Factors affecting predation of red foxes on brown hares during the breeding season in Poland

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Key-words: alternative prey hypothesis, brown hare, habitat diversity, Poland, predation, red fox, voles

Abstract

The aim of the study was to estimate the effect of brown hare *Lepus europaeus* density, vole abundance and habitat diversity on the occurrence of hares in the diet of red fox *Vulpes vulpes* during the breeding season in agricultural landscapes. The average number of adult hares found among food remains scattered around the breeding dens of foxes (10-24 a year) was used, and its temporal variation was analysed from 1997-2006 in an area located in western Poland, while the spatial variation was analysed from 21 areas in various regions of the country. Spring hare density, vole abundance index (logarithm of the number of burrow entrances per km) and habitat diversity (number of structural elements per km) were estimated using line transects (20-61 km). In the low hare density area in western Poland (5-10 indiv/km^2), the number of hares per fox den was influenced by hare density rather than by vole abundance. In various areas with high hare densities (10-28 indiv/km^2), multiple regression analysis showed the positive effect of hare density (R^2 = 40%) and the negative effect of vole abundance index (R^2 = 24%) on the number of hares per fox den, whereas the effect of habitat diversity index (R^2 = 13%) was only close to being significant. In the case of low hare density range (1-10 indiv/km^2), the number of hares per fox den decreased with the habitat diversity index (R^2 = 56%). Therefore, proper habitat management in agricultural areas should lead to reducing red fox pressure on brown hare, especially in areas with weak hare populations.

Introduction

The red fox *Vulpes vulpes* is a generalist predator, which has a broad spectrum of food sources. Analyses of the predator's annual diet conducted in Polish agricultural landscapes between the 1960s and 1980s showed that small rodents were the main prey and made up 32-65% of the total weight or volume of food eaten, while the share of brown hares *Lepus europaeus* was 23-46% (Rzebik-Kowalska 1972, Goszczyński 1974, Pielowski 1976, Goszczyński 1986). Moreover, the proportion of hares in the diet was negatively correlated with the proportion of small rodents, and this varied depending on their changing abundance (Goszczyński 1974, Goszczyński 1986, Goszczyński & Wasilewski 1992). Populations of the main prey species, i.e., the common vole *Microtus arvalis*, in many regions of Poland exhibit annual density changes (Romankow-Żmudowska & Grala 1994). Thus, hares were probably the alternative prey for foxes when voles were scarce.

The characteristics of fox food composition presented previously were developed in a period when hare density in Poland was relatively high. However, during the 1980s and 1990s, the number of hares in the country decreased considerably, especially in western regions (Bresiński 2000). In western Poland in the late 1990s, hares made up as little as 1% of fox stomach content during the autumn-winter season and no significant correlation between the proportion of small rodents and hares was observed (Panek & Bresiński 2002). Therefore, hares have become a rather marginal prey item for foxes, and factors affecting their predation may also have changed. Nevertheless, by the turn of the century it appeared that fox predation was a factor limiting hare populations (Panek et al. 2006).

The aim of this study was to identify the main factors determining the occurrence of brown hares in the diet of red foxes during the breeding season. First, I determined if hares were the main alternative prey of foxes in areas with low hare densities (Angelstam et al. 1984, Norrdahl & Korpimäki 2000). To do this, temporal changes in the occurrence of hares in fox diets were compared with the abundance of the predator's main prey, i.e., the common vole, and with hare density. Second, factors affecting between-area variation in the occurrence of hares in fox diets were estimated. Hare density, vole abundance and farmland habitat diversity were taken into account. I predicted that the impact of these factors may differ depending on hare density level, so analyses were carried out separately for low and high density ranges.

Study areas and methods

Temporal variation of the occurrence of hares in fox diets was observed over 10 years (1997-2006) near Czempiń in western Poland, in an area of about 100 km^2. This agricultural landscape had considerable proportion of large crop fields (>10 ha; 60% of total area), which favoured fluctuations in common vole population (Ryszkowski et al. 1973). Spring densities of red foxes in this area in the years 1997-2000 ranged from 0.9 to 1.1 individuals per km^2 and the density of their breeding dens ranged from 0.29 to 0.32 per km^2 (Panek & Bresiński 2002). Spatial variation of the occurrence of hares in fox diets was studied in 21 areas located in various parts of Poland. Area size ranged from 50 to 100 km^2 and these areas contained mainly farmland habitat (sparse forests >20 ha were disregarded). In each of these areas, the data were collected over one year between 1997 and 2006.

The occurrence of hares in fox diets was described using the average number of adult individuals found among food remains scattered around fox breeding dens. Dens and other shelters used by foxes were located in early spring. These places were then checked in the first half of June, when the cubs began leaving their dens. Breeding dens were identified on the basis of traces left by the cubs (treaded patches, scats, tracks, food remains). From 10 to 24 breeding dens were checked each year in Czempiń and in each of the other study areas. If remains of adult hares were found (mainly limbs), the minimum number of individuals that the remains represented was established, i.e., the number of the same body parts was taken into account. Adults were distinguished from juveniles judging by the size of body parts and the absence of cartilaginous structures in skeleton fragments. Fur or skin pieces were omitted because those did not allow the age of the hares to be determined.

Spring hare density was estimated in March using line transects with perpendicular measurements of flushing-out distances. Transect routes crossed agricultural land and were evenly distributed over the study areas. The length of the routes in Czempiń was 61 km, and in other areas it ranged from 20 to 60 km, depending on their size and the expected level of hare density. If necessary, the routes were traversed repeatedly after about a week to obtain appropriate sample size, i.e., more than 25 observations (Langbein et al. 1999). Between 27 and 62 hares were recorded each year and in each area. The density was calculated using Distance 4.1 software (Thomas et al. 2003).

Vole abundance was estimated on the basis of burrow entrance counts (Mackin-Rogalska et al. 1986). The counts were made in March, on transects 30 km long in Czempiń and 20-32 km long in other areas (hare transect routes or their parts were used). Only active entrances (i.e., entrances with fresh signs of digging, tracks, droppings or pieces of food) up to three meters from the transect route were counted. Logarithmically transformed numbers of burrow entrances per km of transect were used as an index of vole abundance.

The structure of farmland habitat was described on the same spring transects. The count covered all the elements wider than one meter, namely all crop fields (single-crop or ploughed plots) and non-cultivated places with spontaneous vegetation (e.g., drainage ditches, roadsides, tree patches, wasteland). The habitat diversity index was the total number of elements per km of transect.

The relationships between the average number of hares per fox breeding den in individual years or areas and the independent variables were analyzed using correlation and multiple regression (standardized regression coefficients β were calculated).

Results

The average number of adult hares per fox breeding den near Czempiń in the years 1997-2006 ranged from 0.08 to 0.57, spring hare density from 5.1 (SE = 1.2) to 10.2 (SE = 2.2) individuals per km^2, and vole abundance index, i.e. the logarithm of burrow entrance number per km, from -0.92 to 3.61 (Fig. 1). The number of hares per den increased with hare density ($r = 0.642$, $df = 8$, $P = 0.045$), while no significant correlation with vole abundance index was found ($r = -0.557$, $df = 8$, $P = 0.09$). In multiple regression analysis, hare density also had a positive effect, whereas the negative effect of vole abundance index was close to being significant (density – $\beta = 0.597$, $P = 0.03$; voles – $\beta = -0.502$, $P = 0.057$; $df = 7$, $R^2 = 0.663$).

In the 21 study areas, the average number of adult hares per fox breeding den was between 0 and 0.60, hare density ranged from 1.4 (SE = 0.5) to 28.1 (SE = 5.9) individuals per km^2, vole abundance index from -0.92 to 4.23, and habitat diversity index, i.e., the number of structural elements per km, from 3.7 to 20.2. Two of the independent variables were inter-correlated: hare density increased with habitat diversity index ($r = 0.753$, $df = 19$, $P < 0.001$). However, no significant correlation was found between vole abundance index and habitat diversity index ($r = 0.364$, $df = 19$, $P = 0.1$).

The study areas were divided into two groups: one with high hare density (>10 individuals/km^2, N = 11, 0.14-0.60 hares/den, voles -0.92-4.23, habitat 6.7-20.2) and one with low hare density (<10 indiv/km^2, N = 10, 0-0.50 hares/den, voles -0.10-3.99, habitat 3.7-11.4). In the areas with high hare density, the number of hares per fox den was not correlated with any of the variables ($df = 9$; density – $r = 0.275$, $P = 0.4$; voles – $r = -0.487$, $P = 0.1$; habitat – $r = -0.249$, $P = 0.5$). But in the multiple regression analysis all three variables had a significant or nearly significant effect, and the factors that explained the variation in hare number per den were mainly the hare density followed by the vole abundance index (Table 1). In the low-density group, the number of hares per fox den decreased with habitat diversity index ($r = -0.748$, $df = 8$, $P = 0.01$) and no significant correlations with hare density ($r = 0.308$. $df = 8$, $P = 0.4$) or vole abundance index ($r = -0.290$, $df = 8$, $P = 0.4$) were found. In the multiple regression analysis only habitat diversity index entered the regression model (Table 1). Having removed the effect of habitat diversity index, the effects of the other variables were far from significant (density – $\beta = 0.120$, df = 6, P = 0.7; voles – $\beta = -0.012$, df = 6, P = 0.97).

Discussion

In the study area of western Poland with relatively weak hare population, the occurrence of hares in fox diets was related to hare density rather than to the abundance of voles. No clear functional response toward hares was found when the availability of the main prey was limited. Thus, hares did not seem to represent a major alternative prey for foxes in the face of a reduction in their main prey. In an area dominated by forests in north eastern Poland, changes in the proportion of hares in the winter diet of foxes were not related to fluctuations in numbers of small rodents (here, small rodents were also the main prey for foxes), but reflected changes in hare abundance (Jędrzejewski & Jędrzejewska 1992). The density of hares in this area was probably low based on the snow track counts conducted there. Therefore, in both areas, the lack of a functional response of the foxes toward hares when the main prey (voles) was scarce probably resulted from the low abundance of hares, and they were only incidentally preyed upon.

Among the study areas with high hare density, hare occurrence in fox diet depended mostly on hare density, but the abundance of voles was also important. It is possible that hares served as a main alternative prey of foxes in these areas. In central Poland, Goszczyński (1986) and Goszczyński & Wasilewski (1992) found a negative correlation between the percentage of hares and small mammals in fox diets during the spring in an area where hare densities were 12-15 and about 24 individuals per km^2, i.e., similar to the high-density range in this study.

In the areas with low hare density, their occurrence in fox diets did not follow hare density as expected, but was related to habitat diversity instead. On the other hand, Quinn & Cresswell (2004) claimed that the frequency of predation on specific prey may depend not as much on its abundance, but more on its vulnerability to predation. For brown hares, habitat diversity may be important because it ensures a year-round supply of diversified food and shelter (review by Smith et al. 2005) and they tended to aggregate in preferred places, for instance on field borders (Tapper & Barnes 1986, Lewandowski & Nowakowski 1993, Smith et al. 2004, Smith et al. 2005). Such tendencies may lead to increased vulnerability of hares or to a higher encounter rate of hares by foxes in poor habitats. Hence, this may be the reason for the reported relationship between fox predation on hares and habitat diversity.

Conservation of prey populations may be conducted by the removal of predators, but it has often been emphasized that habitat management should be an alternative, and that it may be an even more effective strategy that could limit predation risk (Goodrich & Buskirk 1995, Schneider 2001, Evans 2004, Quinn & Cresswell 2004, Smith et al. 2005). This study showed that fox predation on hares decreased with habitat diversity, especially in low hare density areas. Moreover, the density of hares proved to be positively correlated with habitat diversity, i.e., low-density populations lived in areas with simple structure in the agricultural landscape. This implies that proper management of farmland areas aimed at greater diversification of habitat should decrease fox pressure and lead to increased numbers of brown hares, especially in areas with weak hare populations.

Acknowledgements - I am grateful to all hunters and workers of the Polish Hunting Association who help me to collect field data, and to Robert Kamieniarz, Hubert Niewęgłowski and anonymous referees for critical review of the manuscript. Financial support for this research was provided by the State Committee for Scientific Research within the project No 2 P04F 005 26.

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Table 1. Results of step-wise multiple regression analysis (forward selection) for the occurrence of hares in fox diets during the breeding season in relation to vole abundance index, hare density, and habitat diversity index in various areas of Poland for two hare density ranges. The dependent variable was the average number of adult hares found among food remains near fox breeding dens, while the independent variables were: logarithm of the number of active vole burrow entrances per one km of transect, spring density of hares per km^2, and the number of structural elements in farmland habitat per km of transect.

Analysis/variable	β	P	Change in R^2 (%)	R^2 (%)
High hare density: (>10 indiv./km^2, N = 11)				
vole abundance	-0.784	0.009	23.7	23.7
hare density	0.992	0.005	40.4	64.1
habitat diversity	-0.480	0.08	13.4	77.5
Low hare density: (<10 indiv./km^2, N = 10)				
habitat diversity	-0.748	0.01	56.0	56.0

Figure 1. The occurrence of hares in fox diets during the breeding season (average number of adult individuals found among food remains near fox breeding dens), spring density of hares (±SE) and vole abundance index (logarithm of the number of active vole burrow entrances per km of transect) in Czempiń vicinity (western Poland) from 1997 to 2006.