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Original article

A statistical analysis of the relationship between red fox *Vulpes vulpes* and its prey species (grey partridge *Perdix perdix*, brown hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus*) in Western Germany from 1958 to 1998

Felix Knauer, Helmut Küchenhoff & Stefan Pilz

Predator-prey relationships are of general interest in ecology and have been studied extensively. They are also of interest for effective management and recovery of prey populations. However, quantification of these relationships in the field has remained difficult. We analysed the impact of the predation of red fox *Vulpes vulpes* on brown hare *Lepus europaeus*, grey partridge *Perdix perdix* and rabbit *Oryctolagus cuniculus* using yearly hunting bag records as population indicators in eight German provinces over a period of 41 years. Bag records were tested for deviation from properties of suitable population indicators. We quantified the association between prey and predator populations within the context of other variables such as weather and long-term trends. We used an overall regression model for each prey population and discussed three statistical approaches accounting for the time series structure of the data. Models for all prey species populations display a good fit. The fox population has a significant negative association to the hare population in all models. The results for the rabbit population show only a small effect of the fox population, though it is not significant. The effect of the fox population on the partridge population cannot be clearly distinguished from a general trend. Additionally, there is a strong long-term trend in the hare and partridge populations. This could be due to major changes in the agricultural landscapes over the last decades. It is important to note that this trend is much stronger than the association to the fox population. Our study suggests that habitat improvement could be much more effective in restoring prey populations than fox control due to the minor interactions between the fox and the prey populations.

Key words: agricultural changes, population dynamics, predator-prey, small game conservation, time-series analysis

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Predator-prey relationships are of general interest in ecology, but quantifying these interactions has proven to be difficult. Does the predator just occasionally prey on a certain prey species or does predation decrease at times of low prey density? As a rule, generalist predators can have a significant impact on prey populations, whereas specialists are dependent on the dynamics of their particular prey population. Small game species have declined in the last decades in Germany (German Hunter's Association statistics). Many wildlife biologists, hunters and conservation biologists suspect generalist predators to be responsible for this decline. So we studied the effect of red fox *Vulpes vulpes* on brown hare *Lepus europaeus*, rabbit *Oryctolagus cuniculus* and grey partridge *Perdix perdix*. In Central Europe, the red fox is a generalist predator, preying on a variety of species including these three species (Storch &

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Kleine 1991, Kaiser & Storch 1996). However, in most areas small rodents, especially voles *Microtus* spp., will account for the major part of the foxes' diet (Russell & Storch 2004).

Although much of our understanding of predator-prey relationships derived from theoretical work (Jost & Arditi 2000, Sih et al. 1998, Englund et al. 2001) and laboratory experiments (Murdoch 1969), field studies have provided additional insight. The latter mainly consisted of 1) comparisons of different discrete conditions (such as location or time period; Spittler 1987), 2) predator removal experiments (Goetmark et al. 1990, Palomares et al. 1995, Tapper et al. 1996) or other manipulations (Lindström et al. 1987, Storaas 1988), and 3) analyses of continuous time series (Jost & Arditi 2000, Turchin & Ellner 2000). Removal experiments have the advantage of controlled conditions, but usually they are conducted over short periods of time and often compare extreme situations, which raises the question of their generality. Time series analyses have the advantage of examining the study object under realistic conditions, but are hindered by the long sampling time required, uncontrolled conditions during the sampling period (e.g. changes in sampling methods) and lack of causal relationships. Because of these methodological difficulties, predator-prey relationships have remained relatively poorly studied, even when both predator and prey species are common and their relationship is of high scientific and/or conservational interest.

The purpose of our study is twofold: first, we quantify the association of the population dynamics between fox and three prey species: brown hare, rabbit and grey partridge in eight West German provinces. Being aware that this is only a correlational approach, we secondly assess the usefulness of an analytical strategy in order to estimate the quantitative effect of the fox on the three prey populations.

Material and methods

Data base

We used hunting bag records for a 41-year period (1958-1998) collected in eight West German provinces (Fig. 1 and Table 1; in Bavaria only during 1969-1998), totalling 317 'provinces x years', for grey partridge, brown hare, rabbit and red fox (German Hunter's Association statistics). The remaining three West German provinces (Hamburg, Bremen and Berlin) are mainly urban areas, and East Germany had a different hunting system until 1990. The period for counting the hunting bags is 1 April - 31 March of the following year, e. g. the '1998' data originated from 1 April 1998 - 31 March 1999. The hunting system was constant during 1958-1998. Data were not available in a smaller spatial scale, e.g. districts, municipalities or hunting units.

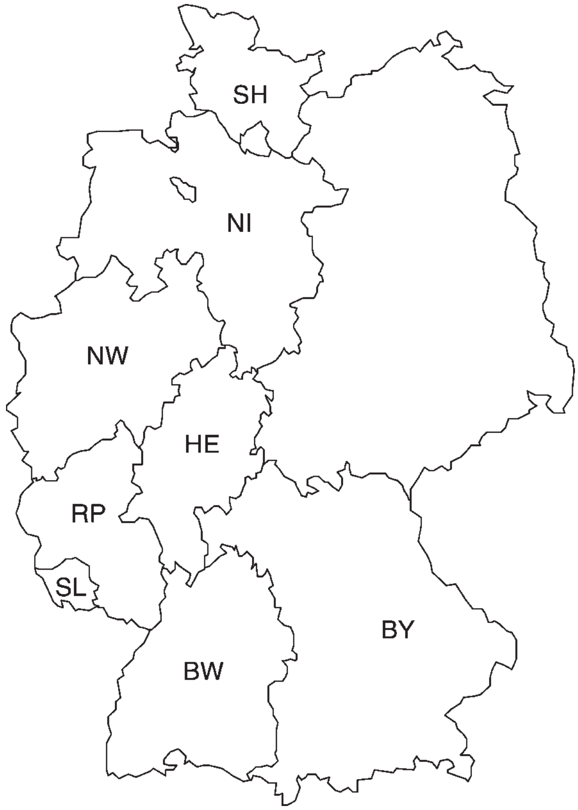

Figure 1. Location of the eight German provinces of concern. For full names of the provinces, see Table 1.

We obtained potential weather variables for the eight provinces from 660 weather stations below 600 m a.s.l. (German Weather Service) since most of the bag records were from hunting units at that elevation. We calculated two different weather indices per month for each province: mean temperature and total precipitation, using the average from all weather stations in each province. We limited the data to include only winter and spring (December - June). We did so, as winter is the most critical period concerning mortality, and in spring until the end of June most offspring of partridge, hare and rabbits are raised (e.g. Potts 1986, Pegel 1986, 1987). Hare

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Table 1. Size (in km2) and percentages of different types of land use in the eight German provinces in 2004 (Federal Statistical Office 2007).

Province	Abbreviation	Total area	Agriculture	Forest	Water	Buildings, Industry, and Traffic	Other
Baden-Württemberg	BW	35.752	46.3%	38.1%	1.0%	13.0%	1.6%
Bavaria	BY	70.552	50.1%	34.9%	2.0%	10.5%	2.6%
Hesse	HE	21.115	42.6%	40.0%	1.3%	14.3%	1.7%
Lower Saxony	NI	47.62	60.9%	21.2%	2.3%	12.8%	2.9%
North Rhine-Westphalia	NW	34.084	50.2%	24.9%	1.9%	20.4%	2.7%
Rhineland-Palatin	RP	19.853	42.6%	41.5%	1.4%	12.4%	2.2%
Schleswig-Holstein	SH	15.763	71.0%	10.0%	4.9%	11.3%	2.8%
Saarland	SL	257	44.2%	33.4%	1.0%	19.1%	2.2%

and rabbits also reproduce later on in the year, but we did not expect strong weather influences at that time due to the higher summer temperatures. By limitation of the variables we avoid problems with overfitting, collinearity and pseudoreplication.

Hunting bag records

The German hunting system differs from the systems used in many other countries. In Germany, hunting rights are given to landowners with a minimum contiguous property area of 75 ha, and landowners of properties < 75 ha can combine their property with other owners within the municipality to obtain the required size. The average size of the hunting units in Germany is about 500 ha. These hunting units are leased to individual hunters for a minimum of nine years. By the end of the hunting year (i.e. March 31) the hunters have to report the bags of all game species to the district authorities. Although there have been cases of hunters overexploiting their units, the long leasing period and an ethical hunting code lead to a sustainable use of the game resources (German Hunters' Association 2000). Therefore, small changes in the length of the hunting seasons do not affect the bag numbers.

The hunting season differs from species to species. Thus, hares can be hunted from 1 October to 15 January, partridges from 1 September to 15 December, whereas red foxes and rabbits can be hunted all year round, but there are slight differences in the hunting seasons between the provinces. Rabbits are primarily hunted during the fall and foxes in winter. It is important to note that small game is hunted before the main fox hunting season starts.

In small game hunting units, foxes are treated as a pest species, but fox control in Germany is not as intense as in Britain (e.g. Heydon & Reynolds 2000 a, b). Small game has a lower economic value and there are legal restrictions, such as the protection of adult foxes with cubs during 16 April - 15 July. In most hunting units fox control is considered unimportant. If game animals are released, it is forbidden to hunt the species in this hunting unit within one year after release.

Are hunting bag records reliable population size indices?

Hunting records are commonly used as population indices (e.g. Angelstam et al. 1985, Danell & Hörnfeld 1987, Lindström et al. 1994, Smedshaug et al. 1999, Post & Forchhammer 2002), though much debated (Ranta et al. 2008). Main criticisms are data quality (noise) and systematic deviations (bias). Noise in the dependent variable should lead to correct estimates of the parameters of the independent variables, but to a lower goodness-of-fit. Noise in the independent variables should lead to an underestimation of the effects. Bias is often believed to be caused by individual hunters who report their bag incorrectly, but the large scale of our study makes this point unlikely. The single positive and negative deviations due to incorrect reports will be averaged out by the large number of participating hunters. Other influencing factors can be changes or 'fashions' in hunting practices, which can cause misleading results. They are difficult to detect, but are not known for Germany during this period and in the eight provinces.

Besides fashions and incorrect records, the slightly increasing number of hunters that occurred in Germany over the last 40 years (a 2% increase before reunification and 0,9% after; German Hunter's Association statistics) could cause higher hunting pressure and therefore bias the records. The actual hunting effort (*sensu* Nichols et al. 2001) is

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unknown, however, it is likely that the effort remained stable since the area is not increasing and the hunting units are leased to individual hunters. In fact, there will be more hunters without a regular hunting opportunity, and the number of practising hunters remains constant. Hunting bag records are suitable as annual population indicators if they can be shown to constitute a constant proportion of the real population over time. The best way to test this assumption is to compare the bag records with direct counts or well-conducted population estimates. In Germany, population estimates are available only at small scales, but not at larger scales (> 1,000 km^2), such as the scale used in our study (the median size of German provinces is 23,900 km^2). Another way of determining the reliability of bag records is to study their statistical properties. At least three properties should be fulfilled by suitable population indices; if fulfilled, we assumed suitability of the bag records as indicators of population trends, though we understand that this is a support for the assumption, not a definite proof. The three properties are:

1) The long-term population trend should be similar in all provinces for each study species, if we expect significant influences from landscape changes caused by agricultural development or by climatic change, these changes should be spatially and temporally correlated at a large scale, i.e. for the whole of Germany;

2) The annual fluctuations of species should be correlated between provinces, since we expect a significant influence of the weather on the annual fluctuations and the weather is correlated over the provinces;
3) The annual fluctuations of species, which use the same habitat and are not influenced by large-scale epidemics, should be positively correlated. This should be true for grey partridge and brown hare (Pegel 1986, 1987), but not for rabbits, which suffered from myxomatosis, or fox, which suffered from rabies.

The linear trends (β-values) of the four game species (log-transformed) in all eight provinces were similar: Partridge (mean: -0.1318; minimum: -0.175, maximum: -0.093) and hare (mean: -0.0380; minimum: -0.0624, maximum: -0.0137) show a negative trend, and fox a positive trend (mean: 0.0294; minimum: 0.0091, maximum: 0.0642), which was caused by vaccination against rabies (see below). Rabbits remained stable (mean: 0.0013; minimum: -0.0086, maximum: 0.0160). Therefore, property 1 was fulfilled.

To evaluate property 2, we analysed the detrended hunting bag records: the pairwise correlations of the data over all provinces for the four species was significantly positively correlated (correlation coefficients average at 0.61 for partridges, 0.57 for hare, 0,70 for rabbit and 0.54 for fox), fulfilling property 2. The fox in Schleswig-Holstein (SH) were less correlated with the other provinces; an explanation might be the lower occurrence of rabies in SH than in the other provinces.

Furthermore, we calculated the correlation coefficients of the detrended data between partridge and hare. The coefficients were positive (mean: 0.36, with the exception of SH), which fulfils property 3.

Statistical modelling - general approach

In this study we analysed the time period in all eight German provinces simultaneously in a single model that can handle factor variables and covariates in the same model as well as the time-series structure of the data. This leads to more robust results than analysis of a single time period, but it requires a special modelling approach. We used additive models (AM; Hastie & Tibshirani (1990) and Kristoffersen et al. (2001)) which allow flexible trend structure in data. The flexible trend can be interpreted as the effects of unknown variables, which change smoothly over time.

However, since the fox population also changed over time, a flexible trend model can lead to an underestimation (or even, masking) of the fox effect. Therefore we also used a less flexible model (regression model with autoregressive error term; AEM). We included a linear trend and a further dummy variable for the crash in the year of 1979, which was obvious in the prey populations (see Figs. 2-4). By using interaction terms we fit different trends to each province, a change in trends in 1979 and assumed an autoregressive error structure (lag of one year) while taking the time-series structure into account. We also included weather variables in our model. Since there are many weather variables, a selection of these variables was necessary. We used the AM with a backward selection procedure, and we used the same variables as for AEM in order to compare the results of both approaches. Finally, in order to be comparable to other studies (e.g.

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Watson et al. 2000), we also used an autoregressive model (ARM) with the time-lagged dependent variable on the right-hand side of the model as a third approach.

Additive model (AM)

In all models, the log (hunting bag records) was the response variable. The additive model is defined as follows:

$$\log_{10}(N_{t,k}) = \beta_1 \log_{10}(F_{t,k}) + \beta_2 \log_{10}(F_{t-1,k}) + \sum_{j=1}^{14} \beta_{j+2} W_{j,t,k} + f_k(t) + \varepsilon_{t,k} \quad (1),$$

where $N_{t,k}$ is the hunting bag record of the prey species in year t in province k. We used the logarithm of the counts (Watson et al. 2000), which corresponds to a multiplicative effect structure. There are three types of regressors in the model:

A. The fox population ($F_{t,k}$) in year t and the fox population ($F_{t-1,k}$) in the preceding year (t-1), as the 'lagged fox population'. The corresponding parameters have to be β_1 and $\beta_2 < 0$, since a positive effect of the fox population on the prey population would have no sensible ecological interpretation. The reason for including the lagged fox population in the model is that hunting seasons for the four species are not identical: hare, partridge and rabbit are hunted in autumn, whereas foxes are predominantly hunted for their fur in the winter.

B. The weather variables $W_{j,t,k}$, denote variable number j in province k at time t. The 14 different variables are described above. The parameter values are limited to $\beta_j > 0$ for temperature variables and $\beta_j < 0$ for precipitation (Pegel 1986, 1987). Temperature has a positive and precipitation a negative effect on population dynamics of the target species.

C. The smooth time effects $f_k(t)$ for each of the eight provinces. We chose a penalised spline approach with splines of degree 2 with 10 equidistant knots.

This analysis was conducted using BayesX (Brezger et al. 2004). The regression parameters were estimated using the maximum likelihood, while the smoothing parameters were estimated through a Reml approach (Ruppert et al. 2003) as a fast alternative to generalised cross validation (Golub et al. 1979), leading to restricted maximum likelihood estimators.

Model with autoregressive errors (AEM)

The used regression models are designed for longitudinal or time-series data (Diggle et al. 2002). It has the following form:

$$\log_{10}(N_{t,k}) = \beta_{0,k} + \beta_1 \log_{10}(F_{t,k}) + \beta_2 \log_{10}(F_{t-1,k}) + \beta_{3,k} C + \beta_{4,k} T + \beta_{5,k} T*C + \sum_{j=1}^{d} \beta_{j+5} W_{j,t,k} + \varepsilon_{t,k} \quad (2).$$

This model is similar to model (1), but unlike the latter, the time-series structure of the data is now taken into account by trend variables T and C and by assuming an autoregressive structure of the error terms:

$$\varepsilon_{t,k} = \rho \varepsilon_{t-s,k} + \upsilon_{t-s,k}, \text{ yielding } \mathrm{Cov}(\varepsilon_{t-s,k}, \varepsilon_{t,k}) = \rho^{\sigma} \quad (3).$$

The parameter ρ is the correlation between two consecutive error terms in the same province and the time lag. It is assumed that the error terms $\upsilon_{t-s,k}$ are independent and identically normally distributed. The trend variable T (year) gives a linear trend over the whole study period. Additionally, a dummy variable C (crash) has been included, with C as 0 for $t < 1979$ and 1 for $t \geq 1979$ (see above). Also interactions between these variables are included, which allow modelling for different time trends in different provinces.

This analysis we conducted using PROC Mixed from SAS (1999). To match the effects of the confounding weather variables, we used the set of weather variables, chosen in the AM for an analysis with the AEM.

Autoregressive model (ARM)

Finally, an autoregressive model was also used by adding the variable $\log_{10}(N_{t-1,k})$ as a regressor. These models are typically used for prediction, since the distribution of $N_{t-1,k}$ is given. The interpretation is slightly different from the other models. Now the influence of the other regressor variables is conditioned on the prey population in the year before, emphasising the dynamic aspect of the model. We did not use lagged variables of the response variable of higher order, because lagged variables of second order were not significant. The time-series structure

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of the model is taken into account by the lagged variable $\log_{10}(N_{t-1,k})$ and no further autocorrelation is assumed in the error term. The complete model is:

$$\log_{10}(N_{t,k}) = \beta_{0,k} + \beta_L \log_{10}(N_{t-1,k}) + \beta_1 \log_{10}(F_{t,k}) + \beta_2 \log_{10}(F_{t-1,k}) + \beta_3 C + \sum_{j=1}^{14} \beta_{j+3} W_{j,t,k} + \varepsilon_{t,k} \qquad (4)$$

with white noise $\varepsilon_{t,k}$. Again we included the set of weather variables from the AM approach in the model.

Results

Relationships between the fox population and the three prey species using the three different modelling approaches differed (Table 2). In the AEM model, the fox was shown to affect the hare both in current and preceding years. The effect of fox on partridge was small in AEM and not significant in the other models. The delayed effect of fox on rabbit was strong in AEM and ARM, but not significant in AM. Overall, the delayed effect of fox was stronger than the current year effect in all models (see Table 2).

Hare

With all three approaches, a good fit was achieved (see Table 2). Furthermore, there was a strong relationship between hare and fox populations (Fig. 2 and Table 2); stronger in winter than in summer since the estimated absolute β-value for the lagged fox population was larger than the β-value corresponding to the fox population of year t. The β-value (AEM) of -0.36 for the lagged fox population

Table 2. Significant negative effects (β-values) of the fox on the three prey species and the fit (R^2) for each model.

Species	Model	$\log(F_t)$	$\log(F_{t-1})$	R^2
Hare	AM		-0.3531	0.91
	AEM	-0.1725	-0.3619	0.9
	ARM		-0.2156	0.84
Partridge	AM			0.97
	AEM		-0.1916	0.97
	ARM		-0.2202	0.94
Rabbit	AM			0.84
	AEM	-	-	0.68
	ARM		-0.2782	0.71

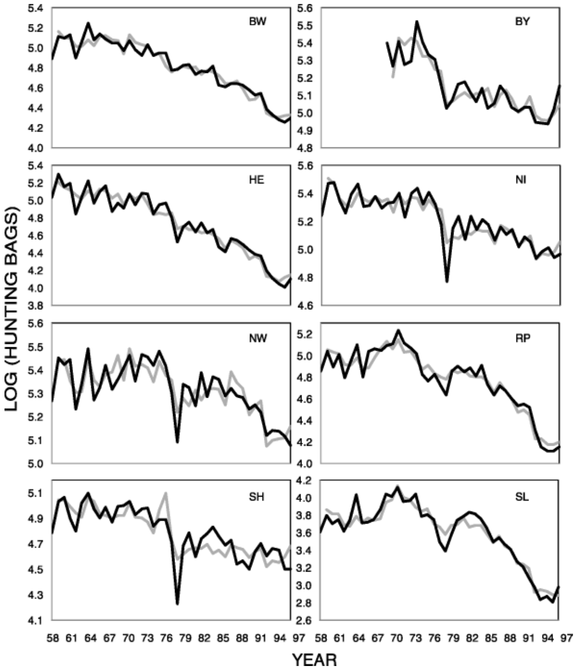

Figure 2. Observed (—) and predicted (—) values of model AEM for the hare in the eight provinces.

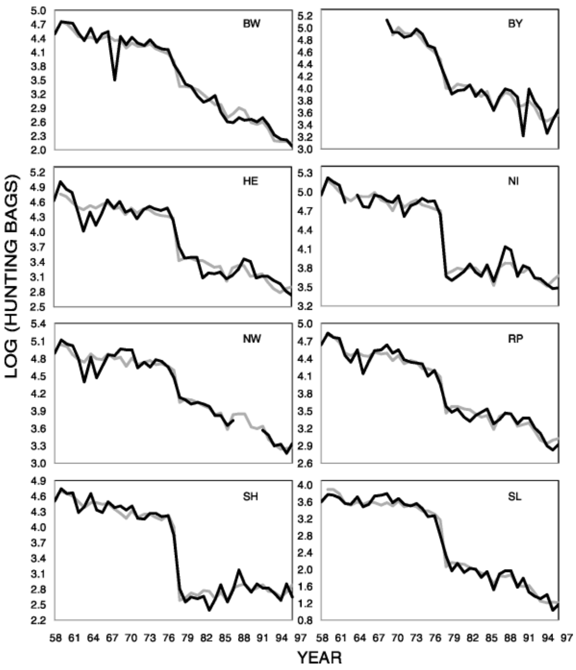

Figure 3. Observed (—) and predicted (—) values of model AEM for the partridge in the eight provinces. During 1989-1992 there was no hunting on partridges in NW, so we excluded this period from the data.

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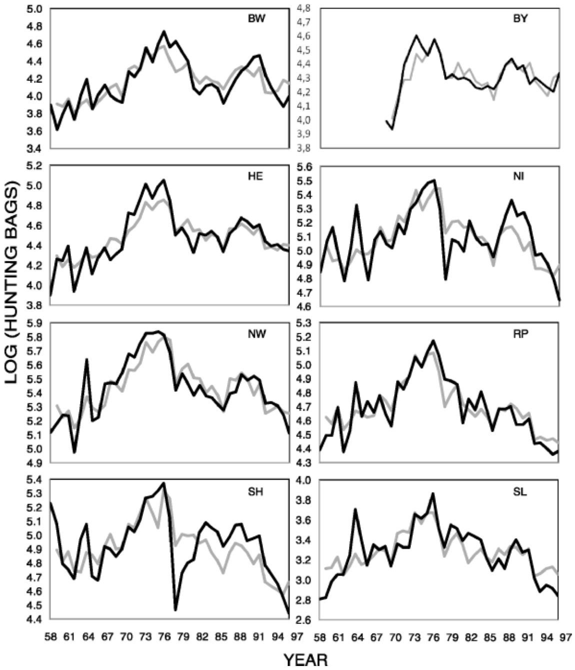

Figure 4. Observed (—) and predicted (—) values of model AEM for the rabbit in the eight provinces.

means that the hare population is reduced by 1-$(1+0.1)^{-0.36} = 3.37\%$ when the fox population of the year before increases by $0.1 = 10\%$ (the relative effect is due to the logarithmic scale).

Partridge

Again a good fit was obtained with the three approaches (see Table 2 and Fig. 3), which was mostly due to the long-term trend. The association between the fox population and the partridge population was always negative, though significant only for the AEM. It was lower ($\beta = -0.19$) than for the hare.

Rabbit

The fit of AEM was lower than for the other species ($R^2 = 0.68$; Fig. 4). The rabbit data show long-term fluctuations, which the model only partly can predict. One possible reason for these fluctuations is the occurrence of myxomatosis, which could not be analysed due to lack of data. The lagged fox population was not significantly correlated to the rabbit population in the AEM.

The other two models fit the data slightly better (see Table 2), although ARM detected a positive association between fox and rabbits, possibly due to an overfitting on the trend (or any unobserved confounding effect).

Discussion

In our study, we tried to quantify the relationship between fox and the three types of prey species, which are also game for hunters. Despite whether hunting bag records indicate real population sizes, we were able to estimate these relationships quantitatively, using a combined approach of different regression techniques. In particular, we detected a stronger lagged effect than the current effect of the fox on prey species. Before discussing the meaning of our results in terms of ecology and management, we first discuss below our methodological choices.

Our time series showed a long-term trend, and therefore the use of additive modelling (AM) of time series may appear striking. We fit a long-term trend using a smoothing parameter, in order to control the flexibility of the trend, as a trend that is too flexible can cause an overfitting of the model. However, in addition, the fox population also follows a trend, so the flexible trend component 'competes' with the fox population trend, a problem known as concurvity, which is the nonparametric counterpart of multicollinearity. Fox populations increased after the rabies vaccination was implemented in 1985. While in the AM model concurvity could be a problem, it is avoided when using a regression model with an autoregressive error term (AEM). The AEM method, however, had also hidden assumptions, such a linear trend and a crash, and the interactions between them. The crash is apparent in the partridge data, but we only can speculate about its ecological meaning. In contrast, the rabbit time series underlines the limits of AEM approach. In this case, we could have made other assumptions about the trend (e.g. quadratic), but then we would have essentially fit a data driven trend, which was already done in the additive model. Finally, we also used an autoregressive model (ARM) with the lagged dependent variable as an explanatory variable, which can be seen as an alternative trend modelling. Interpretation of results is slightly different from the other two models since the influence on the fox population is conditioned to previous year fox abundance. Furthermore, our modelled populations are not stationary, which makes the use of an AR model problematic. We thus

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suggest that a combination of AM and AEM models is the best approach, in selecting first a no-trend confounder (weather) variable with AM, and then use AEM to estimate the effect of fox. This happened to work well for partridge and hare, but less for rabbits, because AEM was not able to model the wave-like long-term fluctuations in these data and therefore might give misleading results on the effect of the fox on rabbit.

The interpretation of the trend variables is more difficult. In AEM and ARM we include a linear trend variable (year T) and an indicator variable (crash C), which models the abrupt change, because the observed data (see Figs. 2-4) of the prey populations indicate a clear population crash in 1978 and 1979. Spittler (1987) already analysed this phenomenon and concluded that harsh winters were responsible for this crash. However, our analyses suggest that winter weather does not actually explain this crash. We have no alternative explanation. In addition, hare and rabbit recovered more or less from this crash within a few years, but partridge did not. Hares do not have very specific habitat requirements, but prefer open agricultural areas (Pegel 1986), rabbits are limited to warm areas with sandy soil, and partridges live almost exclusively in agricultural fields (Pegel 1987). We suggest that after the collapses of 1978 and 1979, larger populations were better able to recover, whereas small populations were not. As hare and rabbit were not only present in agricultural areas, populations living in more forested areas were still healthy and could colonise empty habitats, which was not the case for partridges, because many populations were small and fairly isolated. The negative population trend was obvious before the crash, but after the crash even the larger surviving populations showed a negative trend, indicating that recolonisation of many empty patches did not happen in partridges.

The long-term negative trend in the partridge and hare dynamic (see Figs. 2 and 3) probably results from major changes in the cultivation and management of agricultural areas. Field sizes have become larger, and the use of machines have prevailed at the expense of manual labour (Pegel 1986, 1987). From 1971 to 1990 the area per farm linearly increased by 0,3 ha per year ($R^2 = 0.99$; Federal Statistical Office 2007). We suggest that the long-term hare and partridge population decline is due to change in agricultural management, as was suggested mainly in the UK (Benton et al. 2002, Vaughan et al. 2003, Gates & Donald 2000, Krebs et al. 1999, Gillings & Fuller 1998, Reynolds & Tapper 1995) but seldom demonstrated (see Robinson et al. 2001, Dingerkus & Montgomery 2002, Chamberlain & Fuller 2000, 2001, Donald et al. 2000, Chamberlain et al. 2000, Siriwardena et al. 1998).

Conclusion

Both partridge and hare are red-listed in Germany, but nevertheless are still hunted. Due to the tradition of sustainable hunting and the long leasing periods of the hunting units, hunting might not have a strong influence on their population dynamics. Following our results, we do not expect a major impact by banning hunting on these two species. In addition, given that weather effects cannot be managed, we suggest that management should focus on the long-term trend as well as the fox population size. Although the low impact of hunting seems to be true for the fox as well, the proposal of a stronger hunting pressure on the fox

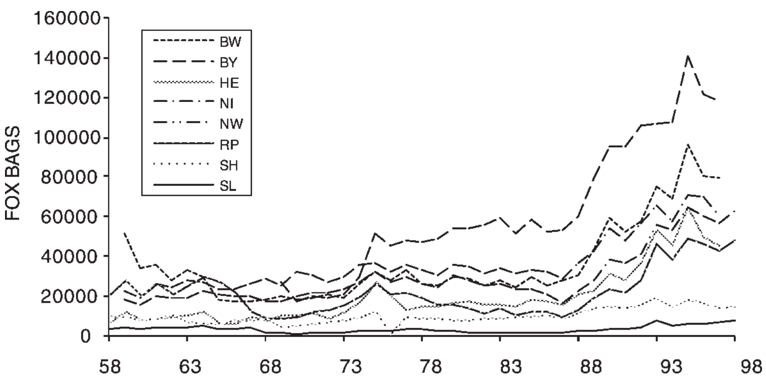

Figure 5. Bag records of foxes in the eight West German provinces. The significant increase after the vaccination against rabies (1987) is obvious.

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population is a major argument between conservationists and hunters' associations (Fig. 5). In our models however, the influence of the fox appears to be much smaller than that of the long-term trend. So, even if the hunters would be able to significantly reduce the fox population, we predict it would not result in a major increase of the small game populations. Based on a large three-year field study in France, Bro et al. (2000) found that the survival of partridge hens was the critical factor for the population trend and therefore concluded that predator control would be a helpful measure, though they did not test their conclusions. Alternatively, a change in the agricultural management would probably have more significant consequences on game species. Present-day policy of the European Union and Germany goes in the direction of a combination of economical oriented agriculture and an improving of the biodiversity in these landscapes. Based on our results this way seems much more promising than the focus on a reduction of the fox population.

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