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Where have all the hares gone?

The decline of the European hare (*Lepus europaeus*) in Basel-Landschaft from 1960 to 1989

The population of the European hare (*Lepus europaeus*) has declined throughout Europe and Switzerland in recent decades. Frequently predators, intensification of agriculture, and sometimes, unfavourable weather are blamed for this decline, but the extent of the different factors is unclear. This study seeks to clarify the main factors of the decline in Basel-Landschaft, Switzerland, and provide a corresponding weighting of the significant factors.

1 Introduction

In 1849, Carl Emil Diezel (1779–1860), a distinguished German expert on small game, wrote: “I regard the [European] hare as the most profitable, hence the most important game in our motherland” (Diezel 1849). The editor of a posthumous edition of Diezel’s classic work *Erfahrungen aus dem Gebiete der Niederjagd* added in 1907 that the importance of the hare for the national economy was even growing, due to its ongoing proliferation and the increased demand for its delicious meat and its multipurpose skin (Diezel 1907). The adoption of the German civil code in 1896 almost failed due to disagreement on whether a landowner’s right to recover compensation for damages caused by hares should be inserted into the civil code (Schulte-Nölke 1995).

Since then a lot has changed. The European hare was placed on the red list of threatened species in Switzerland and Germany (BfN 2015). For decades, hare harvests throughout Switzerland have been declining (figure 1), so that hare hunting was even stopped in many places. The causes of this decline are not yet fully understood. The intensification and industrialisation of agriculture seems to have massive negative effects (Schneider 1978; Kiliass & Ackermann 2001; Holzgang et al. 2005; Gehle 2010; Godt et al. 2010; Wadsack et al. 2010; Kinser et al. 2010; Fischer et al. 2010; Grendelmeier 2011). However, many researchers ascribe an important role to predators (Guthörl & Kalchreuter 1995; Goretzki et al. 1999; Spittler 2000; Guthörl 2001; Panek et al. 2006; Maas 2010). Hare populations are

very prone to bad weather conditions (Schneider 1978; Zörner 1981; Martini 1983; Weber 2014) which is why some researchers assume weather has played a major role in the decline of the hare populations (Eiberle & Matter 1982; Spittler 1987).

This study seeks to clarify the main causes of the decline of the European hare in the Canton of Basel-Landschaft (BL) and their extent.

2 Material and Methods

2.1 Data

The Canton of Basel-Landschaft lies in the northwest of Switzerland and encompasses an area of 51’767 hectares. About 42 percent of this is used as arable land and another 42 percent is covered by forests (BFS 2017a). The weather sta-

tion which provided the weather data is located at 316 meters above sea level. Average precipitation and air temperature are shown in table 1. At the beginning of the analysed period about 2'400 farms existed in Basel-Landschaft, with an average farm size of 10 ha. At the end of the analysed period the number of farms had declined to approximately 1'600 with an average farm size of 14 ha (BFS 2017a, BFS 2017b).

As proxies for the hare and fox populations, hare and fox harvest counts from 1960 to 1989 were taken from the federal hunting statistic (BAFU 2014). The annual harvests were used as a measure for the changes in the population from year to year. This time frame was chosen because the statistical coverage of hare harvests was not fully available before 1960, and, after 1989, hare hunting was increasingly restricted, making subsequent harvests not comparable (Pfister et al. 2002). Unfortunately, the more accurate alternative proxy, counts with the spotlight method, was not available for period and region under investigation.

Factors potentially playing a role in the decline of the hare population were determined in a preliminary literature survey. The factors selected were weather, predators, and the industrialisation of agriculture. For each of the factors, suitable parameters were chosen.

The weather data for the Canton of Basel-Landschaft were obtained from the weather station in Binningen (BL). Summer and winter air temperatures (May to August; December to February), as well as the influence of summer precipitation (May to August) were investigated. These periods were selected because Schneider (1978) ascribes great importance to the weather from July to mid-August and because Zörner (1981) assumes that the yearly variation of the surviving leverets and therefore the annual harvest heavily depend on the postnatal mortality rates of the months May to July. Furthermore, Eiberle & Matter (1982) suggest a negative influence of warmer winters due to increased spread of coccidiosis.

The fox harvest was used as a proxy for the influence of predators, although car-

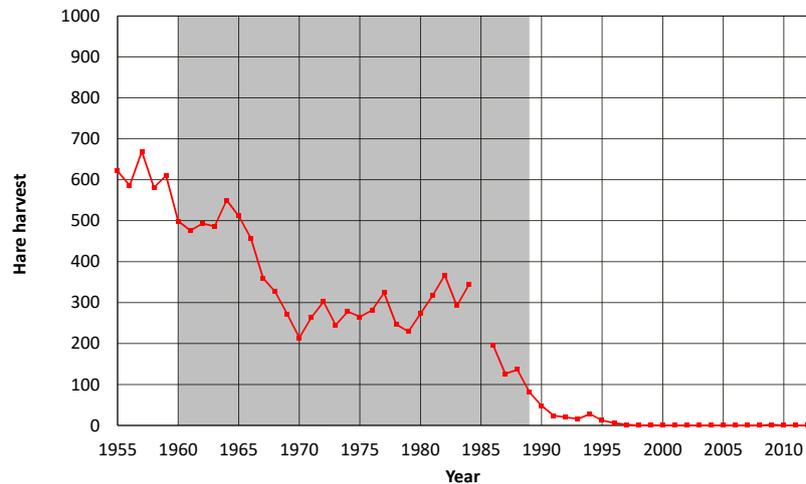


Fig. 1: The annual hare harvests in the Canton of Basel-Landschaft from 1955 to 2013. The area shaded in grey marks the analysed period. The data from before 1960 are not entirely comparable, because the statistical coverage was still under construction. After 1989 restrictions for hare hunting were introduced (Pfister et al. 2002).

	Precipitation in mm	Temperature in °C
December	53	1,8
January	52	0,7
February	49	2,2
May	85	13,1
June	84	16,5
July	78	18,6
August	90	17,8

Tab. 1: Average precipitation and air temperature of the analysed months in BL (1960-1989).

tion crows and feral cats were found to be more likely to kill leverets in arable land (Fernex 2010). For the other species, there were no data available in Basel-Landschaft or the whole of Switzerland. As a proxy for the industrialisation of agriculture, the number of tractors and the number of permanent workers in agriculture in Basel-Landschaft were chosen. The numbers of tractors and permanent workers in Basel-Landschaft were taken from the *Statistisches Lexikon der Schweiz – Historische Kollektion* (BFS 2017c; BFS 2017d). Because farm censuses had only been carried out every five years, missing years were reconstructed by linear interpolation. As Fischer et al. (2010) showed that changes in arable land took six to nine years to affect the hare population, the same lag was used here.

2.2 Statistical analysis

The influence of factors on the annual hare harvest was measured using linear regression analysis. For the selection of relevant factors, each was analysed

in a simple or multiple regression respectively, with a threshold of 0.5 for inclusion. The association between fox and hare harvests was analysed a simple regression. To select the influential air temperature periods, a multiple linear regression with the average monthly air temperatures from December (year prior to the hare harvest count) to February and May to August were used. To assess the influence of precipitation from May to August, a multiple linear regression with each of the four months was conducted. The association between mechanised agriculture and hare harvest was assessed with two simple linear regressions, the first regression for the number of tractors in Basel-Landschaft, and the second for the number of permanent workers in agriculture in Basel-Landschaft. They were analysed independently because both parameters are a proxy for the industrialisation of agriculture and thus an association between the two is highly likely. As previously mentioned, both parameters were analysed with a six to nine-year lag. A

comprehensive model including all pre-selected factors was analysed using a multiple regression with a significance level of 0.05. Despite not fulfilling the pre-selection criterion, the fox harvest was forced into the comprehensive model, because studies of Maas (2010), Reynolds et al. (2010), and Panek et al. (2006) suggest that there is most likely a relationship between foxes and hares. For potentially confounded parameters interaction terms were included, namely for the average temperatures and total precipitation of June and August, and for the number of permanent workers and tractors. For selecting the most relevant lag between the indicator for agricultural intensification and the hare harvest, the Akaike information criterion (AIC) was used to choose the best fitting model. All the statistical analyses were carried out using R 3.2.3.

3 Results

3.1 Preliminary Selection

The results from the preliminary selection analysis can be seen in tables 2 to 5. Of the seven months, only the air temperature in December, June, July, and August had a p-value below selection threshold (Tab. 2). The precipitation in June and August did fulfil the selection criterion (Tab. 3) and was consequently included in the comprehensive model. No significant association between hare harvests and fox harvests could be detected. In addition, the number of tractors as well as the number of permanent workers had a significant association with hare harvests at four different lags (Tab. 4 & 5).

3.2 Comprehensive model

The results of the final comprehensive regression model are given in table 7. The lag of six years between the indicators for agricultural intensification and hare population gave the best fit to the data (Tab. 6). Due to the significant interaction of the workers and tractors ($p = 0.018$), the workers were removed from the model. The annual fox harvest, air temperatures in December, and the number of tractors with a lag of six years had a significant association with the annual hare harvest.

4 Discussion

An important question concerning my method is how suitable hare and fox

Term	Coefficient	p Value
(Intercept)	540,562	0,377
DecemberPrevYear	-11,563	0,337
January	-3,699	0,729
February	1,698	0,854
May	-10,040	0,578
June	34,611	0,129
July	-13,688	0,445
August	-21,869	0,408

Tab. 2: Results of the linear regression of the annual hare harvest in BL on the average air temperatures in December of the previous year, January, February, May, June, July, and August. Significance level $p = 0.5$.

Term	Coefficient	p Value
(Intercept)	264,231	0,047
May	0,446	0,546
June	-0,497	0,483
July	-0,100	0,912
August	0,713	0,263

Tab. 3: Results of the linear regression of the annual hare harvest in BL on the total precipitation in May, June, July, and August. Significance level $p = 0.5$.

Term	Coefficient	p Value
(Intercept)	616,605	2,20E-14
Tractors6Yrs	-0,228	4,70E-08
(Intercept)	600,881	1,16E-14
Tractors7Yrs	-0,225	4,36E-08
(Intercept)	586,257	7,56E-15
Tractors8Yrs	-0,222	4,78E-08
(Intercept)	572,780	5,64E-15
Tractors9Yrs	-0,220	5,77E-08

Tab. 4: Results of the linear regression of the annual hare harvest in BL on the number of tractors with a 6, 7, 8, or 9-year lag. Significance level $p = 0.5$.

Term	Coefficient	p Value
(Intercept)	98,670	0,004
Workers6Yrs	0,060	2,30E-08
(Intercept)	102,200	0,003
Workers7Yrs	0,056	2,83E-08
(Intercept)	103,821	0,002
Workers8Yrs	0,053	3,60E-08
(Intercept)	104,600	0,003
Workers9Yrs	0,050	5,69E-08

Tab. 5: Results of the simple linear regression of the annual hare harvest in BL on the number of permanent workers with a 6, 7, 8, or 9-year lag. Significance level $p = 0.5$.

harvests were as an estimate for the respective population. Hare harvests appear to be a reliable measure because

hunts were essentially carried out at the same time each year (October to December) (BAFU 2014) and in the same

Lag	AIC
6 years	322,062
7 years	327,270
8 years	328,104
9 years	322,848

Tab. 6: Akaike information criterion (AIC) for the comprehensive model using a 6, 7, 8, or 9-year lag.

way (battue) (Weber 2014). Thus, harvests should amount to approximately the same percentage of the hare population each year. Furthermore, as we can see in figures 2 and 3, both fox and hare harvests and road-kills have similar curves. This suggests that harvests were a reliable base of the analyses. Moreover, Reichholf (1981) regarded road-kills as a relatively reliable proxy of the hare population.

The results of the analysis confirm the findings by various authors that the hare population might be strongly influenced by fox predation (Martini 1983; Guthörl & Kalchreuter 1995; Hell et al. 1997; Panek 2006; Knauer et al. 2010; Maas 2010), air temperature in winter (Eiberle & Matter 1982) and agricultural intensification (Holzgang et al. 2005; Gehle 2010; Godt et al. 2010; Kinser et al. 2010; Fischer et al. 2010). In contrast to those studies, the present study provides a combined appreciation of these factors and a corresponding weighting. My analysis shows that most likely not only one factor can be held responsible for the decline of the hare population, as Eiberle & Matter (1982) and Maas (2010) did, but that we have to consider multiple factors. Prima facie, the influence of December air temperatures appears to be much stronger than the influence of tractors and foxes. However, one degree Celsius is a much more significant change than one more fox or one more tractor. Numerically, a reduction of the average December air temperature by 1°C has the same effect as 50 additional tractors or 100 additional foxes in the system. Interestingly, fox harvests nowadays increase or decrease by a few hundred in Basel-Landschaft (Fig. 2), tractors in the sixties and seventies increased by about a hundred per year, and December air temperatures change a few degrees compared to the previous year. Hence, in relation to the annual change rate of the influential

Term	Coefficient	SE	p Value
(Intercept)	1912,284	826,751	0,033
AnnualFoxHarvest	-0,164	0,059	0,012
PrecipAugust	-6,907	6,908	0,331
PrecipJune	-8,142	4,385	0,080
TempAugust	-54,921	37,842	0,164
TempAugust *PrecipAugust	0,340	0,373	0,373
TempDecemberPrevYear	14,741	6,621	0,039
TempJuly	18,780	10,104	0,080
TempJune	-28,907	23,040	0,226
TempJune*PrecipJune	0,453	0,249	0,086
Tractors6Yrs	-0,295	0,037	2,19E-07

Tab. 7: The comprehensive model, including all significant factors of the preliminary selection and the annual fox harvest. Significance level $p = 0.05$.

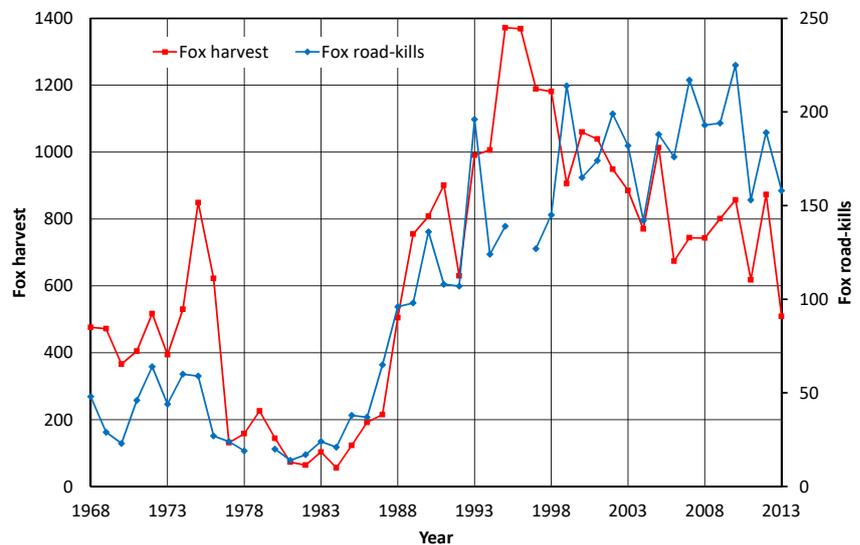


Fig. 2: The annual fox harvests and road-kills in BL from 1968 to 2013.

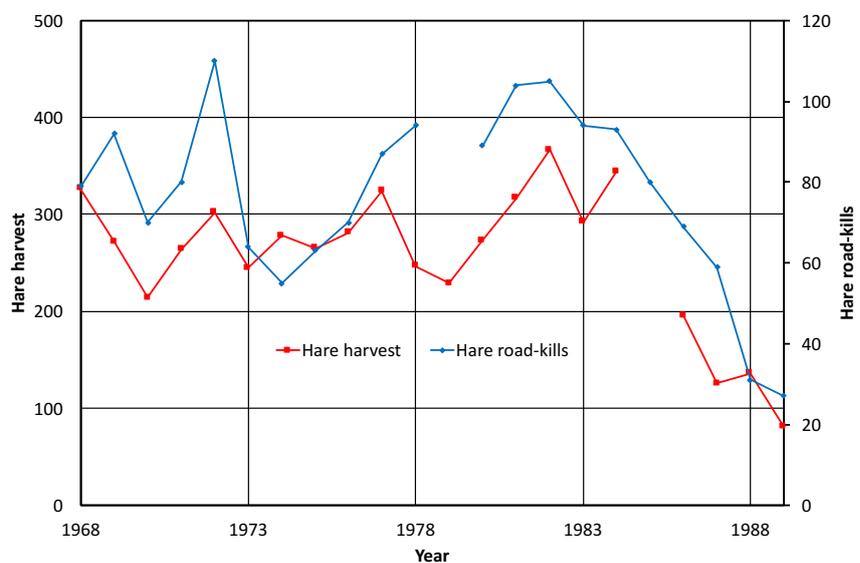


Fig. 3: The annual hare harvests and road-kills in BL from 1968 to 1989.

factors, their effect appears to be equivalent. A further aspect is the certainty of the estimates: while the estimate of December air temperatures and annual fox harvest have a rather large standard error of 44.9% and 35.9%, respectively, the standard error of the tractor estimate is smaller (12.5%), indicating that the effect of agricultural intensification is more probable than the other two. This is also reflected by a significantly lower p-value. The higher probability is plausible, considering the devastating negative influence of tractors on hares shown by Grendelmeier (2011). During the entire harvesting process up to 100% of the dummy-leverets were damaged. Most damage was done by the tractor tyres running them over. Also other studies found a relation of the intensification of agriculture and lower hare populations (Holzgang et al. 2005; Fischer et al. 2010; Godt et al. 2010; Wadsack et al. 2010). The researchers were able to increase the hare population by habitat management, and exactly habitat has been changing for the worse from the hare's point of view to due intensified agriculture. Hare population has even been used as an indicator for intensification of agriculture (Lundström-Gilliéron & Schlaepfer 2003).

Also, the negative influence of higher fox harvests coincides with the pertinent literature (Martini 1983; Hell et al. 1997; Spittler 2000). Many case studies have found a causal relationship between predators, including foxes, and hare population. Maas (2010) managed to increase hare harvests in the hunting district Stoermede-East in North Rhine-Westphalia by 400% within 12 years, by introducing drastic predator control. Panek et al. (2006) intensively culled foxes near Czemiń, Poland, and observed an increase in the hare population, counted with the spotlight method. On the other hand, Wadsack et al. (2010) found that drastically increased culling of foxes did not affect hare densities. The consistent negative association between the fox and hare population should not be ignored when trying to increase the hare population. This is especially true for Basel-Landschaft, as historically high fox harvests and numbers of road-killed foxes indicate a high fox population in past years (Fig. 2). However, this does not mean

that predators, inter alia the fox, are the main culprit of the decline of the hare population, as Maas (2010) concluded. This is unlikely because as Panek (2009) showed that fox predation "decreased with habitat diversity, especially in areas with low hare density", a side effect of the industrialisation of agriculture. This suggests an interdependence of fox predation and a more industrialised agriculture.

The results of my weather analyses were different from the findings of other researchers (Eiberle & Matter 1982; Nyenhuis 1995; Schneider 1978; Zörner 1981). Although like other authors air temperature was found to be more important than precipitation, neither the positive effect of high summer temperatures (Nyenhuus 1995) nor the negative effect of high winter temperatures (Eiberle & Matter 1982) could be confirmed. Nyenhuus' study analysed the influence of weather on hares in the lower Rhine bay, where about sixty percent of land was used for agriculture and only twelve percent was wooded (Nyenhuus 1995). In contrast, Basel-Landschaft is much more wooded; today forest and arable land each make up forty percent of the Canton total area (BfS 2017e). Furthermore, the climate of the lower Rhine bay is milder than in Basel-Landschaft (Schweizer Weltatlas 2010). This may account for the different findings regarding the influence of weather on hares.

Contrary to Eiberle & Matter (1982), who identified a negative influence of high winter temperatures, the present study suggests a positive correlation of warmer Decembers and hare harvests. However, neither juvenile nor adult hares are especially prone to cold weather (Weber 2010; Zörner 1981). The role of coccidiosis claimed by Eiberle & Matter remains to be elucidated as nowadays hare populations are very low and the spread of coccidiosis depends primarily on animal densities and contact rates (S. Rüegg, pers. comm.). To clarify the influence of December and winter temperatures in general further investigations are required.

Zörner (1981) and Weber (2014) stress the detrimental effect of wet weather on leverets, which raises the question why

this effect is not reflected in various statistical analyses. Nyenhuis, Eiberle & Matter, and the present study measure the influence of total precipitation on the annual hare harvests. A problem with this approach might be that the total precipitation does not provide insight into the distribution of rainfall over time. Constant low precipitation can result in the same monthly total precipitation as one or two downpours. These longer periods of wet weather are worse for leverets, because the risk of hypothermia increases (Zörner 1981). A possible approach for future studies would be to count the amount of longer dry periods per year and calculate their association with the hare harvest. This could provide a better insight into the influence of wet weather on hare harvests.

Finally, the use of linear regression for this investigation should be critically assessed, as it assumes independence of data points, which is not the case in a time series. Furthermore, linear associations between hare harvests and the different parameters are assumed, which is not given in ecological systems, where non-linear relations prevail. This could potentially mask causal links or falsely identify significant associations. However, given the short time series and small data sets, linear regression appeared to be the best option despite these shortcomings. It should further be noted that the present study design could only detect associations, no causal relationships. It is therefore important that the results were in line with more reliable evidence from experiments demonstrating causality, such as Panek (2006), Godt et al. (2010), Maas (2010), Zellweger-Fischer et al. (2011), and Grendelmeier (2011).

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