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VEGETATION STRUCTURE AT THE BREEDING SITES OF THE PARTRIDGE (*PERDIX PERDIX* L.) IN CENTRAL EUROPE AND ITS POSSIBLE IMPORTANCE FOR POPULATION DENSITY

ABSTRACT: This paper analyses the abundance of breeding pairs and the location of nesting sites of partridges as related to vegetation structure in the nest surroundings in two areas with very different partridge densities and arable landscape patterns (Central Germany and Eastern Poland). Study objective was to identify underlying causes of the more than 100 fold difference in population density of this species in these two areas of Central Europe. Our results suggests that the very limited availability of appropriate nesting habitats with an open canopy structure and low leaf area index is one of the key factors being responsible for the very low recent population density, and the past rapid decline, of partridge in the modern agricultural landscape of western Central Europe.

KEY WORDS: intensity of agriculture, leaf area index, nesting habitat, population density, vegetation height

1. INTRODUCTION

The size and dynamics of partridge (*Perdix perdix* L.) populations in Central Europe are known to be tightly linked to the type and intensity of agricultural land use. Originally native to steppes and forest-steppes (Glutz von Blotzheim *et al.* 1973), *P. perdix* only migrated from Eastern to Central Europe after large forest areas had been cleared (Glänzer *et al.* 1993). The species has been an abundant and characteristic bird of open agricultural landscapes in Germany and Poland for many centuries. However, in the meantime this situation has fundamentally changed: in the past several decades *P. perdix* populations nearly everywhere in Europe have declined (Aebischer and Potts 1988, Panek 1991, Gossow *et al.* 1992, Kavanagh 1992, Zbinden 1992, Helenius *et al.* 1995, Enderlein *et al.* 1998, Chiverton 1999), often more than 90% (Aebischer and Potts 1994).

Above all, habitat changes due to the intensification and mechanisation of agriculture have been declared to be the main reason for the population decline (Tucker and Heath 1994, Bauer and Berthold 1996, Hagemeijer and Blair 1997). However, the causal links between habitat change and population decrease are complex and have been assessed differentially by different authors. It is often assumed that the loss of structural diversity in open agricultural landscapes represents a key factor with *P. perdix* abundance being linked to the frequency of hedges, field margins, and forest and scrub islands in the landscape mosaic (Rands 1986, Glänzer *et al.* 1993, Mooij 1997, Kaiser 1998, Ranoux 1998, Panek and Kamieniarz 1998, 2000b). These explanations remain unspecific by not identifying the limiting process in *P. perdix* population dynamics in modern agricultural landscapes.

A closer look on the causes of decline is taken by the following authors. Ellenberg (1983, 1992) and Mooij (1998) point out a possible negative correlation of *P. perdix* abundance with the amount of nitrogen fertiliser applied by agriculture. In England, a distinct influence of the increased use of pesticides with the consequence of elevated chick mortality has been recorded (Southwood and Cross 1969, Potts 1986, Potts and Aebischer 1995). Panek (1991) emphasizes the elevated hatchling mortality for Polish populations in the context of decreasing structural diversity in the landscape which he linked to decreases in insect abundance. Potts (1980) suggested the loss of nesting sites as a reason for the population decrease in *P. perdix* in Great Britain. A similar explanation was offered by Kugelschafter (1995) for the decline in Central German populations.

In theory, *P. perdix* population size may be limited by elevated mortality in the non-breeding season, or by reduced population growth in the breeding period. Literature data indicate that, in Central Europe, the former cause seems to be less decisive than reduced reproduction rates, either due to decreased breeding success (Carroll 1992, Panek 1992, Bro *et al.* 2000), or due to elevated chick mortality (Southwood and Cross 1969, Potts 1986, Panek and Kamieniarz 2000a). This points to a key role of abundance and quality of possible reproduction sites which must provide adequate cover and absence of disturbance in a period of at least seven weeks from end of April/early May to June during nest building, breeding and hatching. Thus, the preferred vegetation structure in the immediate vicinity of the breeding site and its location in the agricultural landscape mosaic may be influential factors for *P. perdix* reproduction success. However, related information is scarce for Central European populations.

The recent study investigates vegetation height and ground cover in *P. perdix* nesting sites in two Central European agricultural landscapes with high or low population densities, and analyses the species' preference of different landscape elements as breeding sites. This information is used to draw conclusions on the possible causes of high or low population densities in the two test areas in Germany and Poland.

2. MATERIAL AND METHODS

2.1. Study areas

For comparison of breeding site selection in landscapes with high or low *P. perdix* densities, we selected study areas in Central Germany and Eastern Poland. Both areas comprise 'classical' partridge habitats with open agricultural landscapes and dominance of arable fields with autumn and spring seeds. Because we aimed at a qualitative analysis of vegetation at the breeding sites, the size of the study areas was chosen to include a sufficient number of breeding pairs. We had to choose a much larger study area in Gemany (48 670 ha, study area 1) than in Poland (about 62 ha, study area 2) for including sufficient partridge pairs for analysis, because the density of partridge breeding pairs was about 100 times lower in the German study area (0.2 pairs km^{-2}) with a very heterogeneous metapopulation as compared to the densely populated Polish area (24 pairs km^{-2}).

Study area 1 (51°11'N, 9°30'E) includes substantial parts of the county of Kassel between the cities of Kassel and Wolfhagen in Northern Hesse. It comprises an example of a modern agricultural landscape with a high input of energy and fertilizers, and a high degree of mechanisation as is found in large parts of the Central German highlands. Large wheat, rape and corn fields dominate. The fields today have a typical size of 3 to 10 ha; they were created from former small-holder fields by a consolidation and intensification program in the 1970s and 1980s. This restructuring process of the agricultural landscape may be representative for large parts of western Central Europe.

Study area 2 (50°42'N, 21°43'E), which is located west of Sandomierz near the Vistula river in South-eastern Poland, is characterised by a much lower input of energy and fertilizers and a comparably low degree of mechanisation. The average field size is between 0.3 and 1.0 ha with parts of the landscape being occupied by small hedges, shrub islands and field margins with low use intensities. Both study areas are similar with respect to altitude (140–380 *vs*. 240–270 m. a.s.l.) and the proportion of farmland in the landscape (about 70–85%).

2.2. Methods

In May 2000 and 2001, a determination of the numbers of calling cocks was conducted using the acoustic 'listening method' (cf. Harbodt and Richarz 1992), in which we 'listened' two to four times at dawn or dusk for periods of 60 min in a landscape patch of about 10 ha, at least once at dawn and once at dusk. This was done subsequently in all parts of the two study areas. Since the animals' home range during the breeding period is very small (typically not more than 60 to 100 m in diameter; Blank and Ash 1956, Szederjei and Szederjei 1960, Kugelschafter 1995), repeated observation of a pair in a restricted location in May is a good indicator of a partridge breeding territory. In a number of cases, acoustic decoys proved to be a suitable additional aid for locating the birds. We did not search for the nests because own experience has shown that direct access to the breeding site significantly increases nest predation. Rather, we analysed the vegetation structure in close vicinity of the calling cocks assuming that the nesting site is very close.

The land use patterns of the agricultural landscape in the two study areas (excluding forests and settlement areas) were classified into 10 land use types (see Table 1) to which the breeding sites could be subsequently assigned. In addition, the fractions of the land use types in the total study area were determined in percent. In study area 2 with a continuous distribution of the partridge at a high density in the landscape, this analysis was done for the entire area of about 60 ha. In contrast, in the much larger study area 1 with a highly heterogeneous and discontinuous partridge distribution, we selected by random 20 patches of each 3 ha in size (in total 60 ha) for a landscape pattern analysis. To do so, the spatial extension of the 10 identified land use types was mapped in the field using cadastral maps on a scale of 1:5000. The area per land use type was subsequently calculated with the aid of a geographic information system (ArcView GIS 3.1). In study area 2, we obtained a table of the relative abundance of the 10 land use types in the total area. In study area 1, the results of the 20 random patches were added and set in relation to the total surface area to obtain an estimate of the relative abundance of the different land use types.

In each of the 10 land use types, we selected 10 to 20 plots to analyse vegetation structure as a possible determinant of the plot's suitability to serve as a partridge breeding site. This was done in both study areas. We included land use types which were used as breeding sites and land use types that contained no nests. Vegetation structure was analysed on the plots in a rectangular grid of 20 × 20 m. If partridges were present the plots enclosed the locations where calling cocks were observed most frequently in May. On each plot, twelve locations were randomly selected for analysing vegetation height and leaf area index (LAI), i.e. the one-sided cumulative surface area of leaves of the vegetation related to ground area (in m^2 m^{-2}). LAI was used as a measure of vegetation density and light transmission to the ground. LAI was determined optically with a LAI-2000 system (LI-Cor, Lincoln, Nebraska, USA) which measures the transmissivity of photosynthetically active radiation in a vegetation stand by comparing the radiation flux density in hemispheres above and below the canopy. This was done at all 12 locations per plot; three measurements above the canopy served as reference measurements. All measurements were performed under a cloudy sky as is required by this method of LAI determination. For measuring vegetation height in early May at the starting of the breeding, measurements with a cm-tape were taken at three randomly selected locations per plot. All LAI and height data of a plot were averaged.

We expressed the preference or avoidance of a given land use type by partridges for breeding by a preference factor. In this factor, the proportion of breeding pairs in a land use type as related to the entire population in the study area is divided by the relative size of this land use type as related to the total size of the study area. A preference factor larger than unity indicates that the land use type is chosen more often for breeding than one would expect from a random selection of breeding sites in the landscape.

3. RESULTS

3.1. Preference of land use types as nesting sites

Table 1 shows the land use types which were preferentially selected by partridges as nesting sites in the two study areas in Central Germany and Eastern Poland. A preference is indicated by a more frequent occurrence in a given land use type than its presence fraction in the landscape (i.e. a preference factor > 1).

In study area 1 (Germany), a preference for fallow areas that were at least temporarily out-of-use is visible compared to land use types with current agricultural utilization. The land use types most often used for nesting were: arable fallows, grassland fallows, ruderal areas, and forest or scrub islands within the agricultural landscape. In some cases, grain fields were also selected in study area 1, but only with a very low preference given their large surface area. *P. perdix* never chose spring seeds and grassland areas. Similarly, hedgerows, bushes and field margins were never used as reproduction habitats in the German study area although they are not directly affected by land management.

Although the study area 2 was much smaller and fewer nesting sites were mapped than in area 1, the completely different land use type selection by partridges in the Polish study area was clearly evident. In this area, only agricultural land, above all winter grain fields (autumn seeds), was selected for breeding (preference factor: 35; Table 1). Unlike in study area 1, permanently unused landscape elements such as forest or scrub islands and ruderal areas were nearly absent from the study area 2 as were field margins with or without copses. Consequently, they played no significant role as nesting sites in this study area, although they are typical for other rural areas in Poland.

Table 1. Selection of nesting sites by *P. perdix* in the study areas 1 and 2 as related to land use types (preference factor: fraction of breeding sites/fraction of area; * based on one plot only).

	Area 1 Kassel, Central Germany			Area 2 Sandomierz, Eastern Poland		
Land use type	Fraction of area (%)	Fraction of breeding sites (%)	Preference factor	Fraction of area (%)	Fraction of breeding sites (%)	Preference factor
Autumn seeds	54.4	11.5	0.2	2.7	80.0	35.0
Spring seeds	14.1	0.0	0.0	31.2	0.0	0.0
Arable fallows	1.0	21.2	20.7	0.6	6.7	10.3*
Grassland	8.8	0.0	0.0	6.8	6.7	1.0
Grassland fallows	6.0	28.9	4.8	0.0	0.0	–
Small forest remnants and ruderal areas	3.0	38.5	12.9	0.0	0.0	–
Hedges and bushes	3.7	0.0	0.0	0.0	0.0	–
Margins	0.7	0.0	0.0	0.0	0.0	–
Paths	5.2	0.0	0.0	1.7	0.0	0.0
Other areas	3.1	0.0	0.0	8.7	6.7	0.8

3.2. Vegetation structure in the proximity of the nesting site

Vegetation height and leaf area index measured in early May are used to quantify vegetation density in the nesting site which may determine its suitability for sheltering and accessibility by the birds. Despite the open character of agricultural landscapes, the vegetation structure in the different types of land use available to partridges is highly variable. Figure 1 shows a broad scattering of values with regard to height and leaf area index and definite differences between the investigated types of land use. Rape, the various winter grains, and early-seeded crops each present a very uniform structure, whereas grassland fallows, small forest and scrub islands, and ruderal areas exhibit clearly higher variability among different stands.

Our data indicate that partridges in study area 1 preferred stands with a height of about 20 to 60 cm and with a leaf area index (LAI) of 1 to 3 $m^2\ m^{-2}$ (Fig. 1). Most of the studied agricultural fallows, ruderal areas, and forest and scrub islands had LAI values < 3 in early May; grassland fallows had values between 3 and 7, whereas spring seeds reached values of only 0.2 to 0.6 $m^2\ m^{-2}$ in this time of the year. The LAI in autumn seeds of area 2 was lower than in area 1 (Fig. 2). The vegetation structure of chosen nesting sites in area 2 (autumn seeds) was similar to the preferred structures in area 1 (arable fallows, grassland fallows, and small forest remnants).

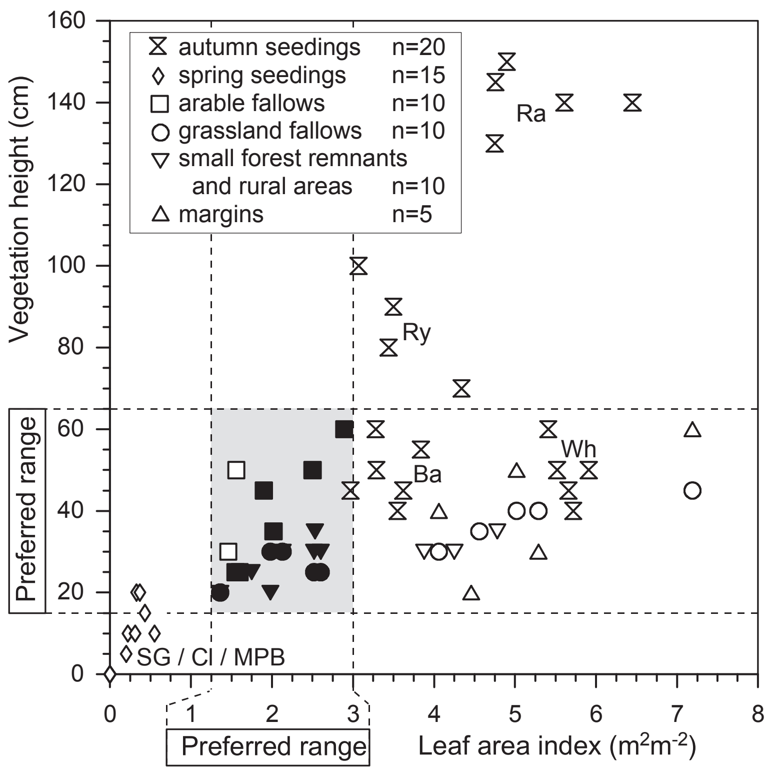

Fig. 1. Vegetation structure of different plots in various land use types in study area 1 (Central Germany). Filled symbols: plots selected by *P. perdix* as nesting sites. Open Symbols: plots not used as nesting sites. The preferred range as indicated (shaded area) was obtained from the extreme values of measured vegetation heights and densities for all plots selected by *P. perdix* as nesting sites in study area 1. Ba = barley, Cl = clover, MPB = maize/potato/beet, Ra = rape, Ry = rye, Wh = wheat (n = 5 in all cases) (For the additional plot types Paths and Other areas listed in Table 1 no meaningful generalising statement about vegetation density could be made).

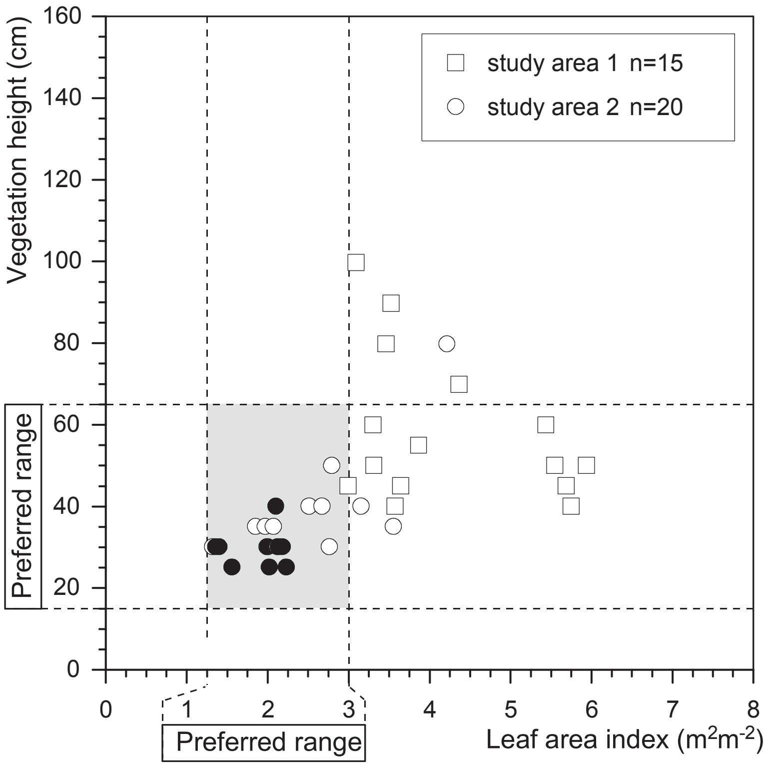

Fig. 2. Leaf area index and vegetation height in early May of autumn seeds in study areas 1 and 2; filled symbols: plots selected by *P. perdix* as nesting sites; open symbols: plots not used as nesting sites. n = vegetation study plots.

4. DISCUSSION

In Central Europe's intensively utilized agricultural landscape, a preference of *P. perdix* for fallows and ruderal habitats as breeding sites has been found recently by different authors in Germany (Flade and Jebram 1995, Eislöffel 1996, Kaiser and Storch 1996, Kaiser 1997), England (Sotherton *et al.* 1998), Finland (Turtola 1998) and Poland (Panek and Kamieniarz 2000a, b). In addition to fallow vegetation, only fields with autumn seeds remain available for first clutches in such areas (cf. Richarz *et al.* 1998). According to older reports, *P. perdix* has bred in Germany in the first half of the 20th century at high percentages in grain fields (Koch 1912, Niethammer 1942). Similarly, Szederjei and Szederjei (1960) mention large numbers of clutches in grain fields in Hungary in the 1940s and 1950s. At the beginning of the 1990s, Kaiser and Storch (1996) still found nearly 50% of the nests in grain in two research plots near Feuchtwangen in Southern Germany (Fig. 3).

In order to be able to interpret the fundamental differences in habitat selection in the two study areas of this study in Central Germany and Eastern Poland, the results of Kaiser and Storch (1996) and Panek and Kamieniarz (2000a) were included in Figure 4 to supplement our own data. The values taken from these publications lie between the extremes of the results from study areas 1 and 2 with respect to both brood pair density and the fraction of breeding in grain fields. The figure shows a clear trend: evidently, the lower the *P. perdix* density, the lower the proportion of breeding in grain fields.

Since partridges require a minimum cover in the nesting site as shelter, substantial parts of the agricultural landscape are inappropriate for this species due to the phenological cycle of spring-seeded annual crops. The spring-seeded crops with leaf area indices <0.6 m² m⁻² were not yet sufficiently developed at the beginning of the breeding period; whereas most of the winter grain fields and field margins already exhibited excessively dense plant covers with LAI values > 3 m^2 m^{-2}. The previously found preference of arable and grassland fallows, rural areas and forest or scrub islands in the agricultural landscape may thus be explained by a preference of *P. perdix* to nest in vegetation of 20 to 60 cm in height and with LAI values of 1 to 3. Given the fact that grassland fallows were only chosen when the LAI was smaller than 3 m^2 m^{-2}, we further conclude that the location of the nesting site in Central Europe is primarily dependent on structural attributes of the vegetation rather than the type and species composition of the vegetation. This is supported by the results from study area 2: the clear preference of winter grain fields in Eastern Poland, which is a major difference to study area 1, is understandable in terms of vegetation structure. The LAI values of the Polish winter grain fields at the beginning of May were lower than those in Central German winter grain stands. The great majority of nesting sites in winter grain had LAI values <3 m^2 m^{-2} and, thus, are in the preference range of this species as specified by the results from study area 1.

The observed dependence on herbaceous vegetation of medium height with only sparse cover is not surprising because *P. perdix* prefers locations that can be surveyed easily in an upright posture, but which simultaneously provide cover (Glänzer *et al.* 1993). On the other hand, the birds have difficulties in moving through, and foraging in, dense vegetation (Kugelschafter 1995, Sotherton *et al.* 1998, Grimm 1999) where food availability may be poor (Litzbarski *et al.* 1988, Heimbucher 1991, Havelka and Ruge 1993, Bräsecke 1995, Litzbarski 1995, Oppermann 1999a, b).

Increasing fertiliser application has resulted in a tendency to higher vegetation density and leaf area indices in most agricultural landscapes. The highest LAI values were measured in highly fertile grassland fallows and field margins with up to 7.5 m^2 m^{-2}.

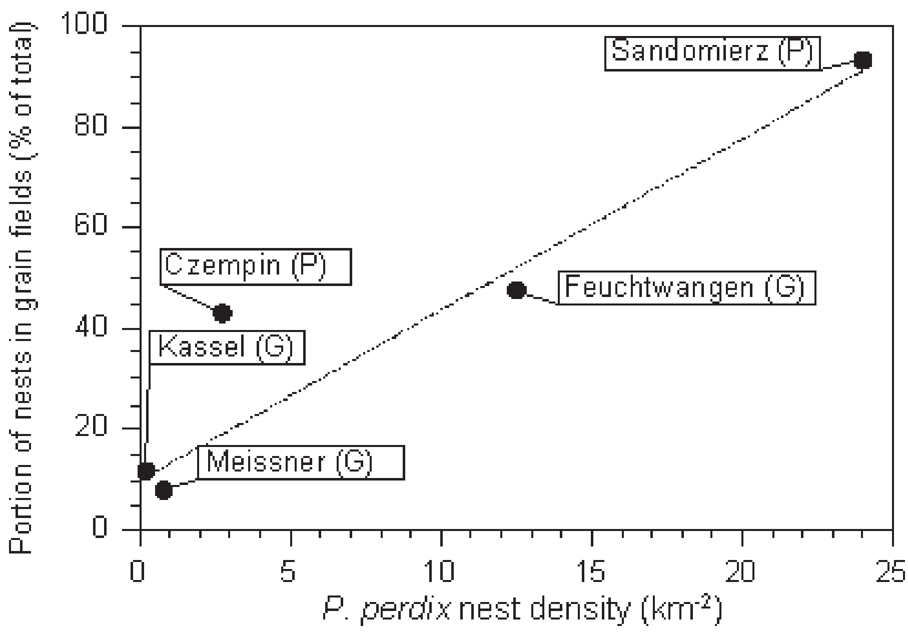

Fig. 3. Portion of *P. perdix* nests in grain fields in five areas with different partridge densities in Germany (G) and Poland (P) (data from Feuchtwangen, Northern Bavaria from Kaiser and Storch 1996, data from Czempin, Western Poland, from Panek and Kamieniarz 2000; for both sources average brood pair densities from several study areas were calculated and used here; data from Meißner, Northern Hesse, from Wübbenhorst 2002). $y = 10.95+3.39x$; r = 0.94; $P = 0.007$.

For this reason, many small residual fallow areas are nowadays inappropriate as breeding habitats for *P. perdix* even when they are not mown during the breeding period. Thus, the hypothesis of Ellenberg (1983, 1992) and Mooij (1998), that widespread eutrophication of agricultural landscapes has to be considered as a prime hazard for the partridge, is confirmed by our data.

If one proceeds on the assumption that the more traditional land use systems in the study area in Eastern Poland today are similar to those existing in Germany approximately 50 years ago, Figure 3 can also be understood as a space-for-time substitution series in which the individual areas reflect different stages of agricultural intensification. The habitat changes resulting from modern agricultural use have apparently resulted in an altered preference of land use types even though the preferred vegetation type of *P. perdix* remained the same. Central European *P. perdix* populations use grain fields as breeding habitats with steadily decreasing frequency. This is because agricultural intensification has not only resulted in an overall increase in vegetation density, but has also led to an impoverishment of the herbaceous field flora and arthropod fauna due to improved weed control methods, and an accompanying increase in chick mortality (Southwood and Cross 1969, Potts 1986, Potts and Aebischer 1995). *P. perdix* increasingly sought refuge in fallows and field islands and, thus, became independent of the insect abundance in the grain fields. Own investigations have shown that the reproductive rates of the birds breeding in the appropriate residual habitat islands and the survival rates of their chicks can be relatively high even if the regional population density is low (Wübbenhorst 2002). According to these data, declining *P. perdix* populations in the agricultural landscape may well have high average chick mortalities although fragments of the population are still reproducing well in restricted optimal habitats.

A number of authors have stressed that a high diversity of habitat types in the agricultural landscape and the existence of small patchy structure may promote high *P. perdix* densities (Glänzer *et al.* 1993, Kaiser 1998, Ranoux 1998, Panek and Kamieniarz 2000b). This factor appears unsatisfactory as the sole explanation for the population dynamics of a species whose original habitat was the steppe. The vegetation structure at the breeding site must be considered to be more decisive. Indeed, the widespread disappearance of hedgerows and field margins (Glänzer *et al.* 1993) does not appear to be a primary reason for the decline of partridge populations in Central Europe. Literature data indicate that hedgerows and field margins may play an important role as a *P. perdix* breeding habitat in certain regions (e.g. in England, Rands 1986), but they do not in the study area 1 in Central Germany. Similarly, hedge and bush islands, which are typical for large parts of the Polish rural landscape, were rare in the study area 2; yet, the partridge population density was high. Apparently, the vegetation structure of the hedgerows and field margins is relevant: the hedgerows of study area 1, which never were selected for breeding, represented dense woody strips that extended directly up to the field border. We speculate that *P. perdix* prefers hedges and field margins only if they are characterised by an open patchy woody vegetation and a sparse herb cover. These habitats are structurally similar to small forest and scrub islands in the study area 1 where high population densities were found.

Our conclusion on the prime importance of vegetation height and density is further supported by the observation that, in study area 1, comparably large partridge populations exist on industrial fallow areas and perspective building land at the outskirts of the cities of Kassel and Baunatal. Since such short-lived ruderal habitats are constantly being re-designated for many years in immediate proximity to one another, *P. perdix* has been able to maintain its populations at relatively high densities there despite the disappearance of the habitats it previously used in the region (Witt 2000, Mitschke and Baumung 2001). Frequent disturbance seems to provide sufficient breeding sites with reduced vegetation density in these ruderal habitats.

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