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Landscape structure, predation of red foxes on grey partridges, and their spatial relations

Research Article

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Abstract: The aim of this study was to estimate the effect of agricultural landscape structure on the predation rate of red foxes *Vulpes vulpes* on grey partridges *Perdix perdix* during the breeding season and on their spatial relations. The number of partridge remains found around fox breeding dens (N=165) was used as an index of the predation rate in 10 study areas. Moreover, the distribution of both species and the searching intensity of partridge nesting habitat (permanent semi-natural vegetation) by foxes in relation to the landscape structure were studied using scat, track and call counts. The predation index (range 0.06-0.46 partridges/den) increased with spring partridge density and decreased with the occurrence of crop boundaries. The distribution of foxes and partridges in large fields was positively correlated with the occurrence of permanent vegetation, but no such effect was observed in small fields. The searching intensity in permanent vegetation by foxes decreased with the occurrence of these structures among small fields, but not among large fields. The study showed that in a differentiated landscape foxes and partridges had various structural elements at their disposal, which led to partial separation of the predator and its prey in the space.

Keywords: *Agricultural landscape • Incidental predation • Perdix perdix • Poland • Predator-prey spatial relations • Vulpes vulpes*

1. Introduction

Generalist predators usually switch their hunting activity between alternative prey species as a result of changes in their relative abundance [1]. However, such a response may fail to happen in the case of prey being a small portion of the predator's diet, *i.e.* the secondary or marginal prey. For example, Finnish researchers did not find any signs of functional response of avian predators to some game bird species, which was explained by a low proportion of these species in the diet of these predators [2]. Such marginal prey may be subject to incidental predation, and its rate may depend on how the predator searches the patchy landscape [3]. However, such predator – marginal prey relations seem to be poorly understood as compared with predator – alternative prey patterns.

This study focused on a generalist predator – the red fox *Vulpes vulpes*, and its prey – the grey partridge *Perdix perdix*, living in an agricultural landscape. In the agricultural lands of Poland, foxes have mainly hunted the common vole *Microtus arvalis,* and as a second choice, the brown hare *Lepus europaeus* (particularly in previous decades); moreover in some regions or time periods their diet contained considerable proportions of birds and livestock carrion, including mammals and poultry [4-9]. According to studies carried out in Poland in the years 1960s-1980s, the grey partridge amounted to less than 5% of the diet of red foxes [4-7]. Thus, the partridge may be considered as marginal prey to this predator. The red fox is, however, listed among significant predators of the grey partridge, in particular during the nesting season [10]. In western Poland in the second half of the 1990s, it was found that the red fox was the most frequent cause of mortality among incubating females and the nest losses of partridges [11].

Grey partridges are known for their preference to nest in non-cultivated parts of the agricultural land covered with permanent semi-natural herbaceous vegetation, such as hedge banks, ditches and roadsides [10]. It was also found that their breeding success increased with

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the availability of such permanent vegetation structures [10], and in the specific conditions of Polish farmland [12], also with the extent of crop field fragmentation [13]. This suggests that the agricultural landscape structure affects the pressure of predators on the nests and incubating partridge females. The probable mechanisms of such a relationship include changes in the availability of safe nesting sites, density of predators, and abundance of their main prey or pattern of area searching by predators.

The study was aimed at estimating the effect of agricultural landscape structure on the predation rate of red foxes on grey partridges during the breeding season. It was predicted that the landscape structure affects the predation rate by modifying spatial relations between the two species. Therefore, in order to understand the mechanism of this impact, the effects of agricultural landscape structure on the distribution of partridges and foxes and on the searching intensity of preferred partridge nesting sites by foxes were also examined. The abundance of the main prey of foxes (voles and hares) as a possible factor affecting the predation rate and fox-partridge spatial relations was controlled.

2. Experimental Procedures

2.1 Predation rate

The study was carried out in 1999-2001 in 10 areas (50-100 km^2) located in various regions of Poland. These areas contained mainly agricultural landscapes (with few forests of up to 200 ha), varying as to the degree of crop field fragmentation (and thus the density of field boundaries) and the occurrence of places with permanent semi-natural vegetation (mainly linear structures along parts of field borders, such as hedgerows, ditches, roadsides).

The average number of individuals found among prey remains around the red fox family dens was used as an index of the fox predation (capture) rate on grey partridges in the nesting season. It was found that this method allows the detection of only a part of birds caught by foxes, but gives a good indication of total prey numbers taken by these predators [14]. The dens of foxes in a given study area were located and checked in one year. In mid June, *i.e.* during the final phase of first clutch incubation of partridges [15], the neighbourhood of each den with cub traces was searched. When partridge remains were found (usually feathers, mainly flight-feathers), the number of individuals was determined on the basis of repeated elements and their sex was identified, if possible. The frequency of females and males among the prey of foxes was compared to the spring sex ratio determined in the Polish partridge populations (47.5% of females [16]).

In each area, in the year of checking the foxes' dens, the spring density of partridges and the indices of the main prey abundance of these predators were estimated. The partridge density was determined in the second half of March or in the first half of April using the method of counting calling males in 10 points randomly selected in each area [17]. The vole abundance was indicated by the number of active burrow entrances [18]. Burrow counts were carried out in March at 15-km random transect routes going across crop fields, and the number of entrances per unit of the transect length was calculated. The brown hare density was estimated using the belt assessment [19] performed in the previous November at the 40-50 km routes in each area. It was assumed that the results of the autumn counts of brown hares were a good index of their spring density since the winter mortality of that species in Poland is relatively low and shows little variation between years [20].

The agricultural landscape structure in the study areas was assessed by line transects (the same as in the case of vole index). Direct boundaries between various crops or between crops and ploughed land (*i.e.* boundaries without permanent vegetation or with narrow strips, <1 m wide) as well as boundaries with strips of permanent semi-natural vegetation (>1 m wide) crossed by the transect route were counted. The indices of the agricultural landscape structure in a given area included the number of crop boundaries and the number of permanent vegetation strips per km.

Relations between the predation index, the indices of main fox prey abundance and the variables describing landscape structure were investigated using multiple regression analysis (forward method).

2.2 Spatial relations

This part of the study was conducted in the years 1999-2001 in an area of 20 km^2 located in western Poland, near Czempiń, south of Poznań. There were two types of spatial management of cultivated land occurring in clusters of several hundred hectares. The first type consisted of crop fields from <1 to 10 ha ("small fields") and the second contained crop fields from 15 to 100 ha ("large fields"). In large fields, most boundaries between crop fields were linear structures comprising permanent semi-natural vegetation (>1 m wide) with a density of 3.7 km/km^2, while the density of direct crop boundaries (without permanent vegetation) was 0.9 km/km^2. The complexes of small fields included similar amounts of permanent vegetation strips – 3.3 km/km^2, but there were numerous direct crop boundaries with a density of 9.7 km/km^2. In this area, 78% of partridge nests were located in permanent vegetation and the fox predation was the most frequent cause of clutch losses and mortality of incubating females in the late 1990s [11]. The density of fox populations in this area was practically stable at the end of the 1990s and averaged 1.0 indiv./km^2 in spring [8]. Partridge densities in the years 1999-2001 were about 1.3 pairs/km^2 (M. Panek, unpublished data). In this region, large fluctuations in numbers of common voles were registered [21]. Brown hare density was relatively low at the turn of the 1990s and 2000s (<10 indiv./km^2 [22]) and the species constituted only 1% of the diet of foxes in the late 1990s [8]. Thus, hare density was not controlled in this part of the study. For the whole study area, maps (1:5000) of permanent vegetation structures were made and updated every year.

Factors affecting the distribution of foxes and partridges as well as fox-partridge spatial relations at the beginning of partridge breeding season on the two field types were examined on 0.5×0.5 km square plots determined on the basis of topographic map grid. Among these, 52 plots were selected, containing only one field type (26 plots with small fields and 26 with large fields). Each plot was evenly covered with transect routes with a total length of 3 km (thus the length of transects in all plots was 156 km). The transect routes were traversed in the end of February and in March to count fresh scats of foxes and active burrow entrances of voles. The index of vole density in each plot was calculated as above. The occurrence of fox scats was used as an index of activity intensity of these predators [23,24], *i.e.* the number of scats per unit of transect length was calculated for individual plots. The occurrence of partridges in individual plots was estimated in March and at the beginning of April (*i.e.* at least two weeks after pair formation, which took place in February in the study years). Partridge pairs were located in the morning or evening during the period of intensive vocal activity of the species, using type playback calls. Each plot was checked three times a year. The average number of pairs found was a measure of the occurrence of partridges in individual plots. For each plot, the length of permanent vegetation strips was estimated.

The searching intensity of permanent vegetation strips by foxes during partridge nesting season in relation to agricultural landscape structure was also studied. Each year, 100 samples of plastic foam (21x23 cm) were randomly placed on boundaries between permanent vegetation strips and crops in late May. The tracks of larger animals were pressed permanently onto the foam. After a month, individual tracks of foxes on a given sample were identified and counted. For the neighbourhood of each sample, *i.e.* in the area of 25 ha around its location, the length of permanent vegetation strips was measured.

The generalised linear model (GLM) was used to analyse the distribution of both species and fox searching intensity in relation to vole abundance, permanent vegetation occurrence, crop field type and year.

3. Results

3.1 Predation rate

Altogether 165 family dens of red foxes were located and in their vicinity the remains of 29 partridges were found. The sex of 22 individuals was determined, and among them 16 females and 6 males were identified. The proportion of females was significantly higher than their ratio in the partridge population during the spring period (χ^2=5.72, P=0.02).

The index of fox predation on partridges in individual study areas, *i.e.* the average number of remains per den, increased linearly with the spring density of these birds (Table 1 and 2, Figure 1). By dividing the average number of remains per den by partridge density in individual areas, it was possible to calculate an index describing the proportion of partridges removed from the population by individual foxes. The removal index proved to be the highest for low partridge densities and decreased asymptotically for higher densities (Figure 1).

Significant correlations found between all variables collected in 10 study areas are shown in Table 2. The index of fox predation rate also increased with the occurrence of permanent vegetation. The partridge density increased with both variables describing the structure of agricultural landscape. The abundance of main fox prey species was partially related to the landscape structure, as the hare density increased with the occurrence of crop boundaries. Moreover, the variables describing the agricultural landscape structure, *i.e.* the occurrence of crop boundaries and permanent vegetation, were positively correlated between each other.

In the stepwise multiple regression analysis of the fox predation index in individual study areas against the variables describing agricultural landscape structure and the indices of main fox prey abundance, controlling for the partridge spring density, only the occurrence of crop boundaries showed a significant negative effect (R^2=0.978, density – partial r=0.982, df=7, P<0.001, crop boundaries – partial r=–0.827, df=7, P=0.006). The significant effect of crop boundaries was maintained (partial r=–0.796, df=5, P=0.03) when the vole density index (partial r=–0.057, df=5, P=0.9) and the hare

No. of study area	1	2	3	4	5	6	7	8	9	10
Fox predation rate index (N)	0.06 (17)	0.08 (24)	0.10 (20)	0.13 (15)	0.14 (14)	0.17 (18)	0.21 (14)	0.25 (16)	0.29 (14)	0.46 (13)
Partridge density	1.0	0.2	0.5	0.8	3.6	4.2	4.4	5.6	5.8	10.5
Main fox prey:										
Vole density index	7.3	1.7	24.0	36.9	68.4	36.5	3.0	30.7	13.2	5.0
Hare density	4.6	3.4	4.4	7.6	34.1	18.6	15.6	14.3	20.8	18.0
Agricultural landscape structure:										
Permanent vegetation	2.0	1.2	1.8	1.9	2.8	2.5	2.9	2.1	3.4	4.4
Crop boundaries	5.5	1.3	3.4	2.9	11.3	9.5	8.9	8.0	8.8	10.6

Table 1. The index of predation rate of red foxes on grey partridges during nesting season (average number of partridges determined by remains found near fox breeding dens; N of dens in parentheses), spring partridge density (pairs per km^2), indices of main fox prey abundance (voles – the number of burrow entrances per km of transect route; hares – individuals per km^2) and variables describing agricultural landscape structure (the number of elements per km of transect route) in 10 study areas in Poland.

Variable	1	2	3	4	5	6
	Correlation coefficient r (df=8)					
1. Fox predation rate index	-	0.966 ***	ns	ns	0.882 ***	ns
2. Partridge density	-	-	ns	ns	0.907 ***	0.787 **
3. Vole density index	-	-	-	ns	ns	ns
4. Hare density	-	-	-	-	ns	0.874 ***
5. Permanent vegetation	-	-	-	-	-	0.803 **
6. Crop boundaries	-	-	-	-	-	-

Table 2. Correlation matrix for the index of fox predation rate on grey partridges, fox prey abundance indices and variables describing agricultural landscape structure (see Table 1 for their definitions) in 10 study areas in Poland (ns – not significant, **P<0.01, ***P<0.001).

density (partial r=0.402, df=5, P=0.4) were also inserted into the regression model. If the occurrence of crop boundaries was excluded from the regression model, both fox prey abundance indices were still not significant (voles: partial r=–0.413, df=7, P=0.3; hares: partial r=–0.563, df=7, P=0.1). Moreover, when both landscape variables were taken into account, crop boundaries still produced a significant effect (partial r=–0.899, df=6, P=0.002), whilst the effect of permanent vegetation strips was not significant (partial r=0.627, df=6, P=0.1). The last variable was also not significant when it was used as only habitat parameter in the regression model (partial r=0.050, df=7, P=0.9).

3.2 Spatial relations

Among the variables estimated in the study plots in western Poland, no significant effect of field type and year was found in the case of the fox activity index and partridge occurrence. The index of vole density did not significantly differ between field types, however changes between years were found. Moreover, the occurrence of

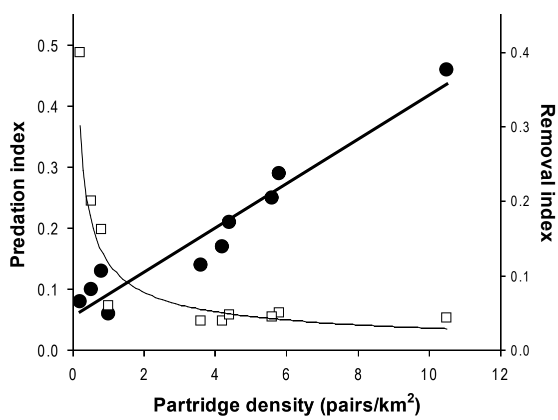

Figure 1. Predation index of red foxes on grey partridges during nesting season (average number of partridges among remains found near fox breeding dens) and removal index (average number of partridge remains per fox den divided by partridge spring density) in relation to spring partridge density in 10 study areas in Poland (predation index: black circles, r^2=0.932, df=8, P<0.001, y=0.0361x+0.0568; removal index: white squares, R^2=0.845, df=8, P<0.001, y=0.117x$^{-0.588}$).

permanent vegetation, which did not show any changes between years, also did not significantly differ between the two field types (Table 3).

The GLM analysis for the index of fox activity in relation to the index of vole density and the occurrence of permanent vegetation as well as the size of crop fields and year as categorical variables showed a significant effect of the field size variable ($F_{1,148}$= 6.080, P=0.01). For this reason, the next analyses were carried out separately for the two field types. In small fields, the fox activity intensity was not significantly dependent on the vole density index ($F_{1,73}$=0.026, P=0.9) or on the occurrence of permanent vegetation strips ($F_{1,73}$=1.146, P=0.3); the year effect was also not significant ($F_{2,73}$=0.432, P=0.7). However, in large fields, the fox activity intensity increased both with the vole density index ($F_{1,73}$=10.68, partial r=0.357, P=0.002) and the occurrence of permanent vegetation strips ($F_{1,73}$=28.16, partial r=0.528, P<0.001), with no significant year effect ($F_{2,73}$=1.422, P=0.2). The occurrence of partridge pairs on the study plots containing small fields was not significantly related to the occurrence of permanent vegetation strips ($F_{1,74}$=0.162, P=0.7) and no significant year effect was found ($F_{2,74}$=1.084, P=0.3). In large fields, however, the occurrence of partridge pairs increased with the occurrence of permanent vegetation strips ($F_{1,74}$=10.74, partial r=0.356, P=0.002), with no significant year effect ($F_{2,74}$=0.184, P=0.8). Nevertheless, a positive relationship between the occurrence of partridge pairs and the fox activity intensity and no significant year effect was found both in small fields ($F_{1,74}$=6.838, partial r=0.291, P=0.01; year effect – $F_{2,74}$=1.491, P=0.2) and in large fields ($F_{1,74}$=7.725, partial r=0.307, P=0.007; year effect – $F_{2,74}$=0.373, P=0.7).

Altogether 81 fox tracks were found on 288 foam samples (the other samples were destroyed during agrotechnical processes), *i.e.* 0.28 tracks per sample on average (SD=0.59). The searching intensity index of foxes by permanent vegetation strips, *i.e.* the number of tracks per sample, did not significantly differ between field types and years ($F_{1,282}$=0.082, P=0.8 and $F_{2,282}$=1.368, P=0.3, respectively; interaction $F_{2,282}$=0.084, P=0.9). When the searching intensity index was analysed for the two field types, no significant effect of permanent vegetation occurrence was found in large fields. However, in small fields the searching intensity decreased with the occurrences of permanent vegetation strips in the surroundings (Table 4).

4. Discussion

The analysis of diet composition of red foxes in central Poland at the turn of 1970s and 1980s showed that the weight percentages of both hares and birds (including the grey partridge) were negatively correlated with the weight percentage of small mammals [7]. This means that the fox responded as a generalist predator, *i.e.* switching its hunting activity between the main and alternative prey species as a result of changes in their abundance [1]. In this study, however, the predation rate of foxes on partridges proved to be unrelated to the between-area variation in the abundance of the main prey of this predator. This indicates the lack of switching

Variable	Mean ±SD	Field type effect	Year effect	Field type/year interaction
Fox activity index	2.6 ±1.6	$F_{1,150}$=3.286 P=0.07	$F_{2,150}$=2.601 P=0.08	$F_{2,150}$=0.347 P=0.7
Partridge occurrence	0.42 ±0.64	$F_{1,150}$=0.759 P=0.4	$F_{2,150}$=0.738 P=0.5	$F_{2,150}$=0.221 P=0.8
Vole density index	20.1 ±30.4 42.1 ±54.7 6.9 ±11.0	$F_{1,150}$=2.756 P=0.1	$F_{2,150}$=12.082 P<0.001	$F_{2,150}$=0.749 P=0.5
Permanent vegetation	0.89 ±0.47	$F_{1,50}$=0.818 P=0.4	–	–

Table 3. Average values and analyses of the field type and year effects for the index of fox activity intensity (scats per km), partridge occurrence (pairs per plot), vole density index (active burrow entrances per km; means for consecutive years are given) and permanent vegetation strips (km per plot; no changes between years) in the 25-ha study plots (N=52) in western Poland.

Variable	Large fields	Small fields
Permanent vegetation	$F_{1,126}$=2.359, P=0.1 partial r=0.136	$F_{1,154}$=15.740, P>0.001 partial r=–0.305
Year	$F_{2,126}$=0.117, P=0.9	$F_{2,154}$=1.969, P=0.1

Table 4. Results of GLM analysis for the searching intensity index of permanent vegetation strips by foxes (the number of tracks per sample) in relation to the occurrence of such vegetation in the surroundings (km per plot), including the effect of year, for the two field types in western Poland.

between partridges and the main fox food components, and this was probably caused by low importance of the aforementioned prey in the diet of foxes [2,7], particularly given that the numbers of grey partridges in Poland decreased considerably in the 1980s and 1990s [20,25]. As such, recently the relative proportion of this species in the diet of foxes may be even lower than in the previous decades. The real predation impact of foxes on partridge populations could not be estimated in this study. However, the largest proportion of partridges removed by individual foxes occurred at the lowest density. This suggests that these predators could potentially depress the growth of weak partridge populations.

The comparison of the sex ratio of partridges found among the remains around the fox dens with the sex ratio in the bird populations indicates a selective predation on females, which supports the susceptibility of this sex to losses during clutch incubation [10]. The predation rate of foxes on female partridge and the searching intensity of preferred partridge nesting sites proved to be related to the agricultural landscape structure. The concept linking the changes in predation rate on various prey species and the habitat use of predators is described by the incidental predation hypothesis [3]. According to this hypothesis, with the declining abundance of main prey the generalist predator may move to habitat patches containing alternative prey, which leads to the reduced incidental predation rate on the secondary prey co-occurring with the main prey or to the increased predation rate on the secondary prey living in patches with the alternative prey. However, in the study area in western Poland, no marked year effect was found on the fox-partridge spatial relations or on the searching intensity of permanent vegetation by foxes, though considerable annual changes in vole densities were observed, particularly in large fields. Thus, the changes in abundance of the main fox prey most likely had no significant impact on the searching intensity of the preferred partridge nesting habitat by the predator. In the Polish agricultural landscape foxes preferred places with permanent vegetation while searching the area, which was probably connected not only with the potential prey occurrence but also with the use of such structures as landmarks, routes of travel, hiding places and shelters when hunting [26]. Therefore, the foxes' use of permanent vegetation structures incidentally enables them to find partridge nests and hunt incubating females.

In the English farmland, local breeding density of partridges (within an area) in agricultural landscapes with relatively large crop fields, surrounded usually by permanent vegetation strips (such as hedges), was correlated with the strip length per area unit, *i.e.* with the availability of the preferred nesting habitat [27]. In a similar landscape, *i.e.* in large fields of western Poland, the same tendency was found. Such partridge preferences in large fields led to these birds choosing home ranges in regions more intensively visited by foxes. As a result, partridges probably nested in places that were relatively frequently searched by the predators. In small fields, the occurrence of partridge pairs was also positively correlated in space with the activity intensity of foxes, but this was not related to the occurrence of permanent vegetation strips. Furthermore, in the same area of western Poland it was found that all partridge nests were located in permanent vegetation in large fields, whereas in small fields half of the nests were located in crops, particularly in cereals [11]. The tendency to nest in cultivated vegetation was demonstrated by pairs settling down in areas with low availability of permanent vegetation structures [28]. Such a tendency in small fields led to avoiding the permanent vegetation strips which were more intensively searched by foxes. Moreover in the same area, the losses of partridge nests were lower in cereals than in permanent vegetation, probably due to the fact that crops were less frequently searched by predators than uncultivated pieces of land [11,28]. On the other hand, nesting in permanent vegetation occurred more often in home ranges containing numerous places with such vegetation, which were visited relatively rarely by foxes among small fields. Therefore, in the agricultural landscape of a simplified structure, red foxes and grey partridges used the same resources, and so probably often met in the space, while in a more differentiated landscape they had various elements of its structure at their disposal, which led to the partial omission of the predator and its prey in the space. These studies on fox activity and fox–partridge spatial relations were carried out in one site, so the obtained results were specific for local habitat conditions. However, the same pattern may be expected in areas with similar landscapes. The described rules of using the agricultural landscape by foxes and partridges were most likely the main mechanism of the identified negative effect of the occurrence of numerous crop boundaries (*i.e.* the extent of field fragmentation) on the predation rate of foxes on partridges in Poland. Moreover, apart from the direct, *i.e.* lethal impact, some non-lethal effect is also probable, for example unfavourable changes in prey behaviour and timing shifted in the presence of predators [29]. It was previously concluded that the presence of foxes indirectly affected birds in farmland of western Poland [30].

One of the reasons for the drastic decline in the grey partridge populations throughout Europe during the last few decades was the decrease of nesting success, which was attributed to increased predator numbers and negative changes in agricultural landscape structure [10,25,31]. This study supported the previous prediction that habitat changes and predation may interact to cause population declines of farmland birds [32]. Moreover, it was also stated that when such interactions occur, conservationists are provided with the opportunity to limit predation impacts through habitat management rather than predator removal [32]. However, habitat improvements in farmland areas sometimes did not result in expected increases in target species abundance because the measures used also proved to be beneficial for their predators [33,34]. Therefore, simultaneous use of both habitat restoration and predator control would seem to be the best solution for grey partridge population management. Habitat improvement may include dividing large fields, creation of hedgerows and grass strips as well as growing special crop mixtures on plots distributed among crop fields [10,31,35].

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