN red list of threatened species (IUCN, 2020a).

3.1.1. Suitable habitats for Grey Partridges

The Grey Partridge is a typical farmland species in Europe (IUCN, 2020a). It avoids forests, settlements, and infrastructure due to its preference for open farmland as well as the higher risk of predation there (Harmange et al., 2019; IUCN, 2020a). It favors a diverse agricultural landscape with small fields of cereals (wheat, barley, millet, maize) or other crops (alfalfa, beet, potatoes) for feeding, and herbaceous, linear features or unmanaged vegetation patches with taller and denser cover as refuge from predators as well as for foraging and nesting (Meriggi et al., 1991; Bro et al., 2000b; Vickery et al., 2004; Ljubojević et al., 2016; Ronnenberg et al., 2016; Černý et al., 2020). Grey Partridges especially profit from a mosaic of linear features, such as rotationally mowed wild-flower strips (Beeke and Gottschalk, 2014), tracks, field margins, hedges, and stripes along paths (Rands, 1987a; Aebischer and Ewald, 2012; Hille et al., 2021). However, the management of hedges is of great importance. If hedges are not of lower height and are not providing enough cover via thick bushes and herbs, they do not function as high-quality habitat for foraging and hiding, but as forest fragments suitable for predators as hideouts or perches (Rands, 1987a; Wübbenhorst and Leuschner, 2006; Hille et al., 2021). In the winter season, winter wheat, barley, rapeseed, and stubbles represent the most important structures promoting the survival of Grey Partridges because these fields provide food and shelter (Sotherton, 1998; Ronnenberg et al., 2016). Especially during winter nights, Grey Partridges avoid field boundaries and linear structures and rather choose to roost in open, preferably plowed, fields. This is an anti-predator strategy, as most nocturnal predators mainly prey along field margins (Ronnenberg et al., 2016; Tillmann, 2009). Therefore, an agricultural environment with a variety of biotopes and structures is necessary for Grey Partridges to survive overall.

3.1.1.1. Home ranges and population density

During the breeding period Grey Partridges maintain smaller HRs (in mean 3.73 ha for pairs in the Czech Republic) than during the post-breeding period, which then account for 8.69 ha in mean (Šálek and Marhoul, 2002). The Grey Partridge population density of 24-33 pairs/100 ha in the suburban region southwest of Prague, which includes many unmanaged areas, is considered high, indicating sufficient availability of good-quality habitats, while 2-5 pairs/100ha in a typical modern agricultural landscape around Písek accounts for low a population density due to poorer habitat quality (Šálek and Marhoul, 1999). Historically (1958 – 1962), average Grey Partridge densities reached 11 – 20 pairs/100 ha in the Beroun region, with local peaks of 40 pairs/100 ha (Nováková and Hanzl, 1965). Similar spring densities were observed in Sussex, Britain (about 21 pairs/100 ha in 1968; Potts and Aebischer, 1995). However, this population density was observed after the beginning of the population decline of Grey Partridges when the average chick survival rate had already decreased. Hence, it can be assumed that the spring density was a bit higher prior to the agricultural intensification. The widespread pesticide usage and overall transformation of the agricultural landscape was a decrease of habitat quality for Grey Partridges, which led to a decline of the spring densities to under four pairs per 100 ha in the Sussex region in 1993 (Potts and Aebischer, 1995). Population densities in France varied from 5 to 25 pairs per 100 ha in different areas (Bro and Crosnier, 2012), indicating different habitat qualities within the whole study area. These studies suggest average breeding densities of Grey Partridges of about 23 pairs/100 ha in a high-quality landscape in Central Europe. Although, a study by Jenkins (1961) observed up to 80 pairs/100 ha in Switzerland, suggesting that Grey Partridges can occur in very high population densities over some periods.

3.1.1.2. Dispersal

The dispersal dynamic of Grey Partridges is also dependent on the habitat quality. Grey Partridge pairs move prior to their breeding to find a suitable nesting site. In landscapes with a higher proportion of suitable habitats pre-breeding movements of Grey Partridge pairs are on average less than 500 m and therefore shorter than its pre-breeding dispersal range in landscapes with lower availability of suitable habitats (> 500 m). Grey Partridges disperse once more after breeding in autumn, which also depends on the habitat quality: in today's typical agricultural landscape with limited supplies of suitable habitats Grey Partridges are moving further, on average 905 m +/- 537 m. Whereas, in landscapes rich in suitable habitats, Grey Partridges only disperse 388 m +/- 256 m on average post-breeding (Šálek and Marhoul, 2008). However, in general, Grey Partridges are highly sedentary birds rarely dispersing more than 10 km (Cepák et al., 2008). Only unpaired males in spring are considered nomadic moving 1828 m +/- 636 m on average (Šálek and Marhoul, 2008).

3.1.2. Reproduction of Grey Partridges

The Grey Partridge's reproduction is a complicated process that is susceptible to numerous external factors, particularly during the breeding season, which might result in a breeding failure. The process starts in the pre-breeding season, which begins around February. Grey Partridges quickly establish couples and disperse before breeding. Although, some males need to disperse further alone because they were not able to find a partner within the male-dominated population during the pre-breeding period. This surplus of males is caused by the high mortality rate of females during the nesting period (Šálek and Marhoul, 2008; Rymešová et al., 2012) which is mainly caused by predation (Kuijper et al., 2009; Rymešová et al., 2012; Rymešová et al., 2013). Due to the huge investment of a female in reproduction (larger fat reserves, additional weight of eggs, exhaustion due to egg-laying and incubation) as well as her behaviour around the nest (covering, egg laying, and incubation), the female's chance to escape a predator is lower than for males, which are also more vigilant (Rymešová et al., 2012). Therefore, the predation risk during the nesting period is high, even though the Grey Partridge hen is performing several anti-predator techniques. The female does not cover the first egg of her clutch to test whether the nest is sufficiently hidden from predators and, thus, whether the nest site on the ground is safe. This strategy is meant to reduce the risk of brood failure due to predation as well as the loss of the huge time and energy investments, that a female provides for her large clutch during the long egg-laying period (Rymešová et al., 2013; Černý et al., 2018; Černý and Šálek, 2020). The hen typically produces 15–17 eggs in her first clutch (McGowan and Madge, 2010), although it can be up to 20-22 eggs locally (e.g. in Prague; Šálek, unpublished data from 2000-2004). However, if the first clutch fails, the hen lays less eggs in her replacement clutch (McGowan and Madge, 2010). During this egg-laying phase the female is covering the eggs with dry plant material to hide the nest from predators as well as to keep the eggs well-tempered. However, when the female is starting with the incubation, she is not covering the eggs again when she is taking short breaks for foraging. Possible reasons are the prevention of a higher risk of predator attraction due to the covering process, or the generally taller and denser vegetation during the incubation period in June, which can provide an appropriate shelter for the nest. During incubation, the female's cryptic plumage together with her immobility are adaptations that contribute to hiding the nest and the female herself as much as possible (Rymešová et al., 2012; Černý et al., 2018). After hatching, the chicks are quickly leaving their nest and are foraging on an insect prey on their own (Šálek and Marhoul, 2002; Rymešová et al., 2012). The covey formation, typical for the non-breeding period, is starting during the late summer; at first with a smaller family covey. Later on, bigger coveys can be formed during autumn and winter due to joining of unpaired, widowed, or unsuccessfully breeding individuals (Šálek and Marhoul, 2008; Rymešová et al., 2012).

3.1.2.1. Nesting sites

Grey Partridges create a little hollow lined with plant material to serve as a nest at the foot of a hedge or other herbaceous vegetation (McGowan and Madge, 2010). Therefore, preferred habitat types and landscape features for nesting are uncultivated areas, such as field margins, ruderal areas, and grassy patches with shrubs and trees (Černý et al., 2020), and linear habitat features with edges along hedges, roadsides, ditches, and dirt roads as well as set-asides within managed agricultural fields (Bro et al., 2000b). However, Bro et al. (2000b) found that Grey Partridges mostly prefer to nest in cereal fields in France, although cereals have been the dominant land use type in most of the study areas, while uncultivated areas were very limited. Furthermore, the nests situated in cereal fields were mostly within 20 m of the field edge. This preference was observed in all but two study areas, where the preferred nesting site was set-asides (Bro et al., 2000b). According to Černý et al. (2020), on the other hand, Grey Partridges prefer uncultivated areas over the predominant cereal habitat. This was particularly evident when the pre-breeding area's habitat diversity and, consequently, the proportion of preferred uncultivated habitat types, were higher. In such cases, nests were more often laid in uncultivated habitats (Černý et al., 2020). Together, both suggest that Grey Partridges prefer to nest in areas with permanent, unmanaged, herbaceous edge vegetation, but sometimes must nest also at the edge of cereal fields, when the agricultural landscape is too homogeneous, and choice of suitable nesting grounds is thus limited.

A favourable nesting site for Grey Partridges is, in general, an open, non-forested habitat that combines several features. Those are 1) a sufficient amount of dead plant material and permanent plant vegetation for nest building, concealment (Rands, 1988; Panek, 1997; Bro et al., 2000b) and clutch covering (Černý et al., 2018), 2) a favourable vegetation height and density as well as banks at the base of the field margin, which both provide shelter for the nest and incubating female from predators (Rands, 1988; Bro et al., 2000b), 3) the occurrence of specific landscape features as landmarks to find the nest easily, and 4) an availability of linear features for everyday departures, serving as a refuge (Bro et al., 2000b), and as a foraging site, as the seed and insect availability is greater in field margins and unmanaged wastelands patches than in crops (Harmange et al., 2019; Panek, 2019). The dependence of Central European nesting sites on specific structural attributes, such as a vegetation height of 20 to 60 cm and a leaf area index of 1 to 3, rather than species composition, was also proven by Wübbenhorst and Leuschner (2006). With this cover, hens can easily hide in a crouching position, while watching out for possible predators when standing (Wübbenhorst and Leuschner, 2006). Consequently, the habitat structure around the nesting site is essential for a successful breeding of Grey Partridges. Therefore, a lack of one preferred habitat or a high percentage of non-preferred habitats can increase the risk of mortality or possibly lead to breeding failure.

3.1.2.2. Breeding success

The breeding success can be described as the brood production rate which mainly regulates the population dynamics and is affected by mortality risks. Those risks increase with predator density, frequency of mowing, and a lack of suitable habitats, especially for nesting. The breeding success varies locally and, thus, can range from 25% to 80% (Panek, 1997). Selection of the nest site is one of the key factors that impact the success of the nest (Ricklefs, 1969). If the preferred nesting habitat with suitable cover and possibly permanent vegetation is available, along with low population densities of Grey Partridges and predators, there will usually be higher general nesting success. Although, when intraspecific competition for nesting sites is high, only pairs having to nest in less preferred habitats experience a lower nesting success, while pairs in preferred habitats had no change of brood production rate (Panek, 1997; Rands, 1987b). Thus, it seems that the carrying capacity of the area and the intraspecific competition together control the population density through the nesting success.

Chick survival is also highly dependent on protein-rich food consisting of a broad diversity of insects (Aebischer and Ewald, 2012). Before the agricultural intensification (prior to 1952), the average chick survival rate in Britain was 49 +/- 3%, however from 1962, after the widespread use of pesticides and the resulting decline in invertebrate diversity, the average chick survival rate was only 32 +/- 1% (Potts and Aebischer, 1995). A lack of preferred insects in the diet leads to reduced chick growth and feather development, resulting in lower chick survival. The malnourished chicks have a lower body temperature and a higher risk of predation, as they have low-quality feathers which disrupts thermoregulation and can delay flying (Borg and Toft, 2000). Most preferred insects for Grey Partridge chicks are grasshoppers (Borg and Toft, 2000), plant bugs, larval sawflies (Panek, 1992; Warren et al., 2017), as well as ground and leaf beetles (Kuijper et al., 2009).

Nesting success and chick survival are affected by weather conditions, too. Colder and rainy days lead to a lower availability of insects for chicks as well as to longer foraging times for chicks, which result in an increased predation risk and longer brooding time (Panek, 1992). Insufficient places to dry the chicks in a uniform agricultural landscape, such as elevated field edges with bare ground or low vegetation, can increase the risk of hypothermia and chick mortality, too (Šálek, pers. comm.). All in all, the breeding success of Grey Partridges depends on a favourable nesting site, appropriate predator densities, and diverse, insect-rich feeding grounds.

3.2. Reasons for a decline of Grey Partridge populations

The Grey Partridge has recorded one of the largest population declines among farmland birds (Kuijper et al., 2009; Gerlach et al., 2019). Kuijper et al. (2009) divided the population trend of Grey Partridges in the UK into three periods, although the described pattern coincides with other European countries with a 10-year lag in each period: 1) The Grey Partridge population was stable until the 1950s. Weather conditions caused mainly the regular fluctuations in the chick survival rate which led to respective population sizes. 2) The second period lasted until 1970 and recorded a steep decrease in chick survival rates with an average of only 33% (between 1955 and 1993). The main reasons for this decline are the intensive use of pesticides and the decrease in habitat quality. 3) Lastly, until now the population decline continues, although the main reasons have shifted. Reduced survival of hens and clutches due to increased predation as well as hunting pressure best explain this decline (Potts and

Aebischer, 1995; Bro et al., 2001; Watson et al., 2007; Kuijper et al., 2009; Aebischer and Ewald, 2012). In the Czech Republic the situation was similar, although due to other reasons: Grey Partridge populations peaked between 1933 and 1937 with 2.4 million individuals. Afterwards, the agricultural landscape was transformed due to the communist regime. The land consolidation of most of the small fields led to large monocultures that were sprayed with pesticides, and therefore led to a massive decline of Grey Partridges (an average of 758,000 individuals in spring between 1966 and 1968). This loss of suitable habitat and increased predation pressures of nests and females continued the decline of Czech populations to only 8-16 000 pairs in 2014-2017 (Šálek and Zámečník, 2020). This accounts for a population decline of 99% in the Czech Republic between 1933 and 2017. In comparison, the Grey Partridge population decreased by 89% between 1992 and 2016 in Germany (Gerlach et al., 2019).

3.2.1. Loss of suitable habitat resulting in a habitat shift

One of the main causes of the decline in the Grey Partridge population is the decrease in the proportion of high-quality habitats, especially habitats for safe nesting, leading to a lower carrying capacity of the environment (Šálek and Marhoul, 2008; Kuijper et al., 2009; Aebischer and Ewald, 2012). The agricultural intensification and mechanisation changes the landscape character on a large-scale (Kuijper et al., 2009). While the size of fields increased, the number of fields as well as the crop variability and length of field borders and margins decreased (Figala et al., 2001, Ronnenberg et al., 2016). In the Czech Republic, for example, agricultural intensification led to an estimated loss of 120 000 km of dirt roads, 800 000 km of grassy boundaries, 30 000 km of linear, herbaceous mosaics including shrubs and trees, and 35 000 ha of groves (Klápště and Franková, 2015). And maize production for biogas and winter crop cultivation increased significantly in Germany, leading to more monocultures, lower crop diversity, and lower proportion of segetal flora along fields (Ronnenberg et al., 2016). The majority of field crops in the Czech Republic are also maize, rapeseed, and winter wheat (Šálek, pers. comm.). As Grey Partridges prefer to breed, forage, and seek a refuge in permanent, linear or patchy features within a diverse and open agricultural landscape (Bro et al., 2000b; Černý et al., 2020), the amount, size as well as suitability of habitat types for Grey Partridges are decreasing (Ronnenberg et al., 2016; Harmange et al., 2019). Another reason for the loss of suitable habitats is the denser vegetation on fields (e.g. grain), fallow grasslands, and field margins, due to the intensification of agriculture, which diminishes the herbaceous structure of early successional stages (medium height, sparse cover) Grey Partridges prefer for foraging and sheltering (Wübbenhorst and Leuschner, 2006). Additionally, the subsidies from the EU for set-asides were stopped in 2008, which led to a decreased abundance of this land use type. It most probably promoted the decline of Grey Partridges, too, because many studies showed that these set-asides had improved the habitat situation for Grey Partridges (e.g. Aebischer and Ewald, 2010; Ronnenberg et al., 2016; Schmitz et al., 2017). All these changes within the agricultural landscape, as well as the ongoing urbanization or seldom afforestation of rural land, are leading to higher fragmentation of original open habitats and therefore to the isolation of the remaining suitable habitats of Grey Partridge populations.

These modern developments of farming techniques and agricultural landscape management influence the habitats of the Grey Partridges and other farmland birds in Europe severely, possibly forcing them to shift their habitat usage (Černý et al., 2020; Hille et al., 2021). Recently, cereal fields have become the most common habitat type within home ranges and the second most selected habitat type for individual occurrence. As this dominant land use type, cereal fields are surrounding the preferred unmanaged habitat types of Grey Partridges, which are simultaneously becoming scarcer. Thus, when the landscape is homogenous and dominated by cereal fields, the occurrence of Grey Partridges in cereal fields is not unexpected (Černý et al., 2020). However, cereal fields were found to be the main breeding habitat of Grey Partridges by Harmange et al. (2019). Although, the authors suggest that these habitat choices were made according to the change of landscape features in modern agricultural landscapes. As cereal cover increases and overall habitat quality as well as food availability decrease, Grey Partridges had to adapt and thus shifted their selected habitats towards lower quality ones, such as cereal fields (Harmange et al., 2019). This is probably promoted by the intensive management of meadows and fallow lands with early mowing which can kill incubating females or chicks and destroy clutches (Rymešová et al., 2012). Therefore, it seems that those habitats are avoided as breeding sites now, even though they used to be a good breeding habitat (Hille et al., 2021). Despite having developed behavioural adaptations for breeding in cereal fields with a high nesting success (Bro et al., 1998), Grey Partridges cannot live only in cereal fields for a long period of time. They also need habitat types with better food availability, such as diverse vegetation stripes as well as insect- and seed-rich fields without chemical treatment (Hille et al., 2021). The preference of Grey Partridges for unmanaged, heterogeneous landscapes was also confirmed by Černý et al. (2020) and Joannon et al. (2008). When there is a higher proportion of uncultivated areas within the pre-breeding home range, thus if the landscape is more heterogeneous, Grey Partridges occur mostly in these preferred unmanaged areas (Černý et al., 2020). Within intensive cash crop landscapes Grey Partridges prefer the most variable field with a crop sequence of at least four different crops and 50% of small grain cereals, that are rotated over the years creating temporal and structural diversity (Joannon et al., 2008).

Therefore, it appears that the scarcity of suitable habitats as well as of food is most likely the cause of the shifting habitat usages because Grey Partridges have fewer and fewer options in the modern agricultural landscape. By now they even select more risky habitats, such as meadows and human infrastructure during the winter (Hille et al., 2021) and are in general decreasingly avoiding other risky habitat types (e.g. woodlands, buildings and roads; Harmange et al., 2019). However, Hille et al. (2021) found that Grey Partridges are still avoiding agricultural land that is too close to buildings because of the higher disturbance rate by humans and dogs.

3.2.2. Decrease in high quality food

An accompanying effect of agricultural intensification is the reduced availability of arthropods, especially insects, due to the increased use of pesticides on fields, leading to a reduced chick survival rate and, therefore, to a decline of the population sizes of Grey Partridges (Wübbenhorst and Leuschner, 2006; Kuijper et al., 2009; Tillmann and Ronnenberg, 2015; Panek, 2019). The loss of insects' abundance and diversity in agricultural landscapes (Benton et al., 2002; Sotherton et al., 2014) is not only caused by the use of insecticides, but also by pesticides that reduce the diversity and abundance of weed species that insects depend on (Kuijper et al., 2009; Panek, 2019). The use of insecticides in summer alone can reduce the availability of insects for Grey Partridge chicks by over 90%. Chicks feeding in areas with such an extensive use of insecticides have a higher mortality than chicks feeding in areas with little or no use of insecticides (Aebischer and Ewald, 2012). Panek (2019) also suggests a correlation between reduced chick survival from 57% to 34% between 1987 and 2013 in Poland and the 2.5-fold increase in pesticide use during the same period.

Another factor contributing to the decreased availability of high-quality food is the expansion of fields with conventional agriculture (e.g. 20% more cereal cover in France since 1994; Bretagnolle et al., 2018), which results in a diminished proportion of a heterogeneous landscape. This transformation of the agricultural landscape decreases, for example, the abundance of field margins or other herbaceous edges (Figala et al., 2001). However, those vegetative boundaries offer the highest availability of appropriate seeds and insects for Grey Partridges (Tillmann and Ronnenberg, 2015; Harmange et al., 2019), which is why the homogenization of the agricultural landscape reduces the availability of high-quality food.

The Grey Partridge chick's survival depends on this high-quality diet, as low-quality insects reduce their growth and flight feather development (Borg and Toft, 2000). Low-quality insects are, for example, many aphids that can be the only insect food found in maize fields (Tillmann and Ronnenberg, 2015) and lead to a higher concentration of toxins in the chick's bodies (Borg and Toft, 2000). Tillmann and Ronnenberg (2015) also found that Grey Partridge chicks, feeding in conventional maize and winter wheat fields as well as in eutrophic grass tracks, significantly lost body weight due to reduced food availability, quality and, therefore, intake. This inhibited growth of chicks decreases their survival rate, as malnutritioned chicks are weaker, have lower body temperature, and are at higher risk of predation because of their low escape ability. In contrast, chick mortality decreases when chicks consume more of their preferred insect diet (Borg and Toft, 2000).

This increased chick mortality causes a dramatic decline of the Grey Partridge populations, since breeding success is mainly regulating the population dynamics (Blank et al., 1967; Panek, 1997; Aebischer and Ewald, 2004).

3.2.3. Direct impact of increased usage of pesticides

Pesticides can also directly poison Grey Partridges by eating besprinkled insects, sown etched seeds, or rodent baits made of grains and pesticides, such as carbamate pesticides and organochlorine insecticides (Novotný et al., 2011; Ljubojević et al., 2016; Rymešova, pers. comm.). Rands (1986) concluded that Grey Partridges feeding in areas with unsprayed headlands of 6 m had a significantly bigger mean brood size and a higher survival rate compared to those feeding in fully sprayed fields. This suggests that pesticides are negatively affecting the reproduction of Grey Partridges as well as increasing their mortality (Kuijper et al., 2009; Novotný et al., 2011). Bro et al. (2015) state that a high proportion of Grey Partridge clutches are potentially exposed to different active substances, such as fungicides, herbicides, and insecticides, of which approximately a quarter can lead to reproductive risks. Most pesticides are diffused during the breeding period of Grey Partridges, leading to a higher risk of contamination of the female and her eggs. Contamination paths incorporate 1) lipophilic pesticides that may be included in the egg yolk, 2) pesticides that may penetrate the eggshell and chorionic membranes after direct contamination or via contact of contaminated feathers of the hen, or 3) chick exposure through contaminated arthropods or directly through air or skin contact (Bro et al., 2015). Grey Partridges that were fed organic grains flew longer during an escape than birds fed conventional grains containing residues of the herbicide Clopyralid, suggesting that pesticide residues may reduce the anti-predator behaviour. Although, this sublethal effect of pesticide residues was mainly observed in captive-bred Grey Partridges, leading to a lower likelihood to try to escape by flying, whereas individuals from wild-strains were mostly unaffected by this low-toxic herbicide (Gaffard et al., 2022). Hence, more research needs to be conducted to assess the actual direct contamination of Grey Partridges with pesticides and their effects, as knowledge of the direct impacts of pesticides on the mortality of Grey Partridges is still minimal. Although, it can be expected that pesticides are negatively affecting their survival and reproduction. Additionally, the contamination risk has increased during the past decades, given that Grey Partridges are progressively breeding in larger cereal fields (Bro et al., 2000b; Černý et al., 2020), that are regularly besprinkled with pesticides.

3.2.4. Higher predation pressure

Predation is a natural component of the regulation of populations, but in weak populations or unbalanced habitats, it may be one of the most harmful causes directly affecting the population decline. An increased predation pressure can be recorded in some populations of Grey Partridges, leading to lower hen and clutch survivals in the last decades (Kuijper et al., 2009). A reduced nesting success decreases the population densities of Grey Partridges (Panek, 1997) and is, thus, also responsible for its decline (Kuijper et al., 2009). Predation was cited in numerous studies as the main cause of nest failure (e.g. Bro et al., 2000a; Rymešová et al., 2012; Rymešová et al., 2013; Černý et al., 2020), accounting for up to 70% of hen mortality throughout the breeding season. In France, most of the predations are executed by ground carnivores (64%), followed by raptors (29%). Although, these proportions are varying across the country (Bro et al., 2001).

One reason of the increased predation pressure is the population increase of most predators: corvids (especially Crows *Corvus* spp. and Eurasian Magpies *Pica pica*), as well as Red Fox (*Vulpes vulpes*) populations have more than doubled in some regions in the last decades (Evans, 2004; Aebischer and Ewald, 2012). The same applies for some raptor populations, such as Common Buzzards (*Buteo buteo*; Evans, 2004), although other common raptors of the farmland are having a stable population trend (e.g. Western Marsh-Harriers *Circus aeruginosus; IUCN*, 2020b, Eurasian Sparrowhawks *Accipiter nisus;* IUCN, 2020e) or a decreasing population size (e.g. Hen Harriers *Circus cyaneus;* IUCN, 2020c, Montagu's Harriers *Circus pygargus;*

IUCN, 2020d). Additionally, other possible mammalian predators of Grey Partridges or their clutches have increased, too, for example, European Badgers (*Meles meles*), American Minks (*Neogale vison*), Rats (*Rattus norvegicus*), and European Hedgehogs (*Erinaceus europaeus*). These higher predator abundances increase the probability of Grey Partridges and their clutches to encounter a predator (Evans, 2004). One possible reason for these increased predator populations is agricultural intensification. Higher livestock densities can increase alternative food options for predators, such as carrion for the Red Fox and corvids (Fuller and Gough, 1999), supporting them toward bigger populations. Additionally, larger fields are attractive foraging grounds for raptors, such as the Hen Harrier in France, which causes higher predation densities and higher predation risks for Grey Partridges in these areas (Bro et al., 2001; Bro et al., 2006). Some of these predators are hunted by humans, which can decrease the predation pressure on Grey Partridges (Tapper et al., 1996; Aebischer and Ewald, 2012). However, when hunting concentrates solely on the top-level predators, such as the Red Fox, the populations of medium-sized predators, like mustelids for example, can increase as a response. Consequently, this meso-predator release effect can lead to higher predation rates of Grey Partridges (Bright, 2000). A higher predation pressure might result in lower long-term fitness of individual Grey Partridges, due to more time spent on guard against predators. Spending more time in vigilance means less time spent foraging, which increases the risk of starvation. Especially when smaller groups become more frequent due to the population decline, causing lower densities of Grey Partridges, individuals need to spend more time being vigilant (Watson et al., 2007; Hille et al., 2021).

Landscape and habitat composition are also responsible for a higher predation pressure, as the reduction of suitable habitats for Grey Partridges is concentrating their occurrences as well as their predators to a smaller area. Red Foxes and Eurasian Sparrowhawks are important predators of Grey Partridges and tend to hunt along field edges and hedges, respectively, which also happen to be suitable habitats for Grey Partridges (Rantanen et al., 2010). This, together with the higher abundances of predators, increases the predation risk significantly and leads to an ecological trap within the decreasing preferred habitats (Bro et al., 2001; Bro et al., 2004; Evans, 2004; Rantanen et al., 2010a; Černý et al., 2020; Hille et al., 2021). On the one hand, this reduces the mortality rate of Grey Partridges in the currently dominant habitat types, like cereals (Rymešová et al., 2013; Černý et al., 2020). On the other hand, this dominance of poor habitats for Grey Partridges can create conditions in which the population dynamic of this farmland bird is more sensitive to predation. Examples can be a lower nest cover or a reduced food availability leading to weaker birds, higher begging and moving rates of chicks, as well as longer foraging times for adults, all of which are increasingly attracting predators. Additionally, Grey Partridges can also be forced to occur in more risky habitat types, such as forests and building areas, where the predation is generally higher (Rands, 1988; Borg and Toft, 2000; Evans, 2004; Hille et al., 2021).

Another reason for the increased predation pressure is the lower abundance of managed game estates. Within these areas, the predators of Grey Partridges have been controlled and Grey Partridges were fed throughout the winter, leading to a lower predation pressure for this farmland bird. However, these game estates also had negative effects on Grey Partridges: In addition to being unintentionally shot when other game birds were released for hunting, they also had an increased risk of contracting diseases like the caecal nematode *Heterakis gallinarum* within the area (Watson et al., 2007; Kuijper et al., 2009).

Overall, this increased predation risk is a great threat in the declining Grey Partridge populations, particularly by reducing the breeding success through hen, egg or chick predation, which results in a further decline of this farmland bird (Panek, 1997; Kuijper et al., 2009).

3.2.5. Hunting

Human hunting of Grey Partridges is often not taken account of in studies that analyse their mortality and/or decline. Reasons for that could be that 1) the amount of shot individuals is comparably small and has therefore no significant impact on population dynamics as in Germany (Knauer et al., 2010; Ronnenberg et al., 2016), 2) hunting is only allowed in restricted game estates or Grey Partridges are even completely under hunting protection (Kuijper et al., 2009); although, the hunting status of Grey Partridges varies over different countries and they can, thus, be legally hunted in some regions, e.g. France (Bro et al., 2006; Besnard et al., 2010) or some federal states of Germany (Tillmann et al., 2012), or 3) hundreds of human-reared Grey Partridges are specifically released for hunting and people, thus, believe that wild populations will stay mainly untouched, stable or are even restored (Bro et al., 2006; Bro and Crosnier, 2012).

However, Watson et al. (2007) showed that human hunting of Grey Partridges is causing higher mortalities (35% to 39%) than the preying of raptors (9.5% to 15%) in the UK. Therefore, de Leo et al. (2004) believe that the continuous hunting activities in the UK probably contributed to the extinction of many subpopulations of Grey

Partridges and that it can endanger the remaining ones. For the current declining populations, this threat of local extinction due to hunting, among other things, is particularly real. Due to other increased mortality factors that cause, for example, lower chick survival, Grey Partridges do not have the resilience to withstand additional threats caused by human hunting (Aebischer and Ewald, 2012). Like this, the survival rate during the hunting season is one of the important demographic factors influencing the population growth rate of Grey Partridges (Bro et al., 2000b). Additionally, some game estates do not have specific hunting limitations on Grey Partridges, which may lead to exploitation (Bro et al., 2006). And the release of human-reared Grey Partridges into the wild or within game estates may have a negative impact on wild populations through genetic introgression (Bro et al., 2006; Bech et al., 2020). Therefore, depending on the country and its laws, hunting of Grey Partridges can be regarded as a significant mortality factor. Grey Partridges have only been a popular hunting bird in the Czech Republic in the past, which accounted for millions of shot individuals. However, since 1971, Grey Partridges have not been hunted in the Czech Republic anymore and it even gained the status of a specially protected species in 1992 prohibiting its hunting (Šálek and Zámečník, 2020).

3.3. Habitat management measures for the protection of Grey Partridges

Such as the decline of Grey Partridges is caused by multiple reasons, the management measures need to consist of a combination of several practices. Thereby, conservationists should first focus on improving safe nesting sites and the availability of high-quality chick food to significantly promote chick survival rates. This is a crucial practice without which the stabilization of Grey Partridge populations is not feasible (Kuijper et al., 2009), as chick survival is the main driver of population growth (Blank et al., 1967; Panek, 1997; Aebischer and Ewald, 2004). Therefore, enhancing nesting and chick-rearing habitats should be the first main measure. Next, a general improvement of Grey Partridge habitat as well as an adaptation of agricultural practices, such as a reduction of the pesticide usage or an implementation of a rotational crop system with herbaceous field margins, is desirable in order to provide the farmland birds with sufficient food and cover, also during winter (Kuijper et al., 2009). In locations with sufficient and suitable nesting and feeding habitats and high Grey Partridge populations, predator control is not required because natural anti-predator measures are sufficient. However, in some regions with very low densities of Grey Partridges, predator control may be supplemental (Šálek et al., 2004). All this together should improve the winter survival rate, hen survival rate during breeding, hatching rate of first clutches, and chick survival rate simultaneously. Then, the declining populations may stabilize (Aebischer and Ewald, 2012).

3.3.1. Improving habitat quality

Habitats used by Grey Partridges have been significantly changed by humans in many ways leading to a dramatic decline in the farmland birds' numbers. Therefore, the improvement of different habitat types necessary for the survival of Grey Partridges should be the main concern of management measures, starting with the nesting and chick-rearing habitats to promote chick survival rates (Kuijper et al., 2009). This means, for example, that 5% of the agricultural land in the UK should be an insect-rich habitat. Together with 6.9 km of nesting cover per km^2, this would suffice to stabilize Grey Partridge populations without predator control (Aebischer and Ewald, 2004). Similarly, Rands (1987a) and Hille et al. (2021) claim that a combination of different-aged fallow lands and flowering strips, which are connectively spread across the agricultural land and are at least 1-2 ha/100 ha in total, are necessary for the survival of Grey Partridges during breeding and chick-rearing time. Specifically, this means an increased creation of rotationally mowed field margins with wildflowers for insects (Beeke and Gottschalk, 2014), as well as other linear, permanent structures, such as ruderal areas or managed hedges for better cover, food and connectivity to rear the chicks (Rands, 1987a; Aebischer and Ewald, 2012; Černý et al., 2020). In order to prevent these improved habitats from becoming an ecological trap for Grey Partridges, as their predators learn that the birds favour these areas (Bro et al., 2004; Rantanen et al., 2010; Černý et al., 2020), it would be better to create a mosaic of bigger patches of improved habitat – minimal size of each block 0.3 ha with a width of 20 m (Sotherton, 1998) - instead of linear features (Bro et al., 2004; Kuijper et al., 2009; Beeke and Gottschalk, 2014). However, the best way to prevent such ecological traps would be by creating a connected, heterogeneous landscape with a high proportion of uncultivated habitats (Černý et al., 2020) that have different goals, such as nesting sites, chick rearing areas, and winter cover patches (Sotherton, 1998). Like this, both Grey Partridges and predators would not be concentrated in the few remaining small areas.

The habitat quality also depends on a considerate management that results in a higher plant diversity as well as structural diversity, which then generates a higher animal diversity: for example, edges of wildflowers record the highest and most diverse invertebrate availability for chicks when 1) the sown mixture is consisting of plants known as host-plants for high-quality invertebrates for Grey Partridges, 2) other wildflowers can disperse there coincidentally, 3) these edges were not sprayed with pesticides, 4) the edges are not tilled for about 5 years so that sensitive soil invertebrates can establish, and 5) the density of the vegetation is managed toward an appropriate structure for the chicks so that they are able to penetrate it (Tillmann and Ronnenberg, 2015). Likewise, rotational set-asides, on which natural herbal pioneer vegetation is allowed to grow without pesticides, provide Grey Partridge chicks with a 3-fold amount of their preferred insects compared to cereal fields (Moreby and Aebischer, 1992). Proper management is also needed to set back natural succession in certain habitat types of Grey Partridges, such as set-asides or hedgerows. Otherwise, set-asides or wastelands would become grassland-like, and hedgerows forest-like habitats that do not contain the supporting structure, vegetation composition and invertebrate fauna Grey Partridges seek for nesting, foraging or sheltering (Rands, 1987a; Sotherton, 1998). Forest-like hedgerows can even feature as an additional threat for Grey Partridges because they provide perches for predators, but no refuge for the farmland bird (Rands, 1987a).

Set-asides can be improved for Grey Partridges and other farmland birds by sowing specific seed mixtures, that secure a continuous food availability as well as shelter during winter and, thus, increase the overwinter survival rate. According to Sotherton (1998) seed mixtures based on kale (*Brassicae*) are the best option for winter crop set-asides. During summer, the sown set-asides can also provide good brood-rearing shelters, which can be supplemented by sowing mixtures based on cereals, especially triticale and oats, that generate insect-rich vegetation (Sotherton, 1998). Another way to improve winter food security can be the provision of supplementary food in hoppers, that are filled with wheat grain and situated along field margins and cover strips (Aebischer and Ewald, 2012). However, the most straightforward method, which is now uncommon, would be to leave undisturbed stubbles standing throughout the winter, as they can serve as important winter feeding grounds for Grey Partridges (Sotherton, 1998). Together with overall habitat improvement measures through set-asides and agri-environment schemes as well as predator control, Grey Partridge abundances increased in the UK like this (Aebischer and Ewald, 2012).

Improved habitats through agri-environment schemes were also the sole key of successful protection measures in the Grey Partridge Conservation Project in the district of Göttingen: Flower strips were established in 0.8% of the agricultural land and divided in spring, where one half was managed by cultivating another seed mixture and the other half was left unmanaged to provide shelter for nests. Whereas the abundances of Grey Partridges declined further in the rest of the federal state, the populations in the district of Göttingen stabilized and even increased locally, where the density of flower strips reached 7% of the agricultural area (Beeke and Gottschalk, 2014).

Therefore, it has been proven that the implementation of a connected network of sufficiently wide and diverse herbaceous linear structures along fields is indeed supporting the survival of Grey Partridges, as they provide both suitable nesting sites and insect-rich foraging grounds. The more such unmanaged areas are available for Grey Partridges in the agricultural landscape, the higher the chances of reversing the population decline. However, the necessary proportion of such improved habitat within the agricultural landscape varies between studies (compare Rands, 1987a; Aebischer and Ewald, 2004; Beeke and Gottschalk, 2014; Hille et al., 2021), although it might also depend on local Grey Partridge population and the composition of the agricultural landscape.

The situation in the Czech Republic might change soon, because so-called 'combined biobelts', herbaceous strips specifically designed to support the Grey Partridge and other farmland animals, are part of the Czech Common Agricultural Policy plan for the years 2023 to 2027. They are composed of two types of biobelts: 1) the annual “fodder biobelt” forms a source of high-quality food that is established with a specified seed mixture to which it is recommended to add barberry, sorghum or phacelia. This biobelt needs to be 6 to 24 m wide and must be installed by 31 May each year. 2) The perennial “clover belt” presents an area used for nesting and rearing the chicks. There is no defined seed mixture, however grasses must represent a maximum of 50% and few specified species are required (alfalfa, lotus, hop clover, wild carrot, caraway, and a minimum of four grass species like oats, dactylis or *Poa annua*). As it is recommended to establish a species-rich clover belt to ensure high invertebrate as well as structural diversity that promotes chick survival, additional plant species suggestions are offered. This biobelt must be 18 to 24 m wide and must be installed by 31 May. Both types of biobelts will remain unmanaged during their existence and no pesticides are allowed (Ministerstvo zemědělství, 2023a; Ministerstvo zemědělství, 2023b).

3.2.2. Suitable habitat decreases predation pressure

Some studies record a targeted, intensive killing of predators of Grey Partridges as a successful management measure, which should increase the nesting success as well as the reproduction rate, particularly in a declining Grey Partridge population (Tapper et al., 1996; Evans, 2004). Especially within less suitable nesting habitats, systematic predator control can stabilize Grey Partridge populations (Aebischer and Ewald, 2004). However, predator control is linked with high financial, temporal, and labour costs as well as with low efficiency for most predator species, as some predators can easily multiply in the next generation as well as with increasing prey density (Evans, 2004; Kuijper et al., 2009). In any way, a more systematic and reliable way to decrease the predation pressure on Grey Partridges is the improvement of their habitats as well as of agricultural practices to reduce the predator-prey meetings (Bro et al., 2001; Knauer et al., 2010), as the predation rate is mostly interconnected with habitat composition (Evans, 2004). This is demonstrated by the fact that the spring pair density of Grey Partridges is 1.5 times higher in areas with habitat and predator management than in areas with sole predation control (Ewald et al., 2020). Therefore, it would be useful to support aspects that Grey Partridges need for successful sheltering rather than predator control, to ensure a long-term positive effect on their populations. This includes maintaining suitable habitat patches that are large enough to protect Grey Partridges from an ecological trap effect (Bro et al., 2004; Evans, 2004; Černý et al., 2020) as well as open and steppe-like habitats in order to see approaching predators soon enough. Additionally, these suitable habitats should be far away from refuges harbouring predators or structures that predators use for orientation (Hille et al., 2021). A network of sufficiently large and abundant herbaceous patches and unmanaged wastelands to take cover within typical agricultural areas is the best option for Grey Partridges. Then, there are enough nesting and overwintering sites, where Grey Partridge populations can persist in these suitable habitats without any predator control (Aebischer and Ewald, 2004; Šálek et al., 2004; Whittingham and Evans, 2004), as their natural anti-predator techniques are sufficient there. For example, the predation rate of Hen Harrier and Marsh Harrier on Grey Partridges decreased, when the mean field size was smaller (Bro et al., 2001), meaning when there was a greater amount of unmanaged edges around the small fields, where Grey Partridges can easily hide.

3.2.3. Improving conventional agricultural practices

Given that Grey Partridges are farmland birds, it is crucial to enhance conventional farming methods and, by extension, the agricultural landscape, in order to protect this species. This, by extension, also affects the heterogeneity and habitat quality of agricultural land, which is why these efforts are also very comparable to habitat improvement measures. Those include especially the set-aside and agri-environment schemes described in chapter 3.1., which can increase the structural and biological diversity and therefore the availability of food, nesting sites, and shelters (compare Sotherton, 1998; Aebischer and Ewald, 2012; Beeke and Gottschalk, 2014). Relevant agri-environmental schemes for Grey Partridges are beetle banks, conservation headlands, wild bird cover, winter cover/food provision (Ewald et al., 2020), and combined biobelts (Ministerstvo zemědělství, 2023b) that should be implemented broadly.

Furthermore, a reduction, or even better an elimination, of the use of pesticides, especially around the field margins, is a key measure to protect Grey Partridges, as this would increase the plant diversity, and thus the invertebrate diversity available for chicks to feed on (Kuijper et al., 2009; Tillmann and Ronnenberg, 2015; Hille et al., 2021). One way to reduce pesticides is through the so-called 'Conservation Headlands', which are the outer 6 to 12 m of a conventional cereal field, which are treated in such a way that a weedy understory grows. This method can support population growth through better chick survival of Grey Partridges, but it is not as effective as set-asides due to its management (Vickery et al., 2002; Kuijper et al., 2009; Aebischer and Ewald, 2012). A reduction in spraying pesticides or irrigation would also decrease the disturbance of Grey Partridges (Bro et al., 2000b). A lower disturbance and mortality rate during the breeding period is especially important and can be reached by a more extensive management of meadows and fallow land with appropriate cutting times (Hille et al., 2021). It is also important to downsize the field size to increase the amount of field edges suitable as linear, unmanaged habitats (Bro et al., 2000b; Joannon et al., 2008). This measure increases the landscape heterogeneity, which can be additionally improved by establishing a diversity of crop sequences and vegetation covers with different field patterns as well as by reducing irrigation measures (Joannon et al., 2008). For these latter measures it is necessary to take farmer needs and constraints into account and offer simple, proven and cheap solutions, to ensure a proper implementation (Bro et al., 2000b; Ewald et al., 2020). To make these Grey Partridge conservation farming practices more appealing to farmers and land managers, demonstration sites, in which appropriate and practical management leads to higher Grey Partridge abundances, should be accessible to farmers as an example (Ewald et al., 2020). Additionally, appropriate subsidy programs, supporting suitable habitats for Grey Partridges within the agricultural landscape as well as farmers, need to be prepared and funded by official institutions, such as the Ministry of Agriculture.

4. Methodology

The analyses of the breeding success of Grey Partridges in dependency on habitat structures were carried out for the whole Czech Republic, since the species is a farmland bird and therefore (originally) widely spread over the agriculturally dominated country (53,25% in 2020; Ministerstvo zemědělství, 2021).

4.1. Grey Partridge data/sample size

I downloaded observations of Grey Partridges within the Czech Republic on the 16th of December 2022, ranging from 01/2012 to 12/2021 from the public database "Avif" (Birds.cz - bird watching (faunistic database ČSO)). After deleting observations that do not have any coordinate values in Microsoft Excel, the Grey Partridge data were prepared for further analyses in the software environment for statistical computing and graphics R (R version 4.2.2). First, the observations were unified by converting all pair observations into two individual observations at the same location. Two groups of observations with certain conditions were created: 1) pre-breeding observations (n = 1875), that contain all observations of two to three individuals between January and April as well as all observations of two individuals in May, representing breeding pairs. The differentiation of individuals within the first four months of a year and in May was chosen because breeding pairs can be accompanied by single males during the early year; however, in May groups of more than two individuals are more likely individuals of unsuccessfully nesting pairs. This selection avoids, therefore, an overlap with the second group of 2) post-breeding observations (n = 648), that contain all observations of more than two individuals between May and September, representing the family covey formation.

Next, it was determined whether a covey, as evidence of a successful breeding, was recorded at this location later in the year. For that, I converted the data into spatial points using the *SpatialPointsDataFrame* function of the package 'sp' and assigned the closest observed post-breeding observation for each observed pre-breeding pair within the same year (post_closest [ID]). Then, I computed the distance (post_distance) of these two observations with the *gDistance* function of the package 'rgeos'. Afterwards, I added a response variable (Success) being 1 (post_distance < 1000 m) or 0 (post_distance > 1000 m), as Grey Partridges usually don't move more than 905 m +/- 537 m. after breeding (Šálek and Marhoul, 2008). Therefore, I assumed that a post-breeding observation, that is closer than 1000 m from the assigned pre-breeding observation, represents a successful reproduction at that location (Success = 1).

4.2. Habitat evaluation

To obtain the necessary habitat variables I was working with the freely available Geodatabase *CORINE Land Cover 2018* (CLC 2018 — Copernicus Land Monitoring Service), an inventory of the European land cover in 44 classes. All further spatial analyses were performed in QGIS (version 3.28 Firenze) with layers projected to the projected coordinate system WGS84/UTMzone33N (EPSG:32633). The Corine land cover layer was clipped to the size of Czech Republic by using a layer of the outlines of Czech Republic obtained by exporting the selected country from a freely available world countries map (Natural Earth » 1:10m Cultural Vectors - Free vector and raster map data at 1:10m, 1:50m, and 1:110m scales (naturalearthdata.com)). Next, all selected Grey Partridge pre-breeding pairs (n = 1875) were imported separately for each year. The next spatial calculations were also performed for each year separately: Using the *Multi Ring Buffer* tool I created ring buffers with a radius of 200 m and 1000 m around each Grey Partridge pair, representing the pre-breeding/breeding HR (based on the mean breeding HR size of 3.73 ha in Czech Republic; Šálek and Marhoul, 2002) and the post-breeding HR (based on the mean dispersal range after breeding of 905 m +/- 537 m; Šálek and Marhoul, 2008), respectively (Fig. 1).

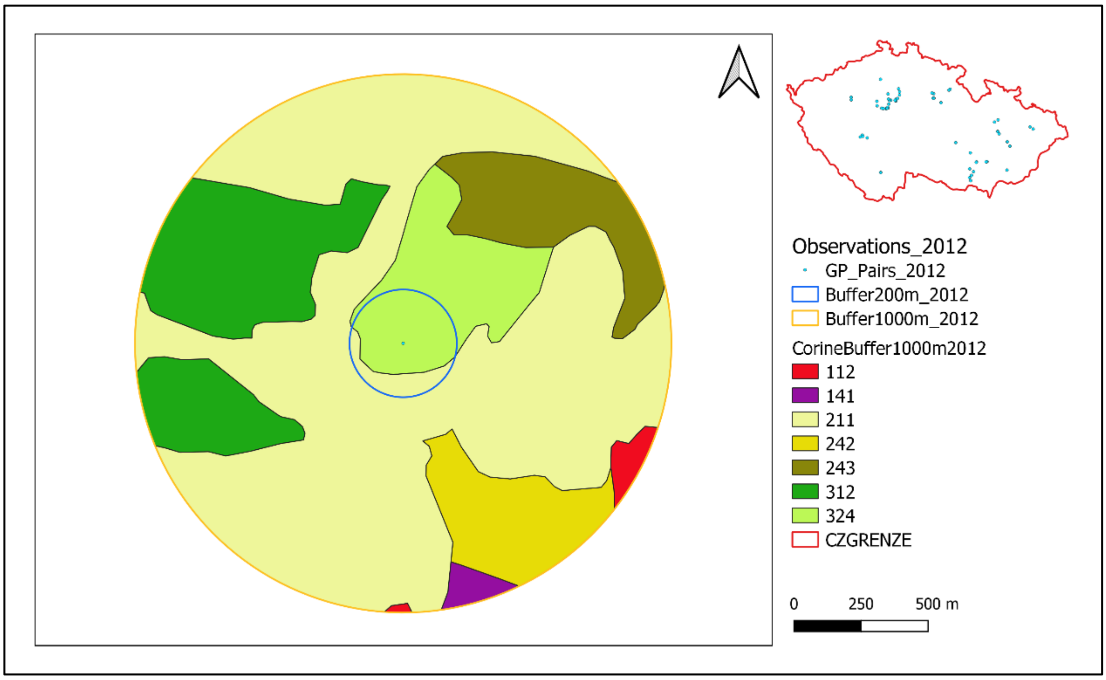

Figure 1 Example of the buffer creation in QGIS. The small map of the Czech Republic in the top-right corner shows all selected observations of Grey Partridge pairs (bright blue dots) in 2012. Around these were two scales of buffers drawn: 1) 200 m (blue circle) representing the pre-breeding/breeding HR, and 2) 1000 m (orange circle) representing the post-breeding HR. The Corine Land cover Classes (CLCs) were intercepted with these buffers. These exemplary buffers include according to my habitat grouping 1) settlements (112, 141), 2) arable land (211, 242, 243), and 3) forest (312, 324).

These two buffer radii are further referred to as scales. First, I clarified how many probable duplicate pairs are in the dataset. According to my definition, a pair was counted more than once when two observations were recorded less than 400 m apart in the same year (based on the average HR size during the breeding period). Thus, if two home ranges represented by two 200 m buffers overlapped in the same year, a duplicate was counted. Those overlaps were computed with the *topology checker* plugin in, using each 200 m buffer layer and the rule 'it must not overlap'. Like this, 256 overlaps were counted in total, accounting for 14,1% of all observations. However, several pairs overlapped with more than one other pair, which is why the actual number of duplicates is lower. These duplicates were retained in the resulting dataset for analysis, although they may be a source of pseudo-replications. However, we also know that many pairs nest in close proximity to each other, so their omission could, on the contrary, underestimate the influence of the tested variables.

Then, I intersected the Corine layer of the Czech Republic with both buffer layers one after another and calculated the area of each polygon within each buffer with the field calculator (geometry, $area) in a new column 'AreaRecal'. Afterwards, I exported the attribute table of the intersect output layer to Microsoft Excel and calculated the total area of each Corine Land cover Class (CLC) within each buffer for each year and both scales separately, using the function SUMIFS. Then, I calculated the proportion of each CLC within each buffer for each year and both scales.

Next, I wanted to obtain the edge lengths of all combined forest polygons as well as of each non-forest polygon. For that I selected the four forest CLCs (311, 312, 313, 324) from the Corine layer of Czech Republic, exported the selection as a new shapefile layer, and dissolved that layer completely by using a newly created unitary column as dissolving field within the *dissolve* tool. Then, I reversed the forest selection and exported the non-forest selection as a new shapefile layer. Afterwards, I converted both layers, the dissolved forest as well as the non-forest one, to lines by using the *polygons to lines* function. Both outcome layers were intersected with each buffer layer of each year to obtain the edges of forests and all non-forest CLCs. Then, I computed the lengths of each forest and non-forest edge in meters with the field calculator (geometry, $length) for each year and both scales and exported the attribute tables to Excel.

Thereafter, I combined the different habitat values in two final documents, one for the 1000 m buffer radius home range (1000 HR) and one for the 200 m buffer radius home range (200 HR), also including data about year and the breeding success. During this step, I merged the original CLCs into seven groups, while excluding the rest of the CLCs:

1) Settlement: mosaic-like surfaces with early succession and disturbances, burdened by human activity (CLC 111, 112, 121, 122, 131, 132, 133, 141, 142)
2) Arable land: predominantly open agricultural landscape with regular farming (CLC 211, 242, 243)
3) Other productive areas: farmed areas, but with a high proportion of woody species, such as vineyards or orchards (CLC 221, 222)
4) Managed grasslands: areas with a predominance of regularly maintained grasslands (CLC 124, 231)
5) Natural grasslands: dry, sparsely vegetated unmanaged areas (CLC 321, 333)
6) Forests: areas with a predominance of woody vegetation (CLC 311, 312, 313, 324)
7) Waterbodies: freshwater waterbodies, such as rivers, streams, lakes, ponds, etc.

According to these habitat groups, I summarized the areas as well as proportions for each buffer with the function SUMIFS in the final document for all years. Next, I summarized the total forest as well as the preliminary non-forest edge lengths for each buffer with the function SUMIF for all years. To obtain the actual non-forest edge length, I subtracted the forest edge length of the same buffer from the preliminary non-forest edge length of that buffer and divided the result by two. Like this, the obtained non-forest edge length only includes those non-forest edges that are not adjacent to a forest, once.

Finally, I calculated the habitat diversity of each buffer as the dominance index of Simpson's Diversity Index (1 – D) and as Shannon's Diversity Index (H) for both scales in R. I used both indices, because Simpson puts more emphasis on dominant habitats, while Shannon also considers the under-represented habitats. Both indices can therefore be important, each with a different interpretive meaning. To calculate those indices, I selected the proportion columns of the final documents as a distinct file and used that in the *diversity* function of the package 'vegan', setting the index argument once as 'simpson' and once as 'shannon'. The results were added as new columns to the final documents and exported after.

4.3. Statistical analyses

Using the final documents from the habitat evaluation, the following statistical analyses were similarly conducted for both buffer scales (200 HR and 1000 HR) in the software environment for statistical computing and graphics R (R version 4.2.2).

First, the year variable was converted into a factor variable, since the years' courses were not important, and the proportion as well as edge length variables were centred and scaled to homogenize the dataset. Next, all habitat variables were tested for correlation to prevent biased model estimates. Only one of two habitat variables was retained, if Pearson's r_s was $r_s > 0.7$ and was therefore indicating a strong correlation. Hence, in both datasets the proportion of forests was removed because it was strongly correlated with forest edge length ($r_s = 0.81$ for 200 HR and $r_s = 0.88$ for 1000 HR). Forest is an unsuitable habitat type for Grey Partridges and therefore less important than forest edges, along which Grey Partridges might occur in poor habitat quality landscapes. Additionally, the proportion of arable areas was removed because it was correlated with both Simpson's Diversity Index ($r_s = -0.78$) and Shannon's Diversity Index ($r_s = -0.75$) in the 1000 HR dataset. Furthermore, arable land cover is the dominant feature in the Czech landscape and therefore suppresses the significance of the other, less represented habitat groups, which are more interesting for these analyses. This is also why I omitted the proportion of arable areas from the 200 HR model. Although, I also considered that its significance was nondescript (p value = 0.9827) and its growth had a small negative impact on the breeding success (estimate = - 0.01040), when included to the model. In addition, I also removed the proportion of watercourses from both datasets because freshwater ecosystems are not suitable habitats for Grey Partridges. Naturally, Simpson's and Shannon's Diversity Indices also correlated strongly ($r_s = 0.99$ for 200 HR and $r_s = 0.98$ for 1000 HR). As both variables seemed similarly important descriptors for habitat diversity, the following Generalized Linear Mixed-Effects Models (GLMMs) and model selection were conducted with one of these correlated variables at a time. The most significant model with a lower Akaike Information Criterion (AIC) was the one with Simpson's Diversity Index as the dominance index for both scales. Hence, Shannon's Diversity Index was removed and GLMMs were fitted to test the hypotheses: "which studied parameters influence the breeding success?". The following predictors were used within each scale: 1) proportion of settlements, 2) proportion of managed grasslands, 3) proportion of natural grasslands, 4) proportion of other productive areas, 5) Simpson's diversity indices for the six habitat groups, 6) forest edge length, and 7) non-forest edge length. I included the years as random effect in the model because the circumstances of the occurrence and abundance of the species could have been different in each year. For the model selection the *dredge* function of the package 'MuMIn' was used. The model with the lowest AIC was defined as the final model.

5. Results

5.1. Breeding success

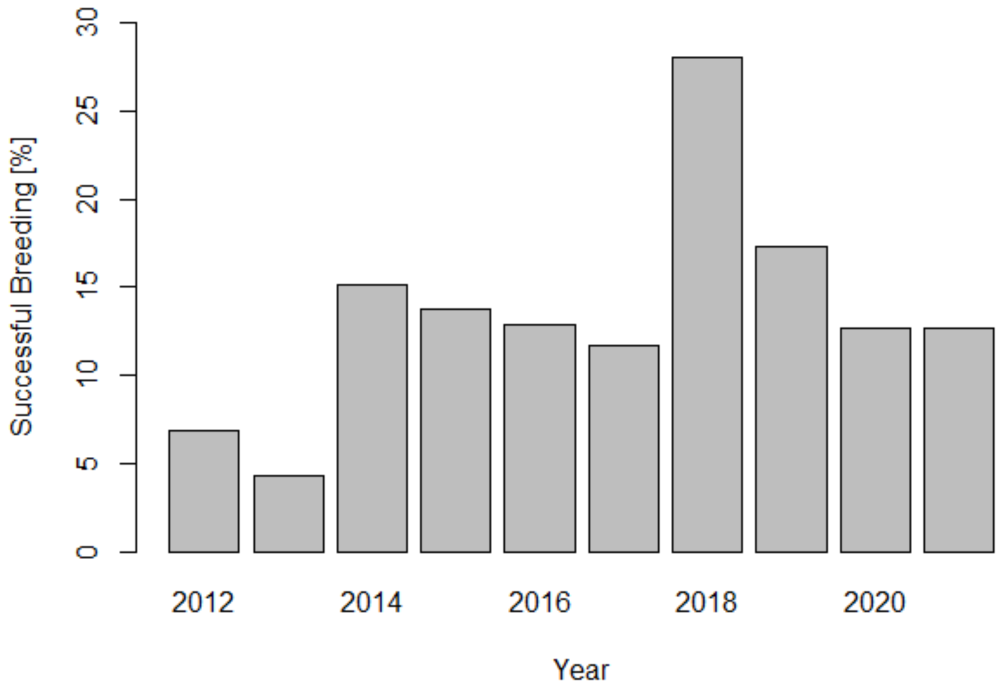

Figure 2 Proportion of successful breeding of Grey Partridges in the Czech Republic over the studied ten-year period from 2012 to 2021.

The breeding success of Grey Partridges varied over the years in the Czech Republic (Fig. 2). The highest breeding success of the observed pairs was recorded in 2018 with 28.04%, whereas the lowest breeding success was recorded in 2013 with 4.30%. The average breeding success of Grey Partridges over the analysed time period (2012 to 2021) was 13.53%. According to the selected Grey Partridge observations and criteria definitions, it seems like the breeding success was relatively stable over the last eight years.

5.2. Influence of habitat variables in 200 HR

I found that the proportion of settlements, managed grasslands, and natural grasslands within the 200 HR as well as Simpson's diversity index as dominance index for the defined habitat groups in the 200 HR, and the length of non-forest edges in the 200 HR were significant predictors of the breeding success of Grey Partridges in the Czech Republic (Table 1).

Table 1 Results of the generalized linear mixed-effects model analysing the effect of several habitat variables on the breeding success of Grey Partridges within a 200 HR (observed covey maximal 1000 m from observed pair of the same year). Predictors: 1) area of settlements in HR, 2) area of managed grasslands in HR, 3) area of natural grasslands in HR, 4) Simpson's diversity index as dominance index (1 – D) for defined habitat groups in HR, and 5) length of non-forest edges in HR.

Factor	Estimate	SE	z	p
Intercept	- 1.70221	0.16585	- 10.264	< 0.001
Settlement	0.22553	0.06778	3.328	0.000876
Managed grasslands	0.18927	0.06172	3.067	0.002164
Natural grasslands	0.12102	0.05043	2.400	0.016399
Simpson	- 1.30047	0.45987	- 2.828	0.004685
Non-forest edges	0.16803	0.08486	1.980	0.047693

The breeding success was higher with an increasing proportion of settlements (Fig. 3a), managed grasslands (Fig. 3b) and natural grasslands (Fig. 3c) in the 200 HR as well as with increasing length of non-forest edges (Fig. 3d) in the 200 HR. On the other hand, increasing habitat diversity within the 200 HR reduced the breeding success (Fig. 3e). Correspondingly, the mean proportions of managed grasslands (Fig. 4a), natural grasslands (Fig. 4b), and settlements (Fig. 4c) were higher in those 200 HR, within which Grey Partridges bred more successfully (successful: 9.57%, 1.76%, 15.49% respectively; unsuccessful: 6.66%, 0.59%, 11.78% respectively). Arable land constituted the largest proportion in most of the 200 HRs, accounting for 67.71% of the 200 HR area with successful breeding and 75.41% with unsuccessful breeding (Fig. 4d). Although, the negative influence of arable land on the breeding success of Grey Partridges in 200 HR was non-significant.

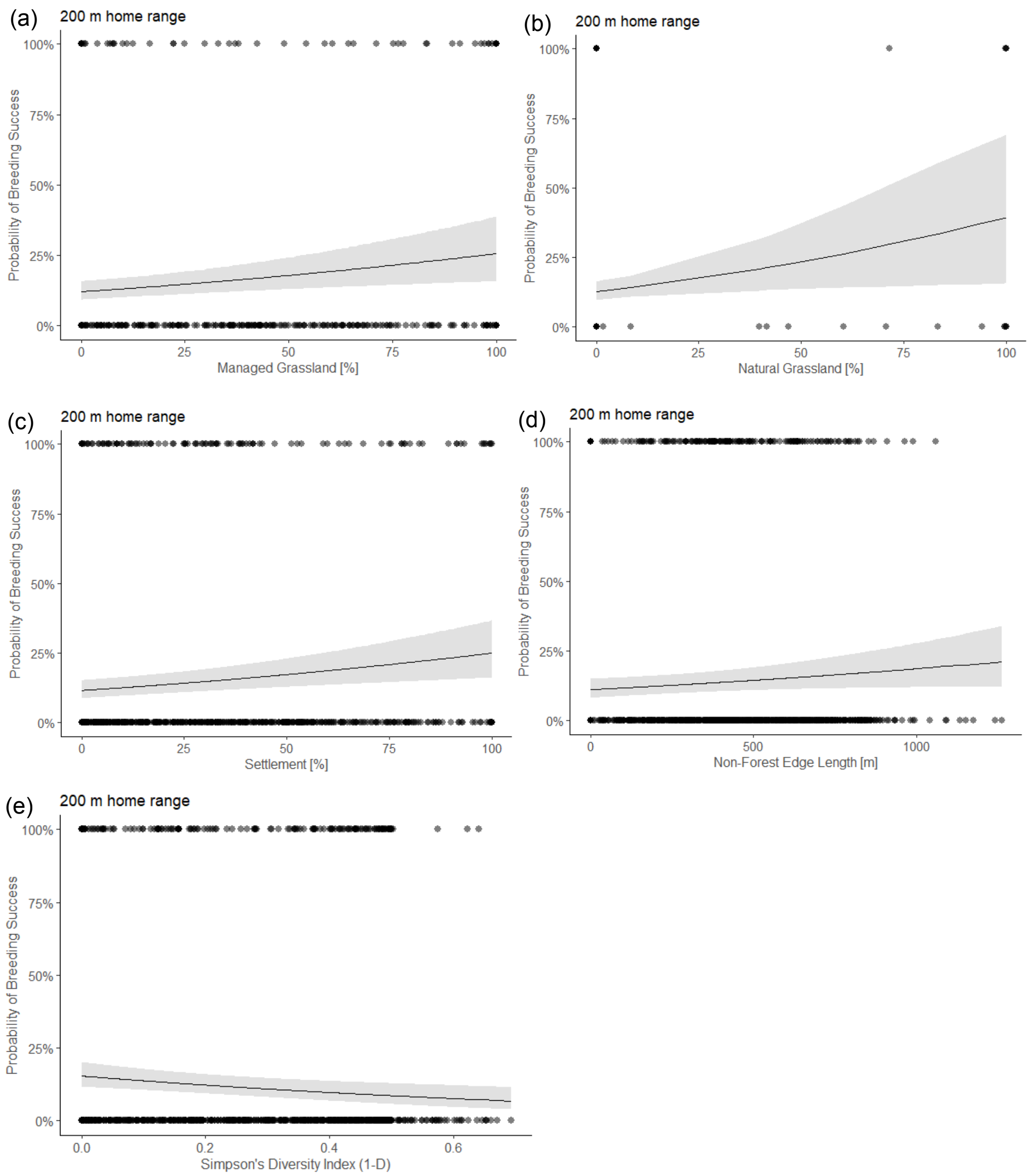

Figure 3 Logistic models of relationships between the estimated probability of successful breeding of Grey Partridges in their 200 HR and the respective predictors with 95% confidence interval (grey colour): (a) proportion of managed grasslands in HR, (b) proportion of natural grasslands in HR, (c) proportion of settlements in HR, (d) length of non-forest edges in HR, and (e) Simpson's diversity index as dominance index (1 – D) for defined habitat groups in HR.

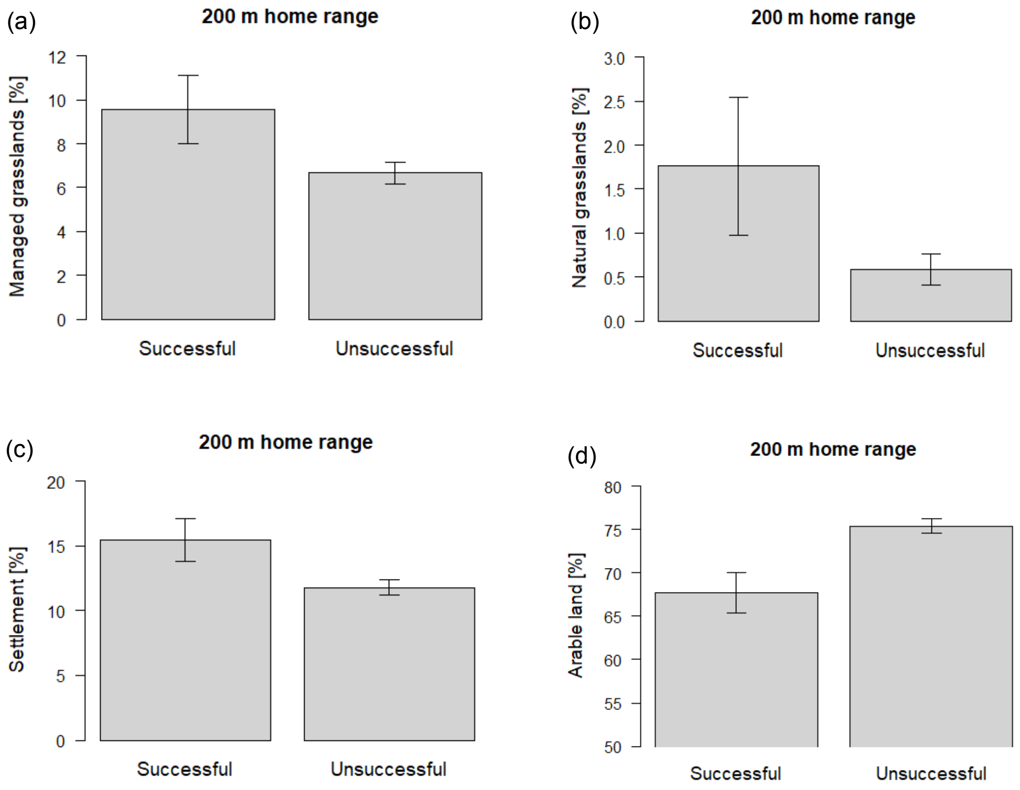

Figure 4 Mean proportions of significant habitat types in the GLMM ((a) managed grasslands, (b) natural grasslands, (c) settlements) as well as the dominant habitat ((d) arable land) in the 200 HR of Grey Partridges, differentiating between successful breeding and unsuccessful breeding within the corresponding habitat. The mean errors are indicated as whiskers.

5.3. Influence of habitat variables in 1000 HR

I found that the proportion of natural grasslands and other productive areas in the 1000 HR as well as the length of forest edges in the 1000 HR and Simpson's diversity index as dominance index for the defined habitat groups in the 1000 HR were significant predictors of the breeding success of Grey Partridges in the Czech Republic (Table 2).

Table 2 Results of the generalized linear mixed-effects model analysing the effect of several habitat variables on the breeding success of Grey Partridges within a 1000 HR (observed covey maximal 1000 m from observed pair of the same year). Predictors: 1) area of natural grasslands in HR, 2) area of other productive areas in HR, 3) Simpson's diversity index as dominance index (1 – D) for defined habitat groups in HR, 4) length of forest edges in HR, and 5) length of non-forest edges in HR. Non-significant variables (*p* > 0.05) are highlighted in italics.

Factor	**Estimate**	**SE**	**z**	***p***
Intercept	- 2.87920	0.23846	- 12.074	< 0.001
Natural grasslands	0.12399	0.05091	2.435	0.0149
Other productive areas	- 0.42483	0.19970	- 2.127	0.0334
Simpson	2.64331	0.49537	5.336	< 0.001
Forest edges	- 0.51164	0.09824	- 5.208	< 0.001
Non-forest edges	*- 0.17492*	*0.09108*	*- 1.921*	*0.0548*

The breeding success was higher with an increasing proportion of natural grasslands in the 1000 HR (Fig. 5a) as well as with an increasing habitat diversity within the 1000 HR (Fig. 5d). A larger proportion of other productive areas in the 1000 HR (Fig. 5b) as well as increasing length of forest edges in the 1000 HR (Fig. 5c) reduced the breeding success. Correspondingly, the mean proportion of natural grasslands (Fig. 6a) was higher, and that of other productive areas (Fig. 6b) was lower in those 1000 HR, within which a Grey Partridge pair was successfully breeding (successful: 1.13%, 0.09% respectively; unsuccessful: 0.35%, 0.52% respectively). Arable land constituted the largest proportion in most of the 1000 HRs, accounting for 66.43% of the 1000 HR area with successful breeding and 73.25% with unsuccessful breeding (Fig. 6c). Although, the negative influence of arable land on the breeding success of Grey Partridges in 1000 HR was non-significant when included to the model (estimate = - 0.15592, p-value = 0.21199).

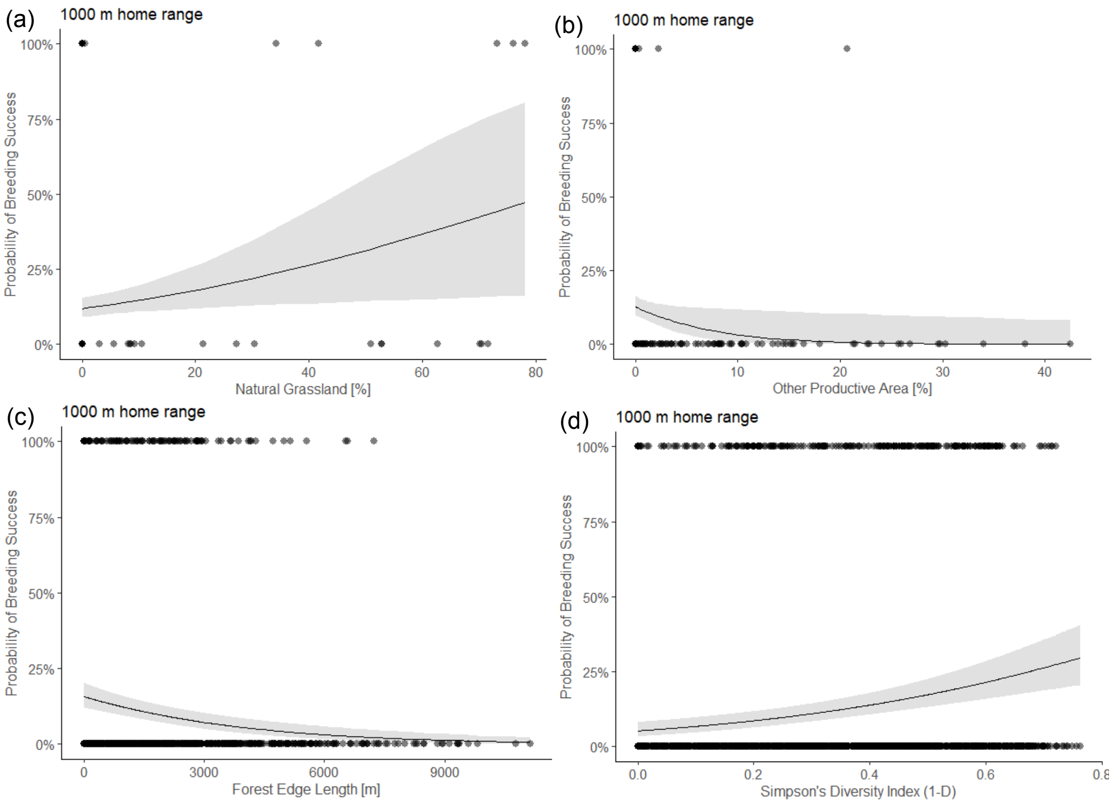

Figure 5 Logistic models of relationships between the estimated probability of successful breeding of Grey Partridges in their 1000 HR and the respective predictors with 95% confidence interval (grey colour): (a) proportion of natural grasslands in HR, (b) proportion of other productive areas in HR, (c) length of forest edges in HR, and (d) Simpson's diversity index as dominance index (1 – D) for defined habitat groups in HR.

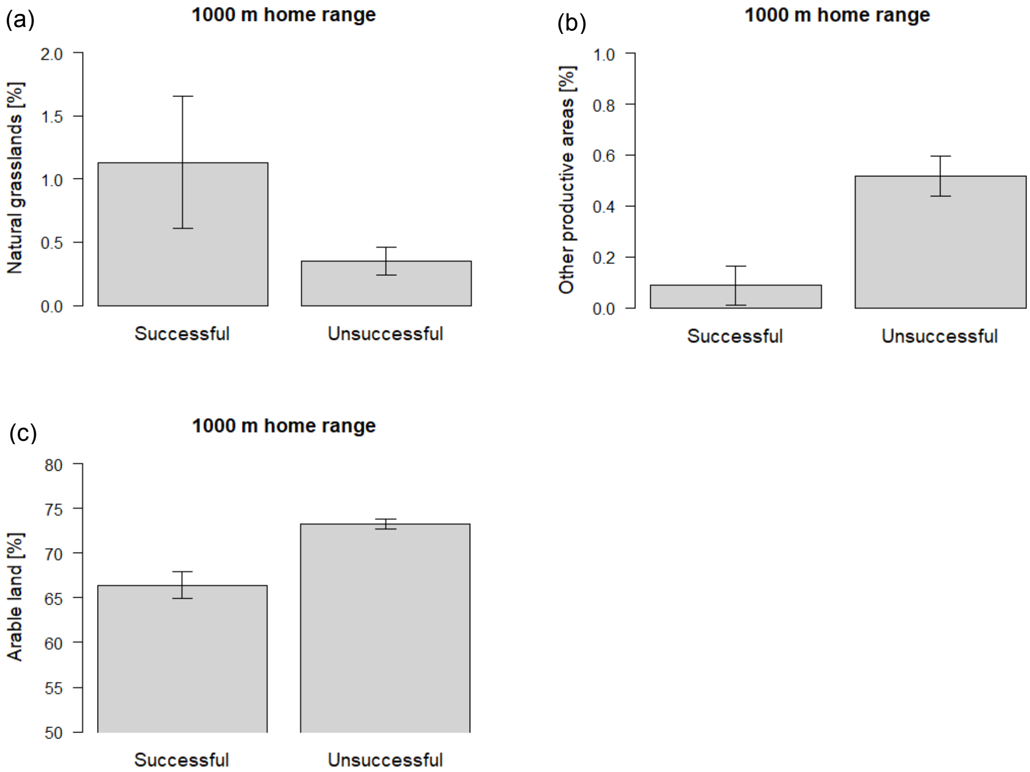

Figure 6 Mean proportions of significant habitat types in the GLMM ((a) natural grasslands, (b) other productive areas) as well as the dominant habitat ((c) arable land) in the 1000 HR of Grey Partridges, differentiating between successful breeding and unsuccessful breeding within the corresponding habitat. The mean errors are indicated as whiskers.

6. Discussion

This study provides evidence that habitat structures, providing Grey Partridges with opportunities of shelter and good foraging grounds, are essential not only for the occurrence itself (Sotherton, 1998; Bro et al., 2000b; Šálek et al., 2004; Aebischer and Ewald, 2012), but also for successful breeding in a modern agricultural landscape dominated by arable land. The study area, the agricultural landscape of the Czech Republic, represents the typical Central European agricultural landscape (e.g. described in Panek, 1992; Wübbenhorst and Leuschner, 2006; Ronnenberg et al., 2016) well, as it consists mostly of arable land and of only a low proportion of unmanaged patches. Therefore, my results can be conferred to other agricultural areas in Central Europe.

6.1. Breeding success

The mean breeding success of this study (13.53%) is lower than the overall nesting success of the species in other studies (e.g. 29% in the Czech Republic; Černý et al., 2020, 31% to 73% in North-Central France; Bro et al., 2000a). This aberrance can have several reasons: First, the analysed data of the studies was recorded in different years, in which the climatic conditions could have been different leading to differing living conditions for Grey Partridges (Panek, 1992). Second, the breeding success might have declined further since the last studies, as the population trend is still decreasing (IUCN, 2020a). Third, there is a difference between breeding success (survival of chicks at least until observation of close by family covey) and nesting success (successful hatching of at least one chick), which is why the data of this study have a longer period including more chances of mortality. And fourth, the Grey Partridge's observation data utilized for this study is possibly skewed because it was obtained from a public database where anybody can input observations. Hobby ornithologists might have entered defective observations and some Grey Partridges were probably overseen or entered more than once, as there is no systematic approach of field mapping. Therefore, the data used might have under- and over-represented Grey Partridge pairs and coveys, as well as misjudged Grey Partridge observations. During my analyses, I was looking for possible duplicates of observed pairs (see methodology), but did not remove them and was therefore risking pseudo-replication in my analyses. In addition to that, Grey Partridges are known to have high breeding densities in the Czech Republic when the habitat quality in the surrounding is good (around one pair per 3-4.2 ha; Šálek and Marhoul, 2002). Assuming that the breeding density is one pair per 3 ha in some regions, removing possible duplicate observations according to my definition (min. 400 m between two different pairs) would result in ignoring relevant pairs in the analyses. And considering that the effect of habitat structures on the breeding success of Grey Partridges is especially expressive in dense populations (pairs having to nest in less preferred habitats experience lower nesting success, while those in preferred habitats experience no change; Rands, 1987b; Panek, 1997), the risk of pseudo-replication might be worth risking, also because these contradictions are partially compensating each other. In either way, I recommend improving the methodology for further, similar analyses by removing the earlier observation of two observed pairs that are closer than 300 m to each other.

6.2. Habitat structures supporting breeding success

The results of the two GLMMs confirm that Grey Partridges depend on different supporting habitat structures for a successful breeding in their pre-breeding/breeding HR (200 HR) than in their post-breeding HR (1000 HR). Only natural grasslands have a strong and positive effect on their breeding success in both HRs. Therefore, my results prove that natural grasslands are the most important habitat structure for a successful breeding of Grey Partridges; even in such little availability as occurred in the study area. Natural grasslands are probably good nesting sites for Grey Partridges, offering permanent and dense vegetation with dead grass and other dry vegetation. All of these structures are known as good factors for the concealment of the nest and the incubating female against predators (Rands, 1988; Panek, 1997; Bro et al., 2000b; Wübbenhorst and Leuschner, 2006). Wübbenhorst and Leuschner (2006) specifically stress the importance of structural attributes of nest sites in Central Europe, such as a vegetation height of 20 cm to 60 cm and a leaf area index of 1 to 3, which coincides with the structure of natural grasslands in spring. Structures like these hide the nest from predators which is an important aspect for nest success because predation is known to be the most common reason for nest failure (Bro et al., 2000a; Černý et al., 2020). This high mortality risk, as well as the corresponding anti-predator techniques during the breeding period, which depend on certain habitat structures around the nesting site, make the nest site choice one of the most important factors influencing nest success (Ricklefs, 1969). The occurrence of natural grasslands as potential nesting sites in the breeding home range is therefore supporting the breeding success of Grey Partridges significantly.

The importance of managed grasslands for the breeding success of Grey Partridges in their breeding HR has probably similar reasons. The structure of managed grasslands during spring and that of natural grasslands is similar, offering Grey Partridges a covered nesting site. Managed grasslands, particularly pastures, are more prevalent and larger than natural ones, which accounts for the larger average size for successful breeding of Grey Partridges. However, the probability of successful breeding of Grey Partridges is lower for the same size of managed grasslands than for natural ones. One reason is probably the risk of nest destruction or incubating hen death, posed by the mowing of meadows during the late breeding season, which can result in nest failure (Rymešová et al., 2012). This mortality is even named as one reason for a shift away from meadows as breeding sites in Hille et al. (2021). Therefore, it can be assumed that unmanaged, natural grasslands would have a greater positive impact on successful breeding of Grey Partridges if they were available more frequently. Furthermore, it is known that Grey Partridges select unmanaged habitats as nesting sites over managed ones if available (Černý et al. 2020), demonstrating the greater importance of natural grasslands.

The importance of unmanaged areas for Grey Partridges might also be the reason for the positive effect of settlements on the breeding success of Grey Partridges in their pre-breeding/breeding HR. In settlements Grey Partridges might be able to find a relatively high proportion of unmanaged areas, such as properties on which infrastructure is going to be build. Those resemble large natural grasslands in which Grey Partridges probably find concealed nesting sites, so that they do not mind the human disturbance that much. This availability of unmanaged areas in settlements, together with the probably lower predation risk by foxes in settlements (Šálek, pers. comm.) as well as the lack of suitable habitats in the agricultural landscape, possibly explain the recent shift in habitat selection toward human infrastructure, among other habitats (Harmange et al., 2019; Hille et al., 2021). Whereas Hille et al. (2021) claim that Grey Partridges are still avoiding areas too close to buildings due to higher disturbance by humans and dogs and are only preferring those habitats during winter, Harmange et al. (2019) state that Grey Partridges are increasingly selecting human infrastructure, especially roads and tracks. Černý et al. (2020) declare that the selection for human infrastructure in HRs is probably a side effect of the selection for field margins that are often located along roads, which would also explain the increasing selection of roads and tracks Harmange et al. (2019) found. Field margins, ruderals, and other linear structures along, for example, roads or ditches are the most selected nesting sites of Grey Partridges (Bro et al., 2000b; Černý et al., 2020), offering shelter for the nesting site as well as during everyday movements, landmarks for orientation, and foraging grounds (Rands, 1988; Bro et al., 2000b; Harmange et al., 2019). However, the Corine Land Cover Classes (CLCs) used for this study do not include any roads or tracks outside of settlements that are narrower than 100 m (Bossard et al., 2000). Therefore, it is probable that the positive effect of linear structures along the roads is under-represented in this study. Hence, the importance of settlements for the breeding success of Grey Partridges in their pre-breeding/breeding HR found in this study probably arises also from the named habitat shift due to the availability of safe nesting sites there as well as the wide occurrence of settlements.

Non-forest edges were found to support the breeding success of Grey Partridges in their pre-breeding/breeding HR which proves the importance of linear, herbaceous habitat structures as nesting sites. This positive impact of non-forest edges would probably be even more significant if distinct fields were distinguished in this study. But the CLCs used do not divide the arable land into distinct fields (Bossard et al., 2000), excluding, therefore, many field margins from the analyses. However, another reason for the lower positive influence of the length of non-forest edges than expected might be the ecological trap they pose for Grey Partridges. Predators can learn where Grey Partridges preferably occur, and, as their preferred habitats are decreasing, the risk of predation within these linear structures increased, resulting in a higher mortality of the farmland bird (Bro et al., 2004; Rantanen et al., 2010; Černý et al., 2020). According to Aebischer and Ewald (2004), Grey Partridge populations stabilize in agricultural landscapes that have 6.9 km/100 ha of nesting cover and at least 5% of habitats that are insect-rich. The findings, however, indicate that these important habitat structures (1.76% of insect-rich natural grasslands and probably less than 6.9 km of non-forest edges) are underrepresented in the average Czech breeding HR of Grey Partridges, which creates optimal conditions for the ecological trap effect.

Later, in the post-breeding HR, not non-forest edges, but habitat diversity had the most significant positive effect on the breeding success of Grey Partridges. Although edge length and habitat diversity are slightly correlated, they do not need to correspond completely, as, for example, the same edge length can lie between patches of two habitat groups (low diversity) or several habitat groups (high diversity). Hence, those results suggest that a heterogeneous landscape (high diversity) is favourable for Grey Partridge family coveys. A diverse landscape inhabits a high plant diversity and, consequently, also a high invertebrate diversity, which is especially present in ecotones, such as non-forest edges (Tillmann and Ronnenberg, 2015). The survival of chicks depends on a constant availability of a variety of high-protein insect-food (Aebischer and Ewald, 2012), as they would be malnourished and weak and, thus, an easy prey otherwise (Borg and Toft, 2000). A heterogeneous landscape therefore promotes the chick survival rate and therefore also the breeding success. In addition to that, a high plant diversity is also promoting good feeding grounds for adult Grey Partridges that feed on a variety of weed seeds as well as corn grain (Potts, 1970; Pulliainen, 1984). Furthermore, in a heterogeneous landscape, the incidence of habitats that are not sprayed with pesticides is higher as well, as there are probably more unmanaged areas. Those unsprayed areas offer a more diverse availability of insects that are important for chick survival and thus covey size (Rands, 1986; Kuijper et al., 2009; Panek, 2019). Habitat diversity therefore supports a healthy chick and adult survival by creating good foraging grounds during the post-breeding period. Another aspect that might improve the breeding success of Grey Partridges through habitat diversity is the increased possibility of shelters due to higher structural diversity (Benton et al., 2003). Especially, a mixture of weedy patches, ruderals and managed hedgerows offer an appropriate combination for sufficient shelter, space for rearing the chicks, and foraging (Rands, 1987a; Sotherton, 1998; Šálek et al., 2004).

In this study, natural grasslands were also important for a successful breeding of Grey Partridges in their post-breeding HR. This habitat group probably represents the best combination of good insect availability, seed foraging ground, and sufficient shelter.

As natural grasslands are unmanaged, the pesticide concentration should be at a minimum resulting in diverse insect and weed communities (Kuijper et al., 2009; Panek, 2019). Additionally, the recorded natural grasslands are probably mostly non-linear which represents a good refuge area for Grey Partridges from predators, as bigger herbaceous patches (best a minimum of 0.3 ha and with at least 20 m width; Sotherton, 1998) protect Grey Partridges from predation through an ecological trap in the current homogeneous agricultural landscape of Central Europe (Bro et al., 2004; Kuijper et al., 2009; Beeke and Gottschalk, 2014; Černý et al., 2020). However, it is important to consider that the 1000 HR used in this study do not represent the real post-breeding HRs of Grey Partridges reliably because these HRs were drawn around the pre-breeding pairs considering their post-breeding dispersal. Therefore, only a part of their real HR is included in the 1000 HR, ranging from about ¼ in poor-quality landscapes to ¾ in high-quality landscapes (calculated according to their mean post-breeding dispersal (1000 m or 500 m, respectively; Šálek and Marhoul, 2008) as well as post-breeding HR size (8,7 ha; Šálek and Marhoul, 2002). Hence, my results are probably not completely accurate, as some effects of habitat structures on the breeding success of Grey Partridges are missing. In addition, CORINE Land Cover 2018 was used for the whole analysis (2012 – 2021) despite the availability of CORINE Land Cover 2012, neglecting possible land cover changes over the years. However, since the CLCs are broadly defined, the recorded land cover changes are probably of minor importance.

6.3. Habitat structures hindering breeding success

Habitat structures that are negatively affecting the breeding success of Grey Partridges also differ between the pre-breeding/breeding and post-breeding HRs. Although, the strongly dominant arable land, which was excluded from my analyses because of its insignificance, among other things, would most likely hinder the breeding success in both HRs. Modern arable land is a highly managed and disturbed area due to the intensification and mechanization of agricultural practices (Kuijper et al., 2009). Modern fields, fallow grasslands, and field margins have denser vegetation, lacking the structure of early-successional stages which Grey Partridges prefer (Wübbenhorst and Leuschner, 2006). Additionally, the crop as well as segetal flora diversity decreased significantly with the agricultural intensification, resulting in a lower availability of food for both adults and chicks (Ronnenberg et al., 2016). This is partially due to the removal of field margins and borders as well as an increase in field sizes, which resulted in a more homogeneous agricultural landscape (Figala et al., 2001; Tillmann and Ronnenberg, 2015). The increased use of pesticides also reduces the availability of food (both corn/seeds and insects) for Grey Partridges (Wübbenhorst and Leuschner, 2006; Kuijper et al., 2009; Tillmann and Ronnenberg, 2015; Panek, 2019). These factors, on top of the higher risk from agricultural machinery of the nest or the incubating female (Casas and Viñuela, 2010), make arable lands unattractive for Grey Partridges. They may be especially negative for their breeding success for various reasons. Pesticides are mostly spread over the breeding season inflicting direct negative impacts on eggs, incubating females, and hatched chicks (Bro et al., 2015). Furthermore, the use of insecticides in summer can decrease insect availability for Grey Partridge chicks by more than 90%, leading to higher chick mortality in those intensively managed areas (Aebischer and Ewald, 2012). The observed habitat shift towards dominant arable lands, such as cereal fields, due to the lower availability of suitable habitats (Harmange et al., 2019; Černý et al., 2020), probably promotes even more the negative indirect and direct effects of pesticide usage on breeding success. Although, Bro et al. (1998) recorded a high nesting success in cereals in the 90s and the predation risk is supposedly lower in cereals nowadays, as predators focus on the preferred habitats of Grey Partridges for hunting (Rymešová et al., 2013; Černý et al., 2020). Hence, the influence of arable land on Grey Partridges should not be underestimated even though I did not analyse its effects in this study. Yet, it can be assumed that modern arable land is disadvantageous for Grey Partridges and their breeding success in both pre-breeding/breeding and post-breeding HRs.

The results show that habitat diversity within the 200 HR has a negative influence on the breeding success of Grey Partridges during the breeding period. There are three possible reasons for this. First, habitat diversity incorporates forests and forest edges, which are ideal habitats for the predators of Grey Partridges, increasing the predation risk there (Rands, 1988; Evans, 2004; Hille et al., 2021). Second, with higher habitat diversity comes higher structural diversity that provides predators with good ambush and perch possibilities, which are best in forest-like structures (Rands, 1987a; Hille et al., 2021). Third, habitat diversity should come along with more preferred, unmanaged habitats for Grey Partridges, especially in the more favourable, rectangular patch shape that decreases the predation risk (Sotherton, 1998), and should, therefore, have a positive impact on the breeding success. However, as long as this habitat diversity is not creating a highly heterogeneous landscape (5% insect-rich habitat and 6.9 km/100 ha nesting cover; Aebischer and Ewald, 2004), the preferred breeding habitats probably function as ecological traps, as predators learn to hunt in the few unmanaged habitats (Bro et al., 2004; Rantanen et al., 2010; Černý et al., 2020). Therefore, assuming that this ecological trap effect and my results are true, nests and incubating females might be better hidden in a more homogeneous landscape with low diversity, as predators might not find the farmland birds that easily then. On the other hand, the reduced nest cover and lower food availability for adult Grey Partridges increase their sensitivity to predation (Rands, 1988; Evans, 2004; Hille et al., 2021) and their time spent on vigilance, which results in less foraging time and, thus, lower fitness (Watson et al., 2007; Hille et al., 2021). In addition, the findings of a positive effect of non-forest edges as well as natural grasslands on the breeding success of Grey Partridges in 200 HR contradict with the negative effect of habitat diversity, as the preferred unmanaged habitats of Grey Partridges are represented by those habitat types in this study. Therefore, I assume that my results regarding the negative effect of habitat diversity on the breeding success of Grey Partridges are defective, due to the inaccuracy of the used CLCs. The missing non-forest edges, for example, along roads or between fields, as well as the missing crop diversity (Bossard et al., 2000) are probably decreasing the expected positive effect of habitat diversity on the breeding success of Grey Partridges. However, why habitat diversity supposedly has a negative impact in 200 HR and a positive impact in 1000 HR in my results cannot be explained properly. I assume that the accompanying insect diversity is so important for the survival of chicks in the post-breeding HR (Borg and Toft, 2000; Aebischer and Ewald, 2012), that the effect of habitat diversity is more significant in the 1000 HRs. Yet, further, more detailed as well as accurate research is necessary to distinguish these effects better.

The negative effects on the breeding success of Grey Partridges within their post-breeding HRs clearly show the strong impact of predation. Forest edges as well as other productive areas, such as vineyards or orchards, provide ideal structures for predators while lacking good hiding spots for Grey Partridges (Rands, 1988; Evans, 2004; Hille et al., 2021). Forest edges might often be adjacent to suitable habitats for Grey Partridges, which is why the chance of an encounter between the predator and the Grey Partridge might be even higher there. Especially inexperienced chicks, juveniles or reintroduced Grey Partridges might underestimate the danger of being close to forest-like structures. The decreased avoidance of risky habitats, such as woodlands, among other habitats, due to a lack of suitable habitats (Harmange et al., 2019; Hille et al., 2021) is increasing the predation risk of Grey Partridges even more. The strong, negative impact of small other productive areas on the breeding success of Grey Partridges in post-breeding HRs implies that those half-open woody structures of orchards and vineyards seem like good alternative habitats with sufficient food and shelter possibilities for rearing the chicks, but end up as optimal ecological traps, as the woody structures are advantageous for predators (Rands, 1987a; Rands,1988; Evans, 2004; Hille et al., 2021). However, the inaccurate representation of post-breeding HRs, possibly leading to biased results in this study, must be considered again.

6.4. Management recommendations

Several management measures aiming to improve the breeding success of Grey Partridges can be derived from my results and from findings of other studies. To increase the probability of a breeding success, two main factors have to be present: 1) a suitable nesting site concealed from predators and 2) sufficient availability of high-quality food for chicks (Kuijper et al., 2009). As a rapid creation of the optimal habitat structures, supporting the breeding success of Grey Partridges (a heterogeneous agricultural landscape that provides a diverse network of wide unmanaged, herbaceous patches as well as linear, herbaceous structures that are not sprayed with pesticides and are located between small fields with segetal flora; Rands, 1987a; Sotherton, 1998; Šálek et al., 2004; Černý and Šálek, 2020) is far from possible, I recommend concentrating on the following: First, protect and improve existing natural grasslands, including resembling areas in settlements, and possibly create new ones, while ensuring that those grasslands are big enough to prevent the ecological trap effect there (best a minimum of 0.3 ha and with at least 20 m width; Sotherton, 1998). This will provide Grey Partridges with suitable nesting sites with permanent vegetation and dry plant material (Panek, 1997; Rands, 1988; Bro et al., 2000b; Wübbenhorst and Leuschner, 2006). Second, promote the correct implementation of the combined biobelts in the Czech Republic (Ministerstvo zemědělství, 2023a; Ministerstvo zemědělství, 2023b) or other similar agri-environmental schemes (examples in e.g. Beeke and Gottschalk, 2014; Ewald et al., 2020). Those wide linear, herbaceous structures along fields will provide Grey Partridges with further safe nesting sites, as well as sufficient and diverse food, particularly invertebrates that are important for the healthy development and survival of chicks (Borg and Toft, 2000; Aebischer and Ewald, 2012). Third, reduce the general use of pesticides to increase the availability of segetal flora and invertebrates that serve as suitable food for Grey Partridges (Kuijper et al., 2009; Aebischer and Ewald, 2012; Panek, 2019). And fourth, ensure that these improved and suitable habitats are not adjacent to forest-like structures, as these are favourable habitats for predators of Grey Partridges (Rands, 1988; Evans, 2004; Hille et al., 2021) and an overlap of their habitats would therefore result in higher chances of prey-predator encounters.

7. Conclusion

This study provides evidence that the breeding success of Grey Partridges depends on slightly different habitat structures in their pre-breeding/breeding and post-breeding HRs. Within their smaller pre-breeding/breeding HR the farmland birds prefer unmanaged habitats, such as natural grasslands and linear, herbaceous structures along non-forest edges, roads, tracks, ditches, and field margins. These habitats provide Grey Partridges with sufficient dry plant material and vegetational structure to conceal their nest and the incubating female from predators (Rands, 1988; Panek, 1997; Bro et al., 2000b; Wübbenhorst and Leuschner, 2006). As predation is the most common natural reason for nest failure (Bro et al., 2000a; Černý et al., 2020), directly deteriorating the breeding success, the availability of herbaceous cover without human disturbance during the breeding time appears to be essential. During the post-breeding time, on the other hand, an availability of a variety of high-quality food for the chicks is vital for the breeding success because the chick's survival depends on a diverse diet high in protein (Borg and Toft, 2000; Aebischer and Ewald, 2012). This is why a heterogenous landscape with unmanaged patches of natural grasslands, offering a diversity of high-quality food without pesticides for both adults and chicks as well as shelter, are the key structures for rearing the chicks successfully. Additionally, it seems important to limit the occurrence of forest-like habitat structures in the HRs of Grey Partridges, such as forest edges, as those are favourable for predators (Rands, 1987a; Rands,1988; Evans, 2004; Hille et al., 2021). It appears that these woody structures are especially hindering the breeding success in post-breeding HRs, probably because of the proximity of foraging grounds of the family coveys to those forest-like structures. The observed habitat shifts of Grey Partridges toward dominant arable land and human infrastructure – both often lying close by forests – as well as the decreasing avoidance of woodlands (Harmange et al., 2019; Černý et al., 2020; Hille et al., 2021) probably enhance this predation risk even more. Additionally, ecological trap effects in the remaining preferred habitats as well as in alternative habitats, such as other productive areas, are increasingly threatening Grey Partridges in the modern homogeneous agricultural landscape, too (Bro et al., 2004; Kuijper et al., 2009; Beeke and Gottschalk, 2014; Černý et al., 2020). This is probably one reason why my results imply that a more uniform landscape is promoting the breeding success of Grey Partridges during the breeding time. However, due to my partially biased and defective data as well as analyses, I assume that the effects of habitat diversity as well as of non-forest edges are underestimated. According to other studies and to most of my results, Grey Partridges overall depend on a heterogeneous landscape with a variety of unmanaged patches of sufficient size and shape (Sotherton, 1998; Šálek et al., 2004; Beeke and Gottschalk, 2014; Černý et al., 2020) as well as on small-sized fields (Joannon et al., 2008) for a successful breeding and survival. This is fundamental for stabilizing the population and thus halting the decline of this farmland bird (Bro et al., 2000c; Aebischer and Ewald, 2004). As the establishment of such a diverse network within the agricultural landscape is a great challenge, I recommend focussing on the creation and protection of wide natural grasslands in addition to wide and diverse linear biobelts along unsprayed fields for the beginning. However, to further reduce the risk of an ecological trap, those suitable habitats for Grey Partridges should not lie next to habitats favourable to predators. In the end, I recommend conducting further and more detailed research, based on a systematic, large-scale field mapping of both Grey Partridges (pairs and coveys), as well as their surrounding habitat structures, to prove the effects of particular habitats on the breeding success of Grey Partridges in their HRs more reliably. I would specifically concentrate on studying the effect of natural grasslands on the breeding success of Grey Partridges, as this habitat seems to be of particular importance over the whole breeding period.

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