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Why Did Brown Hare *Lepus europaeus* Disappear from Some Areas in Central Poland?

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Abstract: Brown hares originated in the open steppe grasslands of Eurasia and have adapted very successfully to a mixed, arable agriculture environment. In the last decades of the 20th century, a decline in brown hare populations has been observed in many European countries. In this study, we documented a long-term (1965–2018) decline in the hare population in a field and forest mosaic in central Poland (from over 30 ind./100 ha in the mid-1960s to 1–2 ind./100 ha in the past decade). We showed that the recent autumn densities were the same as compared to the preceding spring densities (suggesting a low recruitment rate) and that the recent densities recorded in the fields were no longer higher than in the forests (probably due to a decrease in the habitat quality of arable lands). We also showed that the share of hares in a red fox diet was now very low (0.1% vs. 13% in the past). We compared the recent (2004–2018) population estimates to another area that was located 70 km east (with a similar habitat structure, a community of predators and climate conditions, but with less intense agriculture), where the hare population was increasing. We suggested that the farming practices were the most important factor for the hare population decrease in our study area.

Keywords: long-term population decrease; farming practices; intensification of agriculture; red fox predation; recruitment rate; density estimation; density in open and wooded areas; field and forest mosaic

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1. Introduction

The brown hare, *Lepus europaeus*, has a vast natural range in Eurasia and was introduced by humans to all the continents, except Antarctica [1–3]. In a primeval condition, the species inhabited natural grasslands, shrublands and open forests [1] but had later adapted very successfully to the mixed arable agriculture environment [4]. For thousands of years, human activity was beneficial for the brown hare and other species related to these agricultural areas. Yet, numerous studies have documented the declines in farmland biodiversity caused by agricultural intensification since the mid-20th century in Europe (review in: [5]), with the brown hare being one of the suffering species [6–9]. Consequently, in the last decades of the 20th century, the decline of brown hare populations has been observed in many European countries [1–3]. Among the different factors that affected the brown hare populations negatively, were listed: agriculture intensification [6–9], predation [7,10–13], toxic and poisonous chemicals [14], diseases [15–18], poaching [19], road mortality [20], and inbreeding depression [21]. Nevertheless, it was shown that the monocausal explanations of the population dynamics of the species are unlikely (review in: [22]).

Habitat changes, caused by the intensification of agriculture, are considered the crucial causes of the brown hare populations' decline [23,24]. Mostly, land use changes impaired the forage quality and diversity of brown hares dramatically [22,25]. An increase in field size is mostly negatively associated with an abundance of brown hares [23]. Habitat diversity is crucial for brown hares, as this ensures a year-round supply of diversified food and shelter [12,23]. A more homogenous field structure also results in the limited availability of various crops that are suitable for feeding in a home range of hares [26]. Indeed, in the farmlands with a high proportion of small fields, hares have much smaller home ranges, as they have access to various resources over a small area (review in: [27]). With the larger fields, field edges (important as a source of wild vegetation) are less accessible (review in: [26]). Brown hares selectively feed on plants with a high fat and energy content, as they enhance energy assimilation, thus, allowing the animals to reduce their foraging activity (hence, their predation risk) and minimize the weight load of the ingested food (which is crucial for species that rely on high running speeds to flee from predators) (review in: [25]). Within the arable habitats, hares only use cereal crops for foraging when they are short, however, herbs and grasses make up the majority of their diet. Thus, in monocultures areas, food availability decreases during summer, as crops reach maturity at the same time (review in: [23]). Due to a site's fidelity and the range size stability of the hares, poor food resources at the local level during the period of reproduction and leveret growth may affect the number of reared juveniles [28]. Indeed, in the areas of low landscape diversity, the mortality rate is higher, while the body condition of the hares (hence, the litter size) is lower [23]. Moreover, in Poland, hares were less frequently caught by their main predators, i.e., red foxes (*Vulpes vulpes*), in the more diversified habitats than in homogeneous ones, especially in the areas with low hare densities [12].

An increased predation has been also suggested to be a driver of the brown hare population decline [29]. Brown hares are preyed upon by numerous mammalian and avian predators [13,30], including domestic cats, *Felis catus* and dogs, *Canis familiaris* [31,32]. Yet, in Northern Europe, the red fox is the main predator of the brown hare [7], affecting population dynamics [7,11,33,34]. Still, it needs to be kept in mind, however, that in other studies, there has been no effect of the fox density on the abundance or decline rates of hares that was found [13,35,36], and that the factors characterizing the agricultural habitat were found to be more important than predation pressure [36,37].

There is no reliable and complex data on the abundance of the brown hare in Poland. However, a decrease in the hunting bag was substantial, i.e., in 2020, only 396 individuals were harvested [38] as compared to the almost 700,000 hares in the 1975/1976 hunting season [39]. The brown hare is an important game species—much research on its habitat preferences and abundance has been conducted in various European countries [23]. It was also shown to be among a set of appropriate indicators to measure the intensification of the habitat changes and human disturbances [40]. It was claimed to be an excellent species to examine regarding the agricultural changes across fields [22,36].

In this study, we showed long-term (i.e., over 50 years) data on a brown hare density in a focus area in central Poland. By combining the current and historical data, we showed how the relations between the spring vs. autumn and field vs. forest hare densities over time with the declining hare populations have changed. We compared the red fox diet composition between the studies to show its preying intensity on brown hares in periods of decreasing hare abundance. We also compared the recent estimates of the population of brown hares and the red foxes in the main study area to another study area with less intense agriculture, to check if the density of the predatory species explains the difference in the brown hare abundance.

2. Methods

2.1. Study Area

We conducted our study in the two areas located in central Poland: Rogów (the focus area) and Dobieszyn (a reference area) (Figure 1). Those rural areas in central Poland represented a typical field—a forest mosaic with a prevalence of open areas. Woods of a few hundred hectares were surrounded by a fine mosaic of patches of different crops, pastures, fallow land, and groups of trees. The villages (primarily consisting of a row of settlements along a road) and single farms were evenly distributed in the main study area and the reference area, within a distance of no more than a few kilometers from each other.

The first study area, where most of the research was done, was located in the vicinity of the village of Rogów (51.8183, 19.88715). This study area encompassed the hunting units no 99 and 122 and covered 9441 ha of field and forest mosaic (Figure 1). The forest covered 1599 ha (approx. 17% of the area). This area was managed by the Warsaw University of Life Science (WULS) as an experimental research area, which is dedicated to science activity and education. Forestry and wildlife management were conducted by WULS. The arable lands were mostly private, and the soil was relatively rich, which was favorable for intensive agriculture. The second (a reference) study area was located 70 km east of the main study site, in the vicinity of Brzeźce village (51.67258, 21.00143). It encompassed hunting unit no 532 and also represented a field and forest mosaic, and was similar in size (7354 ha) (Figure 1). The forests (25% of the area) were managed by State Forests (Dobieszyn forest inspectorate), and the arable lands were private. Wildlife management was conducted by a local hunting club. In contrast to the Rogów area, a poor, sandy soil dominated. The Pilica river is located in this area, with vast areas of extensive pastures and meadows that are located along the watercourse.

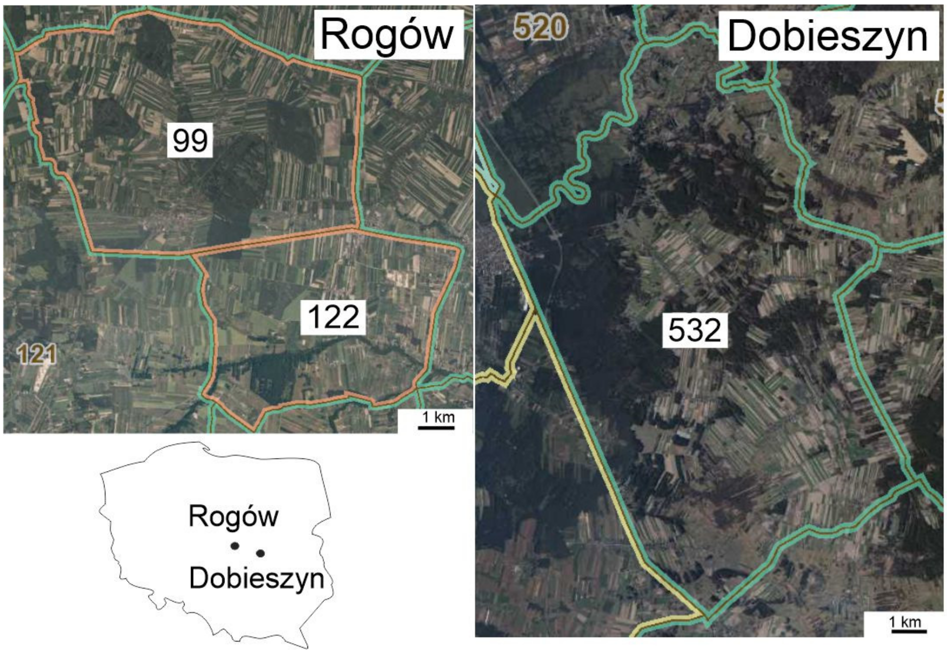

Figure 1. The two study areas are located in central Poland: Rogów (the focus area) and Dobieszyn (a reference area). The studies were carried out in the areas of hunting units no 99 and 122 (Rogów), and 532 (Dobieszyn), with their borders marked in orange (Rogów) and green (Dobieszyn). Source of the maps [41].

The agriculture was much more intensive in Rogów than in Dobieszyn. The farms were generally bigger in Rogów: small farms of up to 5 ha accounted for around 40% as compared to more than 60% in Dobieszyn. Similarly, farms over 10 ha were more numerous in Rogów (24%) than in Dobieszyn (13%). The use of agricultural areas was much less intensive in Dobieszyn: the arable lands accounted here for 50% as compared to 80% in Rogów, and at the same time, there were more fallow lands and extensively used grasslands in Dobieszyn. Agriculture was less mechanized in Dobieszyn (0.7 vs. 2.6 combines/100 ha in Dobieszyn and Rogów, respectively). Horses were still in use in some of the agricultural works in Dobieszyn and were more numerous than in Rogów (4.1 vs. 1.4/100 ha, respectively) and the share of farms that kept horses was also higher (12.6 vs. 2.9%, respectively) [42].

Both study areas were affected by the mild oceanic climate of Western Europe and the harsh and dry continental climate of Eastern Europe and Asia. The duration of the growing season was approximately 210 days. The total precipitation was as much as 600 mm per year, and the mean ambient temperature ranged from −4 °C in January to +18 °C in July.

There were no large carnivores present in the study areas; other carnivores included the red fox, pine and stone martens (*Martes martes*, *M. foina*), badger (*Meles meles*), polecat (*Mustela putorius*), stoat (*Mustela erminea*), least weasel (*Mustela nivalis*) and domestic cats [31,42–44]. In both of the study areas, numerous free-ranging domestic dogs were present [32,44]. The most numerous birds of prey in both study sites were the common buzzard *Buteo buteo*, sparrowhawk *Accipiter nissus*, and the Northern goshawk *Accipiter gentilis* [30,45–48].

2.2. Field Methods

The monitory of density (and a hunting bag) of the brown hare in the main study area (Rogów) started in 1965 and was continued until 2018. Data, which was collected with two standard methods that can be applied in open fields (belt assessment) and forest (driving census), was mostly used. In recent years, the standard belt assessment could not be continued due to the very low abundance of hares. Thus, a new method (spotlight counts) was implemented in 2004. This enabled us to show the long-term trend in the brown hare abundance in Rogów.

To compare the recent brown hare densities between Rogów and Dobieszyn, apart from the spotlight counts, other methods were implemented (snow tracking and pellet counts). A certain bias is attributed to each of the methods used [49] but here, we mainly used them to compare the densities between the seasons, habitats or study areas. According to our experience, with very low brown hare densities, the belt assessments (and also spotlight counts when the densities are close to zero) become ineffective, thus, pellet counts (and also snow tracking) were used to obtain a relative index of abundance in the two study areas.

As the red fox is often thought to be an important reason for the brown hare population decline [7,11,34], the densities of this predatory species were compared between Rogów and Dobieszyn by implementing the spotlight counts and snow tracking. Moreover, the changes in a red fox's diet (and their predation on brown hares) in the main study area (Rogów) were analyzed.

2.2.1. Belt Assessment and Spotlight Counts

The density monitoring of the brown hares in the field started in 1965 (Table S1). At first, the standard belt assessment method was implemented [49]. The census was organized within a framework of game management classes by the students of forestry of the Warsaw University of Live Science, twice a year, in spring (March) and in autumn (November) (data from the Department of Zoology and Wildlife Management, WULS). Around one hundred students were divided into several groups. Each group formed a line of people (no fewer than one person every 15 m), walking slowly through fields along a route of defined breadth (100 m), and extended over several kilometers, representatively sampling the habitat. All the escaping brown hares were counted. On the basis of the known length of the route and its defined breadth, the total area monitored was calculated. The density was simply based on the number of hares recorded, divided by the total belt area covered. This procedure was conducted every year, in the same places, until 2003. The belt assessment data was collected for 19 years (autumn), and in 14 years, also for the preceding springs.

At the beginning of the 21st century, such a classic belt assessment was difficult to conduct. This was due to the very low densities of brown hares and mild winters (with few frosty days). This made walking through clay soil difficult and affected the crops, which led to conflicts with the local farmers. As a result, another method was implemented—nocturnal spotlight counts [8,24,50]. They were accomplished with a spotlight from a car (always with two observers, being the authors—one driving the car, while the other conducted observations and took notes, and were engaged at the same time), driving at an average speed of less than 20 km/h [42]. The maximum beam range (i.e., the strip of land surveyed) was estimated at 100 m. We attempted to choose days with clear weather because rain, snow or fog diminished visibility [51,52]. The counts were conducted from ca. 10 p.m. until midnight. One count took ca. two hours. The inventories were done in November/December (data for autumn) and/or in March (data for spring), in the areas where the traditional daily belt assessments were done in the years 1965–2003. The transect route length was approximately 30–40 km, and the same route was repeated but could be slightly modified due to the poor road conditions (i.e., snow cover, deep mud). We only included the areas where the vegetation cover made animal sightings possible, i.e., shrubs, woods, and built-up areas were excluded from the inventory. During all counts, the same spotlight reflector was used (1 mln cd). In the years 2004–2018, 36 nocturnal assessments were done (Table S1).

In the Dobieszyn area, only the spotlight counts were done (2004–2015), along a route of approx. 20 km; there were 25 night counts done in total (Table S1).

In both study areas, during the spotlight night counts, red foxes were also counted.

2.2.2. Hunting Bag Data

Hunting statistics can be used as a robust indicator of the long-term trends in the European brown hare numbers [7,36,40,49]. Here, we used the annual data on the hunting bag of brown hares taken from the Experimental Forest Station in Rogów (both hunting units, Figure 1, from the years 1965–2018).

2.2.3. Driving Census

In the forest areas, brown hare densities were assessed with the aid of the driving census. The census was done by the students of forestry and biology (WULS), in early March, between 1983 to 2018 (data from the Department of Zoology and Wildlife Management, WULS) (Table S1). The driving census was done only in Rogów forest, not in Dobieszyn. The animals were counted in selected plots (forest compartments). The total number of plots (usually 3–4 plots, each 12–24 ha) depended on the total area of the forest complex (i.e., the censused area accounted for around 30% of the whole forest complex). The censused area was representative from the point of the stands' age, species composition, the distance from the forest edge and soil richness. Around one hundred students were simultaneously involved in the driving census. Each rectangle plot to be censused was surrounded by observers, who stationed themselves 50–100 m apart (to maintain visual contact). The observers along three sides of an estimated compartment, remained stationary, while those along the fourth side moved inward and went through the entire area. When the rectangle-shaped plot was surrounded by people, the students from one side started moving and roused the animals from the plots. The observers (both stationary and moving) noted the animals passing through the line of observers and the closed area that was being censused. Each person counted only the animals passing by on their left side to avoid duplications. On the basis of the number of observed hares and the total area of the plots, the density of animals was calculated. The data was collected for 27 years (Table S1).

2.2.4. Snow Tracking

In order to compare the brown hare and red fox densities between the two study sites (Rogów and Dobieszyn), a relative index of abundance (n tracks/1 km/24 h was assessed on the basis of snow tracking on transects (Table S1). The fieldwork was done in the winter season of 2010/2011. Snow tracking was conducted on linear transects of different lengths (1 km on average) that were sparsely distributed in the area (66 transects in Rogów and 43 in Dobieszyn, Table S1), and both were conducted in the field and forests (60% and 40% of the route was in the forest, respectively). The number of brown hare and red fox trails crossing 100 m of the transect was registered and then the index of species density was calculated (n tracks/1 km/24 h). Tracking was carried out 1–3 days after a snowfall (the number of tracks registered was adjusted for 24 h of snow cover persistence). The total length of the transect route was 71.1 and 45.4 km in Rogów and Dobieszyn, respectively.

To calculate an absolute density of red foxes, the formula presented by Priklonski [53] was used: D (n ind./100 ha) = 1.57 × (n tracks/km/24 h)/DMD, where D stands for density, 1.57 is a constant value and DMD indicates the daily movement distance. The DMD values were 13.8 km for the red fox as calculated for central Poland [54].

2.2.5. Pellet Group Counts

Another method used to compare the relative indices of the brown hare density between the study sites (Rogów and Dobieszyn) was the pellet group counts (Table S1). The pellet groups were counted on transects that were sparsely distributed in open areas, in late March and the beginning of April 2011 (i.e., the period after the snow melt, but before the vegetation started). The transects were two meters wide and the whole route was 53 and 38 km long in Rogów and Dobieszyn, respectively. The number of pellet groups was attributed to a stretch of a given length (counted in meters) that crossed homogenous habitat (fallow land/early succession, ploughed field, winter crops, grassland, extensive orchards/berry plantations, strawberry plantations/after-crops, stubble/fallow land with low vegetation, dirt road/wasteland) and the number of pellet groups per 1 km of the transect was calculated. The total number of stretches was 575 in Rogów and 428 in Dobieszyn (Table S1).

2.2.6. Red Fox Diet Analysis

The red fox diet composition was assessed in the Rogów study area (but not in the second study area) on the basis of the prey remnants found close to fox dens. Data was collected at known and monitored natal dens (around 15 to 20 dens yearly), during the breeding season (April–July), in the years 2011–2021. To see the changes in the frequency of brown hares in the red fox diet, our data were compared with data collected in the same area and with the same method used in previous periods: 1978–1991 [55] and 1999–2002 [56].

2.3. Analysis

To show the long-term trend of the brown hare decline in Rogów, the autumn density assessments in open areas (i.e., the belt assessment and spotlight counts) were combined. If more than one assessment was done in one year, a medium value was presented. Continuous data from 1965 to 2018 was shown (records for 34 years are available). Similarly, the trend in the hunting bag statistics was shown (data for 51 years). The Mann–Kendall trend test was used to assess whether the time series had a monotonic upward or downward trend. Pearson's correlation was used to show the relation between the brown hare density and the corresponding annual hunting bag in Rogów.

To compare the (1) spring vs. autumn, and (2) field vs. forest densities of the brown hares in the Rogów area, the density estimates were grouped into three 10-year periods, i.e., 1980–1989, 1990–1999, and 2000–2009. In the first case, the estimates obtained by the belt assessment and spotlight counts for the spring and autumn of the same year were compared with the two-sample paired *t*-tests (1980–1989: n = 7, 1990–1999: n = 3, 2000–2009: n = 5). Second, we compared the brown hare density in spring in the open areas (assessed with the belt assessment and spotlight counts) and forests (assessed with the driving census). We pooled data from the two first ten-year periods together (1980–1999) due to the small sample sizes collected from the forests in the first period. Here, we could not use the paired *t*-tests in the numerous years' assessment, for only one of the habitats was available. Thus, in either of the two compared time periods, we pooled the density assessments into two groups: fields vs. forests (1980–1999: field n = 10, forest = 8; 2000–2009: field n = 5, forest n = 10). As the data did not follow a normal distribution (Shapiro–Wilk test, $p < 0.05$) we used the Kruskal–Wallis test to show the differences between the habitats in the two periods.

To compare the density assessments of the brown hares (spotlight counts, snow tracking, pellet group count) and red foxes (spotlight count, snow tracking) between the two study areas, Kruskal–Wallis tests (data did not follow a normal distribution) were used. In the case of the spotlight counts, only the autumn assessments were taken into account. To show the trend in the autumn brown hare density (based on the spotlight counts), continuous data from 2004 to 2018 (Rogów) and 2004 to 2015 (Dobieszyn) was shown (Table S1). A Mann–Kendall test was used to check if data had an upward or downward trend.

The Fisher (two-tailed) exact test was used to determine if there was a significant association between a share of a given food group in the red fox diet and a given study period in Rogów. The share of a selected food category (domestic birds, *pheasant Phasianus colchicus* and grey partridge *Perdix perdix*, carrion, brown hare, human refuse) and the sum of the remaining food occurrences in the red fox diet were taken for analysis. The Bonferroni correction was applied ($p < 0.01$), as the same dataset was used for multiple comparisons (n of tests = 5). In the case of human refuse, a comparison was done between the second and third periods only, as in the first period, the sample size was zero.

The analyses were done in the Past 4.05 [57] software.

3. Results

3.1. Trends in the Density and Hunting Bag of Brown Hares in Rogów

The autumn brown hare density decreased throughout the decades (1965–2018) (Mann–Kendall trend test, S = −438, $p < 0.001$). In the mid-1960s, the density was 36, then in the 1980s, it was between 24 to 31 ind./100 ha. In the 1990s, it was between 11 to 19 ind./100 ha, and finally, it dropped to fewer than 2 ind. per 100 ha between 2010 to 2018 (Figure 2).

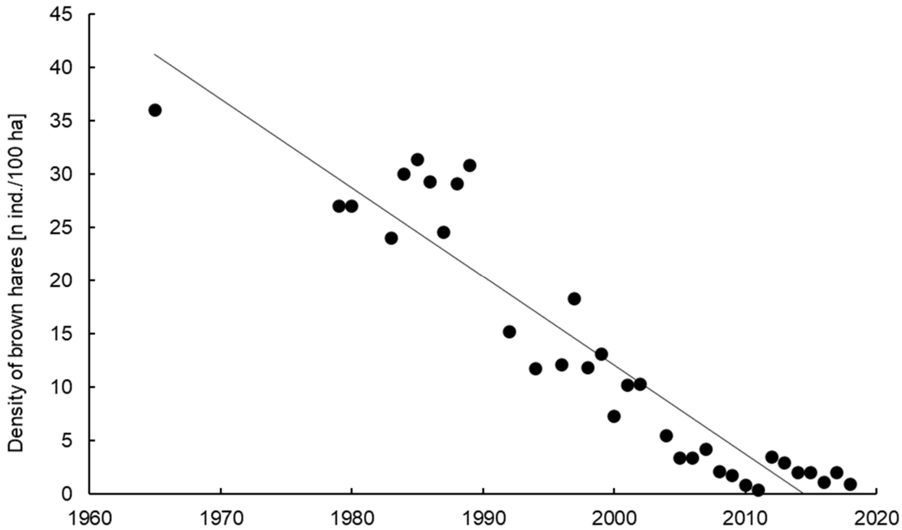

Figure 2. Decrease in the autumn brown hare density in the study area (Rogów, central Poland) as assessed on the basis of the belt assessment and spotlight counts along transect routes, in open fields, in autumn.

A decrease in the hunting bag of brown hares in Rogów (Mann–Kendall trend test, S = −758, $p < 0.001$, Figure 3) was correlated with a decrease in the density of the species in question (Pearson correlation, r = 0.869, $p < 0.001$). The biggest number of hares shot yearly was reported in 1969, when 505 individuals (5.3/100 ha of the hunting ground) were killed. In those times, the autumn hare densities were around 30 individuals per 100 ha. As a result, hunters killed around 16% of the available animals. In the early 1990s, harvest dropped dramatically. The last collective brown hare dedicated hunt was organized in December 2000; approximately 7% of the autumn stock was hunted that season. In the following years, hunters were allowed to shoot hares during hunts organized in the forest (i.e., focused mainly on ungulates). The last hare was shot in 2006.

3.2. Changes in Brown Hare Densities in Spring vs. Autumn and Field vs. Forests, in Rogów, in Three Ten-Year Periods

We compared the brown hare spring and autumn densities in Rogów, in the three defined periods. In the first of them (1980–1989), the mean brown hare density was lower in spring (mean = 23.1, SD = 1.9 ind./100 ha) and increased in autumn of the same year (mean = 27.8, SD = 2.7 ind./100 ha) (two-sampled paired *t*-test, t = −4.36, n = 7, $p < 0.005$). In the next period (1990–1999), the pattern reversed, i.e., in spring, the density was 21.7, SD = 1.85 vs. 14.4, SD = 1.99 in autumn, yet this difference was not statistically significant (t = 2.22, n = 3, $p = 0.16$). In the last period (2000–2007), the spring and autumn densities were the same (t = 0.01, n = 5, $p = 0.97$) and equaled 5.7, SD = 4.65 in spring and 5.7, SD = 2.98 in autumn (Figure 4).

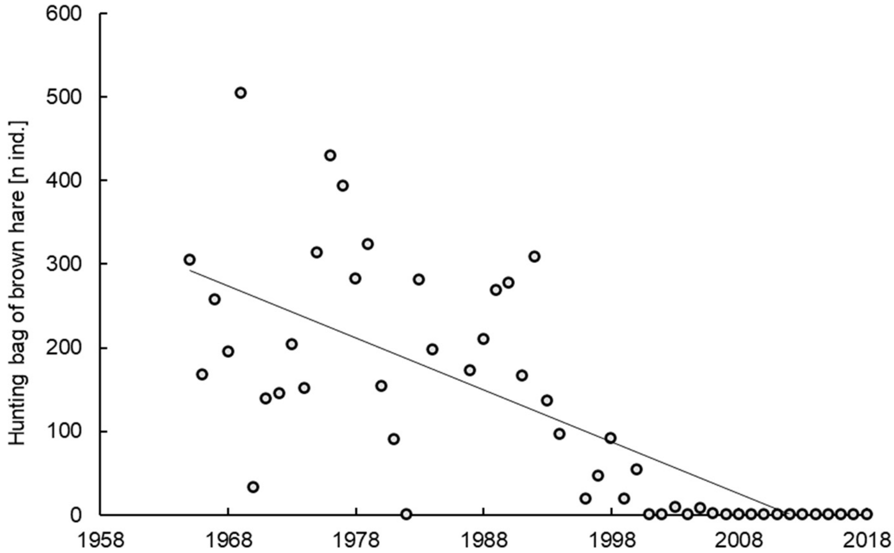

Figure 3. Decrease in the annual hunting bag of brown hare in the study area (Rogów, central Poland).

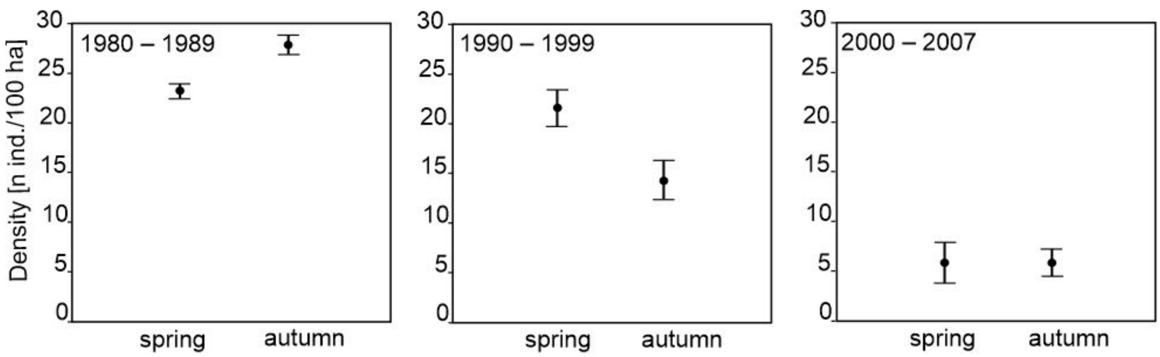

Figure 4. Mean (±SE) brown hare densities in spring and summer in Rogów (central Poland), as assessed with the aid of the belt assessment and spotlight counts along transect routes, in open fields, in the three study periods (1980–1989: n = 7; 1990–1999: n = 3, 2000–2009: n = 5). Data for spring and autumn of the same year were compared.

We also checked how brown hare densities changed in the fields and forests in Rogów. In the first two study periods pooled together (1980–1989 and 1990–1999), the brown hare density was much higher in the open fields (22.7, SD = 2.30 ind./100 ha, n = 10) as compared to the forests (13.7, SD = 7.47 ind./100 ha, n = 8, Kruskal–Wallis test, H = 8.60, $p < 0.005$). In the third period (2000–2009), there was no differences between the densities in the two habitats, i.e., 11.4, SD = 4.65, n = 5 vs. 8.8, SD = 2.02, n = 10 (H = 0, $p = 1$) (Figure 5).

3.3. Brown Hare and Red Fox Densities in Rogów as Compared to a Reference Area (Dobieszyn) in the First Two Decades of the 20th Century

The brown hare densities in the past decades, assessed with the aid of the three different methods (Table S1), were always lower in Rogów than in the reference area (Dobieszyn) (Table 1). In the case of spotlight counts, the density in Rogów was ten times lower than in

Dobieszyn, and for the pellet group counts, the difference was even larger. The smallest difference (i.e., threefold) was found when the snow tracking indices were compared (Table 1).

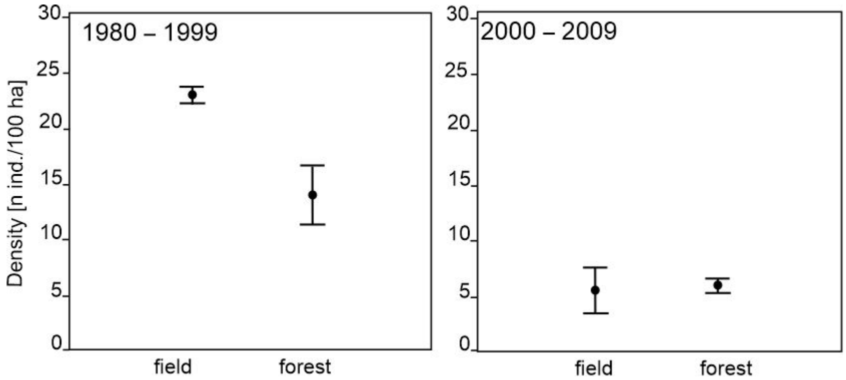

Figure 5. Mean (±SE) brown hare density in spring in open fields and forests in Rogów (central Poland), as assessed with the aid of the belt assessment and spotlight counts along transect routes (fields) and the driving census (forests) in the two study periods (1980–1989 and 1990–1999, pooled together: field n = 10, forest n = 8; and in 2000–2009: field n = 5, forest n = 10).

Table 1. Comparison of indices of brown hare densities between the study area (Rogów) and a reference area placed in central Poland (Dobieszyn) in the past decades (Table S1). Values of the Kruskal–Wallis test (H) and *p*-values are given.

Mode of Estimation	Density Index	Study Area		H	*p*
		Rogów	Dobieszyn		
Spotlight counts	n ind./100 ha	2.2	24.0	34.04	<0.001
Snow tracking	n tracks/1 km/24 h	7.8	23.5	11.95	<0.001
Pellet group counts	n pellet groups/km	0.1	13.9	29.06	<0.001

In the case of Rogów, the hare density ranged between 0.4 and 4.2 ind./100 ha, but no trend was found (Mann–Kendall trend test, S = −32, $p > 0.05$). In turn, in the case of the Dobieszyn, densities, this was between 16.4 and 37.5 ind./100, and the trend was uprising (S = 22, $p < 0.05$, Figure 6).

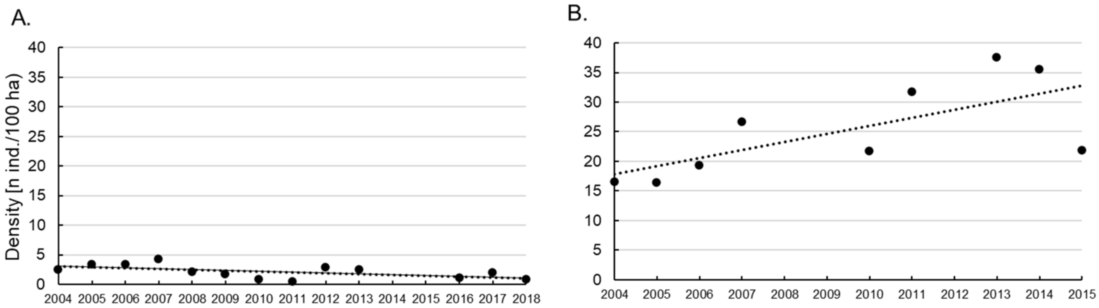

Figure 6. Comparison of brown hare densities between (**A**) the study area (Rogów) and (**B**) a reference area placed in central Poland (Dobieszyn). The method of spotlight counts along transect routes, in open fields, in the autumn/winter period was used.

At the same time, the red fox density, which was assessed with the aid of spotlight counts and winter snow tracking along the transects, did not differ between the study areas (Table 2). In both sites, it was around 1 ind./100 ha (as defined by snow tracking).

Table 2. Comparison of red fox density indices between the study area (Rogów) and a reference area placed in central Poland (Dobieszyn), in the past decades (Table S1). Values of Kruskal–Wallis test (H) and *p*-values are given.

Mode of Estimation	Density Index	Study Area		H	*p*
		Rogów	Dobieszyn		
Spotlight counts	n ind./100 ha	0.7	0.8	0.00	>0.05
Snow tracking	n tracks/1 km/24 h	9.2	8.5	0.47	>0.05

3.4. Red Fox Predation on Brown Hare in Rogów, Now and in the Past

The share of brown hare in the red fox diet decreased in Rogów when past and current data were compared. Between 1978–1991, it accounted for almost 13% (n = 606) of all the food items found at the fox dens [55], while between 2011–2021, the brown hares were preyed on only occasionally (n = 959, 0.1% of all the food items). Similarly, small game birds, i.e., pheasant and grey partridge, were caught occasionally in the last period. At the same time, carrion and various foods of human origin (human refuse) were found more often at the den sites in the last period (Tables 3 and S2).

Table 3. Changes in the share of selected food categories (% of all food items recorded) in the red fox diet in Rogów (central Poland), in the three periods, as based on the food remains collected at natal dens. Results of the Fisher (two-tailed) exact test are given. Bonferroni corrected *p*-value of 0.01. In the case of human refuse, only the second and third periods were compared. Source of data: 1978–1991 [55], 1999–2002 [56], 2011–2021 (this study). The complete diet composition is shown in Table S2.

Food Type	Period			*p*
	1978–1991	1999–2002	2011–2021	
Domestic birds	58.3	38.3	37.6	<0.001
Pheasant, grey partridge	4.5	4.1	0.6	<0.001
Carrion	5.0	14.8	20.1	<0.001
Brown hare	12.7	4.1	0.1	<0.001
Human refuse	-	2.6	9.2	<0.001
Total number of items	606	196	959	<0.001

4. Discussion

In this study, we documented a constant and very severe decline of the brown hare population in a field and forest area of central Poland (Rogów). The brown hare densities dropped from over 30 ind./100 ha in the mid-1960s to 1–2 ind./100 ha in the past decade. Nowadays, the abundance of the brown hare is so low that it is often not recorded with typical counting techniques (i.e., the belt assessment or spotlight counts [24,49,50]).

It should be highlighted, however, that not only the hare population declined among the field dwelling species in the Rogów area. A similar trend, and at the same time, was detected in the case of the partridge, pheasant, quail *Coturnix coturnix*, wild rabbit *Oryctolagus cuniculus*, and the European hamster *Cricetus cricetus* [43,48]. On the basis of the available data, and our own observations and reports from the local inhabitants, we can conclude that farming practices changed dramatically in the last 50 years in Rogów [47]. In the late 1970s, most of the fieldwork was done by horses, which completely disappeared from the farms at the end of the 20th century. Mechanized crop harvesting can be an important source of mortality, mainly for leverets [14]. Moreover, the crop structure changed over the years. In the 1980s, medicago *Medicago* spp., other alfalfa crops, and vegetables accounted for more than 11% of the whole cultivated area. Presently, these plant species are not cultivated anymore. A similar fate applies to the cultivation of oats *Avena sativa* and potatoes *Solanum tuberosum*—their cultivation frequency was severely reduced. Today, the cultivated areas are dominated by wheat *Triticum* sp., oilseed rape *Brassica napus* (the first two mostly for winter crops) and maize *Zea mays*; the last two were unknown in the area 40 years ago [47]. Grain is often an important forage for hares, but mostly during the period when cereals are low and of high nutritional value [24]. Thus, winter cereals are an important food source in winter but are of little nutritional value in further periods (from late spring–summer), when they still occupy large areas of arable lands [7,14]. It was shown that the winter cereals [7] or cereals in general [36] had a significant negative association with the European brown hare numbers, while the cultivation of legumes (such as peas and beans) positively influenced the hare populations [22]. Although winter oilseed rape is used (and in some cases is preferred by hares [9]), it might also be avoided due to its content of glucosinulates, and is used more often only in the absence of an alternative food [4]. Additionally, an increase in maize production was shown to be unfavorable for hares [9]. Although hares may benefit from moderate maize cultivation, as it serves as a cover opportunity, its large cultivation might force hares to use it as a food source, which (through changes in intestinal flora) leads to a reduction in fitness and may affect hare abundance [9]. Wild rich flora (i.e., herbs and grasses) in a diet of brown hares is crucial [24,58,59]. This can be found in field boundaries and uncultivated pieces of land, which become less available in more homogenous arable habitats [24,26]. It was shown that a 5% increase in permanent set-asides is strongly favored by hare population development, i.e., the herbaceous field margins showed a strong influence on female abundance [22]. In intensively used agriculture, wildflower strips (used as agri-environmental scheme tools) were highly beneficial for hares [9]. Moreover, root crops (absent now in our area) positively affected brown hare numbers [7]. Moreover, the area covered by grasslands diminished during the last decades in the study area [47]. The shares of extensive pastures and meadows, wasteland and shrubland were higher in Dobieszyn, as were the hare numbers, probably due to the better feeding conditions and a larger offer of hiding places. Indeed, the densities of hares were positively related to the amount of meadows of high ecological quality [50] and also to the hay meadows [8]. Moreover, as the farms in Dobieszyn were smaller than in Rogów, the crops were probably more diverse, thus, more field margins were available—being crucial for the hares, both for feeding as well as for periods of inactivity [5,9,24,58,59]. Increasing negative effects of large fields on the hare densities were shown in other studies in Poland [26,36], and the population numbers were higher in the areas with smaller fields, which highlighted the species' preference for heterogenous landscapes [27].

Several studies focused on the risk of pesticide exposure to many invertebrate and vertebrate species [60]. Although brown hares are suggested not to be affected directly by pesticides [7], the animals are subjected to chronic environmental levels that, while not lethal, may be exerting some adverse effects [61]. Moreover, pesticides are applied repeatedly over a vegetation period, which leads to regular pesticide exposure, and it is likely that pesticides accumulate in the body over time (review in: [60]). It was shown that pesticide uptake may be very high in brown hares, both due to overspray/oral grooming and foraging [60]. In the vicinity of Rogów, until the 1960s, DDT was used on a massive scale. In the early 1970s, these highly toxic pesticides were prohibited in Poland. Among the chemicals used by farmers in 1984, the most popular pesticide was those containing deltamethrin and tetradifon. A commonly used fungicide was Triadimefon. In the case of herbicides, farmers used MCPA, Ethofumesate and Phenmedipham [62]. It was proven that one brown hare individual was lethally intoxicated by the pesticides in the Rogów area [62]. Most of these chemicals are still in use in agriculture. Unfortunately, we have no detailed data on chemical use in Dobieszyn, now or in the past.

An increased leveret mortality (low recruitment) is one of the most important determinants of the decline in European brown hare populations, and neonatal survival can be one of the key factors affecting population dynamics (review in: [63]). We showed in our study that in the first period (1980–1989), autumn densities were higher than the densities of the preceding spring. This changed later when the spring and autumn densities were at the same level. Other studies from our study area (1985–1989) also showed that the autumn densities fluctuated, ranging between 25 to 30 ind./100 ha, and were the same or only slightly (yet, statistically insignificant) higher than the preceding spring densities. That study also showed a high mortality of juveniles in spring and autumn and a very low recruitment rate of the young [64]. It was suggested that reducing leveret mortality, i.e., by promoting habitats where leverets can seek shelter from predators or inclement weather conditions, should be a priority for declining populations [63]. It was also suggested that low access to high-energy food in modern agricultural landscapes (with reduced plant diversity) may impair the lactation processes in females, and therefore impact their ability to meet the high-energy demands of their precocial juveniles [25].

In our study, we also showed changes in the pattern of habitat use by brown hares, i.e., in the last two decades of the 20th century, densities in the fields (i.e., open spaces) were higher than those in the forest. This changed in the first decade of the 21st century, when the densities of hares were similar in the two habitats. Reports on the increased use of forests by hares also came from Sweden. Assumingly, brown hares may have been relatively successful in survival and reproduction in forest habitats as an effect of a general decrease in the suitability of agricultural landscapes [65]. Additionally, in Great Britain, promoting scattered woody vegetation in agricultural landscapes was suggested to be a powerful tool for improving brown hare habitat quality, as greater proportions of woodland-shrub and small woody features were accompanied by sharp increases in hare densities [66]. The woodlands and hedges were recorded to be widely used as sheltering habitats [6,67]. We may assume that in our study area, the woods became important refuges for brown hares. Numerous open spaces within the forests in places of felling, with woody seedlings planted and often overgrown with grasses and raspberries (*Rubus* spp.), can offer food and hiding places. Similarly, it was shown that roe deer *Capreolus capreolus* concentrated in the winter in areas with plentiful raspberries [68].

As the predation by red foxes is often thought to be an important reason for brown hare population decline [7,11,34], we compared the red fox densities between the two study sites (Rogów and Dobieszyn) in the first two decades of the 20th century and found similar red fox densities in both areas (i.e., around 1 ind./100 ha). Although in the Rogów area, the red fox population increased lately, due to the rabies vaccination [69], and this correlated with the brown hare population decline [56], the share of hares in the fox diet in the Rogów area was very low (as shown by this study). Thus, fox predation should not be claimed to be responsible for a hare population collapse. Diets of all predatory birds and mammals (including domestic dogs and cats), living in the vicinity of Rogów, were studied in detail, however, in our case, none of them preyed regularly on brown hares [30–32,42,46–48,70–74]. According to Goszczyński and Wasilewski [10], in the late 1980s, the reduction in hare populations by foxes in Rogów was around 20%. According to Juszko [56], in the years 1999–2002, all predators consumed, yearly, around 30% of the hare population in the Rogów area. Among these, red foxes were responsible for 95% of the hare mortality (i.e., consumption) caused by predators. Nevertheless, it must be kept in mind that among the consumed hares, an unknown fraction constituted of carrion or individuals lethally ill or injured, and only some hares were killed by predators. Thus, the real predatory pressure was probably much lower [56]. The predator–prey interaction depends on many factors, such as habitat structure [75]. Increased habitat diversity is thought to be able to limit predation [12]. According to Goszczyński [76], in the case of highly intensive agriculture, alternative prey availability is very high because of a massive common vole *Microtus arvalis* occurrence. Nevertheless, in our study, the area densities of common voles were never high, and they also decreased in the last years, due to changes in the farming practices [47]. Nowadays, the red fox, as a typical opportunistic predator [55], often feeds on carrion and human refuse.

Diseases can be one of the reasons for the brown hare population decline [15–18]. There is not much data on brown hare diseases from the Rogów area, and there are none from Dobieszyn. Nevertheless, the main cause of death of the 16 hares examined in the years 1963–1969 in Rogów was pneumonia, caused by *Staphylococcus* spp. and *Pasteurella rodenticum*. Coccidia was also frequently detected (*Eimeria leporis, E. semisculpta*) [62].

Nevertheless, there was no correlation between the share of infested individuals and juvenile mortality or the recruitment rate or the mortality of adults during the reproductive period [77]. Furthermore, nematodes, from the genus *Protostrongylus*, and unidentified species of tapeworms and leukaemia, were detected in the study area [62]. During the years 1997–1998, hares shot by hunters were clinically examined in the Rogów study area. The most frequently detected parasite was *Eimeria* protozoan (mainly *E. leporis*), and the presence of antibodies of the European Brown Hare Syndrome virus was also detected. Brucellosis was not confirmed. Additionally, there were some genetical, physiological and toxicological studies done, but again, none of the analyzed factors was found to be responsible for such a dramatic population decline, as shown in the present study [39,78,79].

Although hunting statistics revealed a long-term trend in the brown hare population in our case, they did not reflect the changes in the hare density from year to year, as annual hunting bags accounted for as low as 0–7% to as much as 200–400% of the hunting bag from the previous year. In the vicinity of Rogów, in 1970 and 1981, the hare harvest was very low, and in 1982, not a single hare was shot. This was attributed to political rather than ecological situations. During this time, huge protests against the communist regime took place in Poland, and in 1981, martial law was implemented. Due to this, hunting weapons were temporally confiscated by the police. Additionally, the number of hunters and organized collective hunts differed yearly. Finally, apart from the animals that were shot by hunters, our hunting bag data also included live individuals being net-trapped and exported for restocking populations in western Europe.

Overall, in our study, we documented a long-term decline in the European brown hare population in field and forest mosaic in central Poland. We showed important shifts in the population densities, i.e., the low autumn densities as compared to the preceding spring (resulting, assumingly, from the low recruitment rate) and an increase in the hare densities in forests as compared to the open fields (which was probably a response to the low quality, both in terms of the feeding opportunities and hiding possibilities, of arable lands). We compared the brown hare population abundance in Rogów with another area, where the brown hare population was increasing. The two regions differed in terms of the agricultural intensification and structure of the arable lands but not in terms of a red fox density, which suggested that farming practices were the most important factor for the brown hare population decrease in Rogów.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14060465/s1. Table S1: Methods used to assess the density of brown hares in the two study areas (R-Rogów, D-Dobieszyn); Table S2: Changes in food composition (% share of food items) of red foxes in Rogów (central Poland) in three periods, as based on food remains collected at natal dens.

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