Factors Affecting Predation of Red Foxes Vulpes vulpes on Brown Hares Lepus europaeus During the Breeding Season in Poland

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Short communication

Factors affecting predation of red foxes *Vulpes vulpes* on brown hares *Lepus europaeus* during the breeding season in Poland

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The aim of my 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. I used the average number of adult hares found among food remains scattered around a number of breeding dens of foxes (10-24/year), and analysed its temporal variation during 1997-2006 in an area located in western Poland; furthermore, I analysed the spatial variation based on results from 21 areas in various other regions of the country. Spring hare density, vole abundance index (logarithm of the number of burrow entrances/km) and habitat diversity (number of structural elements/km) were estimated using line transects of 20-61 km. In the low hare density area (5-10 individuals/km^2) in western Poland, the number of hares/fox den was influenced by hare density rather than by vole abundance. In the various areas with high hare densities (11-28 individuals/km^2), multiple regression analysis showed a positive effect of hare density ($R^2 = 40\%$) and a negative effect of vole abundance index ($R^2 = 24\%$) on the number of hares/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 individuals/km^2), the number of hares/fox den decreased with the habitat diversity index ($R^2 = 56\%$). Therefore, proper habitat management in agricultural areas should lead to a reduction of red fox pressure on brown hare, especially in areas with low-density hare populations.

Key words: alternative prey hypothesis, brown hare, common vole, habitat diversity, Lepus europaeus, Microtus arvalis, Poland, predation, red fox, Vulpes vulpes

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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). The proportion of hares in the diet was negatively correlated with the proportion of small rodents, and this varied depending on the small rodents' changing abundance (Goszczyński 1974, Goszczyński 1986, Goszczyński & Wasilewski 1992). In many regions of Poland, populations of the main fox prey species, i.e. the common vole *Microtus arvalis*, exhibit annual density changes (Romankow-Żmudowska & Grala 1994). Thus, brown hares probably made up the alternative prey for foxes when common 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 the late 1990s, in western Poland, hares made up as little as 1% of fox stomach content during the autumn-winter season and no significant correlation was observed between the proportions of small rodents and hares (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).

In my study, I aimed at identifying the main factors determining the occurrence of brown hares in the diet of red foxes during the breeding season. First, I determined whether hares made up the main alternative prey of foxes in areas with low hare densities according to the definition given by Angelstam et al. (1984) and Norrdahl & Korpimäki (2000). To do this, I compared temporal changes in the occurrence of hares in fox diets both with the abundance of the predator's main prey, i.e. the common vole, and with the hare density itself. Secondly, I estimated the factors affecting the between-area variation in the occurrence of hares in fox diets. I took hare density, vole abundance and farmland habitat diversity into account, and I predicted that the impact of these factors may differ depending on hare density level, so I carried out analyses 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 of which 90% was agricultural landscape with considerable proportions of large crop fields (>10 ha), which favoured fluctuations in common vole population (Ryszkowski et al. 1973). During 1997-2000, spring densities of red fox in this area ranged from 0.9 to 1.1 individuals/km^2, and the density of their breeding dens ranged from 0.29 to 0.32/km^2 (Panek & Bresiński 2002). Furthermore, I studied spatial variation of the occurrence of hares in fox diets in 21 areas located in various parts of Poland. The sizes of these areas ranged from 50 to 100 km^2, and they contained mainly farmland habitat (sparse forests > 20 ha were disregarded). In each of the areas, 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. In the first half of June, when the cubs began leaving their dens, these places were checked. Breeding dens were identified based on traces left by the cubs (e.g. treaded patches, scats, tracks and food remains). In Czempiń, and in each area, 10 - 24 breeding dens were checked each year. If remains of adult hares were found (mainly limbs), I established the minimum number of individuals from which the remains originated, i.e. by taking the number of the same body parts into account. I distinguished adults from juveniles judging by the size of body parts and based on the presence/absence of cartilaginous structures in skeletal fragments. Fur or skin pieces were omitted, because they did not allow the age of the hares to be determined.

Spring hare density was estimated in March based on line transects with perpendicular measurements of flushing-out distances. Transect routes crossed agricultural land and were evenly distributed over the study areas. In Czempiń, the length of the routes was 61 km, and in other areas, it ranged from 20 to 60 km, depending on the size of the area and the expected level of hare density in the area. If <25 observations were made, to obtain a sample size of >25 observations (Langbein et al. 1999), the routes were traversed again after about a week. Each year and in each area, 27 - 62 hares were recorded. I calculated the density by use of Distance 4.1 software (Thomas et al. 2003).

I estimated vole abundance based on counts of burrow entrances (Mackin-Rogalska et al. 1986) made in March, along transects 30 km long in Czempiń and transects of 20-32 km in the other areas (I used hare transect routes or some parts of them). Only 'active' entrances (≤ 3 m from the transect route), i.e. entrances with fresh signs of digging, tracks, droppings or pieces of food, were counted. I used logarithmically transformed numbers of burrow entrances/km of transect as an index of vole abundance.

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

The relationships between the average number of hares/fox breeding den in individual years or areas and the independent variables (hare density, vole abundance index, and habitat diversity index) were analysed using correlation and multiple regression (standardised regression coefficients β were calculated).

Results

In 1997-2006, the average number of adult hares/fox breeding den near Czempiń ranged from 0.08 to 0.57, spring hare density from 5.1 (SE = 1.2) to 10.2 (SE = 2.2) individuals/km^2, and vole abundance index, i.e. the logarithm of burrow entrance number/km, from -0.92 to 3.61 (Fig. 1). The number of hares/den increased with hare density ($r = 0.642$, $df = 8$, $P = 0.045$), whereas no significant correlation with vole abundance index was found ($r = -0.557$, $df = 8$, $P = 0.09$). In multiple regression analysis, hare density also showed 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/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/km^2, vole abundance index from -0.92 to 4.23, and habitat diversity index, i.e. the number of structural elements/km, from 3.7 to 20.2. Two of the independent variables were intercorrelated: 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 21 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 individuals/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/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/den were mainly the hare density followed by the vole abundance index (Table 1). In the low-density group, the number of hares/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 the habitat diversity index entered the regression model (see Table 1). Having removed the effect of habitat diversity index, the effects of the other variables were far from significant (density:

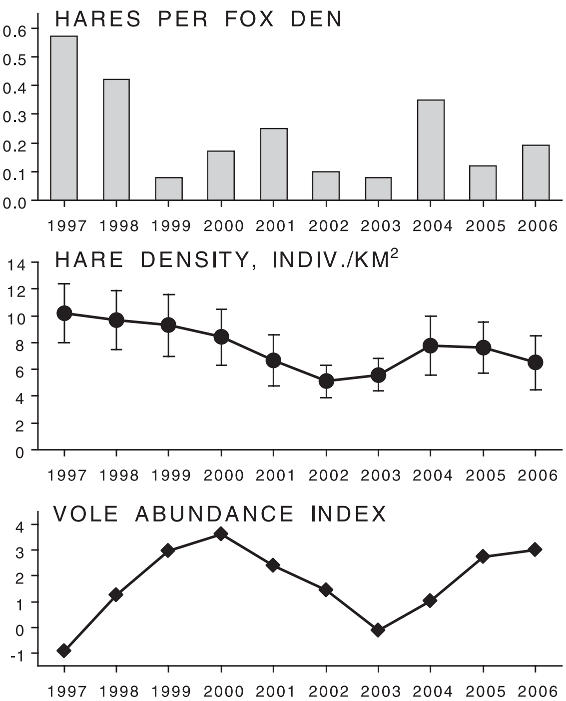

Figure 1. Occurrence of hares in fox diets during the breeding season expressed as average number of adult individuals found among food remains near fox breeding dens, spring density of hares (± SE) and vole abundance index expressed as logarithm of the number of 'active' vole burrow entrances/km of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

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 high (> 10 individuals/km^2) and low (< 10 individuals/km^2) 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/km of transect, spring density of hares/km^2 and the number of structural elements in farmland habitat/km of transect.

Analysis/variable	β	P	Change in R^2 (%)	R^2 (%)
High hare density (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 (N = 10):				
Habitat diversity	-0.748	0.01	56.0	56.0

$\beta = 0.120$, df = 6, P = 0.7; voles: $\beta = -0.012$, df = 6, P = 0.97).

Discussion

In the study area of western Poland with a relatively low-density 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 an alternative prey for foxes in the face of a reduction in their main prey (voles). 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 (small rodents also made up the main prey for foxes in this area), but reflected changes in hare abundance (Jędrzejewski & Jędrzejewska 1992). The density of hares in this area seemed to be low based on snow track counts conducted. 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 a 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 spring in an area where hare densities were 12-15 and about 24 individuals/km^2, which is similar to the high-density range in my 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 hares tend to aggregate in preferred places, e.g. 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 between hares and 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 emphasised that habitat management would make up 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). My study showed that fox predation on hares decreased with habitat diversity, especially in areas with low hare density. 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 a low-density population.

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References

Angelstam, P., Lindström, E. & Widén, P. 1984: Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. - Oecologia 62: 199-208.

Bresiński, W. 2000: Sytuacja populacji zająca w Polsce w latach 1998-2000 (wyniki monitoringu). (In Polish with an English summary: The condition of the hare population in Poland in the years 1998-2000 (the results of monitoring)). - In: Kubiak, S. (Ed.); Zwierzyna drobna jako elementy bioróżnorodności środowiska przyrodniczego Włocławskie Towarzystwo Naukowe, Poland, pp. 101-107.

Evans, K.L. 2004: The potential for interactions between predation and habitat change to cause population declines of farmland birds. - Ibis 146: 1-13.

Goodrich, J.M. & Buskirk, S.W. 1995: Control of abundant native vertebrates for conservation of endangered species. - Conservation Biology 9: 1357-1364.

Goszczyński, J. 1974: Studies on the food of foxes. - Acta Theriologica 19: 1-18.

Goszczyński, J. 1986: Diet of foxes and martens in central Poland. - Acta Theriologica 31: 491-506.

Goszczyński, J. & Wasilewski, M. 1992: Predation of foxes on a hare population in central Poland. - Acta Theriologica 37: 329-338.

Jędrzejewski, W. & Jędrzejewska, B. 1992: Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. - Ecography 15: 212-220.

Langbein, J., Hutchings, M.R., Harris, S., Stoate, C., Tapper, S.C. & Wray, S. 1999: Techniques for assessing the abundance of brown hares *Lepus europaeus*. - Mammal Review 29: 93-116.

Lewandowski, K. & Nowakowski, J.J. 1993: Spatial distribution of brown hare *Lepus europaeus* populations in habitats of various types of agriculture. - Acta Theriologica 38: 435-442.

Mackin-Rogalska, R., Adamczewska-Andrzejewska, K. & Nabagło, L. 1986: Common vole numbers in relation to the utilization of burrow systems. - Acta Theriologica 31: 17-44.

Norrdahl, K. & Korpimäki, E. 2000: Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. - Oikos 91: 528-540.

Panek, M. & Bresiński, W. 2002: Red fox *Vulpes vulpes* density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. - Acta Theriologica 47: 433-442.

Panek, M., Kamieniarz, R. & Bresiński, W. 2006: The effect of experimental removal of red foxes *Vulpes vulpes* on spring density of brown hares *Lepus europaeus* in western Poland. - Acta Theriologica 51: 187-193.

Pielowski, Z. 1976: The role of foxes in the reduction of the European hare population. - In: Pielowski, Z. & Pucek, Z. (Eds); Ecology and management of European hare populations. PWRiL, Poland, pp. 135-148.

Quinn, J.L. & Cresswell, W. 2004: Predator hunting behaviour and prey vulnerability. - Journal of Animal Ecology 73: 143-154.

Romankow-Żmudowska, A. & Grala, B. 1994: Occurrence and distribution of the common vole *Microtus arvalis* (Pallas) in legumes and seed grasses in Poland between 1977 and 1992. - Polish Ecological Studies 20: 503-508.

Ryszkowski, L., Goszczyński, J. & Truszkowski, J. 1973: Trophic relationships of the common vole in cultivated fields. - Acta Theriologica 18: 125-165.

Rzebik-Kowalska, B. 1972: Studies on the diet of the carnivores in Poland. - Acta Zoologica Cracoviensia 17: 415-506.

Schneider, M.F. 2001: Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. - Journal of Applied Ecology 38: 720-735.

Smith, R.K., Jennings, N.V. & Harris, S. 2005: A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. - Mammal Review 35: 1-24.

Smith, R.K., Jennings, N.V., Robinson, A. & Harris, S. 2004: Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? - Journal of Applied Ecology 41: 1092-1102.

Tapper, S.C. & Barnes, R.F.W. 1986: Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). - Journal of Applied Ecology 23: 39-52.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. & Bishop, J.R.B. 2003: Distance 4.1. Release 2. - Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Available at: http://www.ruwpa.st-and.ac.uk/distance/