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ORIGINAL PAPER

Influence of weather factors on population dynamics of two lagomorph species based on hunting bag records

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Abstract Weather conditions can have a significant influence on short-term fluctuations of animal populations. In our study, which is based on time series of hunting bag records of up to 28 years from 26 counties of The Netherlands and Germany, we investigated the impact of different weather variables on annual counts of European rabbits (*Oryctolagus cuniculus*) and European hares (*Lepus europaeus*). Overall, the long-term dynamics of both species could be described by higher-order polynomials. On a smaller time scale, the number of European hares shot was lower in years with higher amounts of precipitation during late summer/autumn, and the number of European rabbits shot was lower in years with high precipitation in spring of the respective year. We suggest that rainy weather conditions might have lowered the survival of young rabbits in spring and might have generally facilitated the outbreak or spread of diseases in rabbits as well as in hares, specifically in autumn. In addition, the results showed a time-delayed, interactive effect between precipitation in spring and winter weather on European rabbit dynamics: rabbit numbers were limited by low temperatures of the prior winter season, but only when precipitation was high during spring of the previous year. The latter result might be explained by the lowering effects of rainy spring weather on the body condition of the animals, leading to higher sensitivity to harsh winter conditions. In conclusion, our study provides evidence for the impact of weather conditions on the population dynamics of both study species and particularly highlights complex interactions between the prevailing weather conditions during different seasons in the European rabbit.

Keywords European hare · European rabbit · *Lepus europaeus* · *Oryctolagus cuniculus* · Precipitation · Temperature

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Introduction

The question of which factors are involved in shaping the dynamics of animal populations is certainly one of the major issues in population ecology. Next to density-dependent processes, there is a large body of evidence that variation in climate and weather can significantly affect vital rates and thus can be decisive for changes in density in many populations (e.g. Stenseth 1999; Aars and Ims 2002; Saether et al. 2007). For example, weather effects, i.e. stochastic variation in parameters such as temperature and rainfall among or within years, have been reported to influence body condition, survival and reproduction in many mammalian species (small- and medium-sized mammals: Van Vuren and Armitage 1991; Fichet-Calvet et al. 1999; large mammals: Loison et al. 1999; Delgiudice et al. 1990). Such weather effects are often complex and have the potential to interact on multiple levels. For example, the effect of one weather factor on an organism can intensify the effect of another—for example, in the combinations of low temperature with rain and wetness or low temperature and wind (Seltmann et al. 2009; Mercer 1998). Furthermore, the effects of weather conditions that an animal experiences during different seasons or developmental stages might interact. For example, a study on European rabbits (*Oryctolagus cuniculus*) in Germany showed that individuals that experienced high amounts of rain during their early post-weaning life showed comparatively lower growth rates until the end of their first vegetation period. Later on, such animals suffering from stunted growth had a lower chance to survive during the winter season, in particular, when winter temperatures were low (Rödel et al. 2004a).

Various mechanisms can underlie apparent correlations between weather and changes in population size. On the one hand, weather effects have the potential to directly influence health, survival and body condition of the animals, e.g. by increasing the costs of thermoregulation or by thermal stress (Seltmann et al. 2009; Rödel et al. 2009a; Myers et al. 1981). On the other hand, weather effects might act indirectly. For example, low temperatures and snow cover can limit the quality of or access to food (Rödel 2005; Crawley 1983). Moreover, adverse or extreme weather conditions, such as persistent rain and wetness, can favour the spread of diseases (O'Connor et al. 2006; Stromberg 1997), thus affecting health and survival. Furthermore, unfavourable weather conditions can increase the animals' chance of being predated by lowering their body condition or by directly hampering their mobility—for example, by high snow depth (Cederlund 1982; Mech et al. 1987). Knowledge of such potential mechanisms, i.e. of how different weather conditions can affect the health and survival of a species, might help to conduct specific and targeted studies in order to assess the effects of different weather variables on population dynamics by considering potentially sensitive periods of an animal's life history.

In the present study, we focus on two lagomorphs, the European rabbit and the European hare (*Lepus europaeus*). Both species underwent a decline in Europe during the last decades (Smith and Boyer 2006; Smith and Johnston 2008). In the European rabbit, this decline started in Europe in the 1950s and was certainly in large part due to the outbreak and spread of two viral diseases, myxomatosis and rabbit haemorrhagic disease (RHD), the latter spreading in Europe (including Germany) in the late 1980s (Moreno et al. 2007; Delibes-Mateos et al. 2009) and arriving in The Netherlands in the early 1990s (Drees et al. 2009; van Strien et al. 2011). A strong decline from the 1960s and 1970s of the last century onwards was also observed in European hares (Mary and Trouvilliez 1995; Smith and Johnston 2008)—the factors causing this population trend appear to be more complex than in the European rabbit (Smith et al. 2005). It has been widely accepted that habitat changes caused by the intensification of agriculture are a key factor in driving the long-term decline in this species (Edwards et al. 2000; Smith et al. 2005; Santilli and Galardi 2006; Zellweger-Fischer et al. 2011). However, other factors such as diseases (Lamarque et al. 1996), predators (Reynolds and Tapper 1995; Schmidt et al. 2004; Knauer et al. 2010), landscape fragmentation (Roedenbeck and Voser 2008) and climatic conditions (Kilias and Ackermann 2001; Jennings et al. 2006; Spittler 1997) are also reported to play a role in shaping European hare population trends.

In both species, several mechanisms of how weather and climate can affect vital rates and population dynamics are known from experimental as well as observational studies in the wild or in the lab. In particular in European rabbits, such studies have proven strong effects of weather conditions on individual growth, health, survival and reproduction during different life stages (reviewed Tablado et al. (2009); Rödel and von Holst 2008). During early juvenile life, young rabbits and hares are particularly sensitive to low temperatures and wetness, leading to increased metabolic costs with potential implications for their health and survival (Hackländer et al. 2002; Rödel et al. 2009a; Seltmann et al. 2009). In addition, wetness in spring and early summer has been shown to limit growth and body condition in young rabbits (Rödel et al. 2004a). Later in the season, low winter temperatures are reported to limit population densities (Bijlsma 2004), in particular by lowering the survival probability of first-season animals (Rödel et al. 2004a; Rödel and von Holst 2008). In accordance, a study on survival rates of yearling European hares conducted at the northern edge of this species' distribution revealed lower survival rates during harsh winters (Marboutin and Hansen 1998).

In a comparative approach based on long-term data sets of European rabbits and European hares in The Netherlands and in Germany, we explored the effects of weather conditions (ambient temperature, precipitation) during different times of the year on population dynamics. As direct and long-term population counts in these species are rare and only available on a local scale, we use time series of hunting bag data as proxy for changes in population size. Based on our assumptions on potential mechanisms as stated earlier, we focus on weather conditions during spring, i.e. around the onset of the breeding season, during summer/autumn when population densities are usually high and diseases are known to spread in populations of both species (Lenghaus et al. 2001; Brooks 1986) and during winter when the availability of high-quality food is low (Reichlin et al. 2006; Rödel 2005; Rödel et al. 2004b). Correcting for long-term population trends, we (1) considered short-term effects of different weather variables on the population dynamics in both species in our models. We also tested potentially relevant interactions among weather variables (2) within and (3) across different seasons. In particular, we predict (a) that high amounts of precipitation could enhance the detrimental effects of low temperatures, e.g. during winter or spring, (b) that adverse weather conditions during the vegetation period might have the potential to increase the susceptibility of animals to harsh conditions during the subsequent winter, or vice versa, and (c) that low temperatures during the winter might increase the susceptibility of the animals to harsh conditions (low temperatures, high levels of precipitation) during the early vegetation period.

Materials and methods

Study period and sample sizes

For this study, hunting bags (both species) from The Netherlands were available over a period from 1980 to 2007 for 11 counties. Data from Germany were available from 1982 to 2007 for the counties of former West Germany (n=10) and from 1987 to 2007 for the counties of the former German Democratic Republic (n=5). We did not consider the county of Berlin (Germany), where hunting of European hares is prohibited by law. Given some missing values for some years in particular counties, this resulted in a total number of N=661 annual hunting bag records of European rabbits and European hares from 26 different counties.

Hunting bags were calculated as the summed up animal numbers per annual hunting season (see Fig. 1). Data from The Netherlands were provided by the Koninklijke Nederlandse Jagersvereniging (Royal Dutch Hunter Association, KNJV), which validated and stored this information. Hunting bag records from Germany were obtained from the homepage of the Deutscher Jagdschutz Verband at http://www.jagd-online.de.

Weather data

Data on precipitation and temperature for The Netherlands were available from the Royal National Meteorological Institute (www.knmi.nl). Data for Germany were available from the Deutscher Wetterdienst (www.dwd.de). For analysis, we averaged the freely available weather data from all meteorological stations (in total, n=54) within each county. On average, data from 2.1±0.3 SE (min, 1; max, 8) stations per county were used. We excluded data from stations situated higher that 1,000 m asl since the abundance of the two study species in such regions is low. We used averaged data per county since we only had access to summed-up annual hunting bags from each county but not to detailed information about the local origin of the hunting bag records on a finer scale.

The weather variables repeatedly measured during the years of study differed significantly among counties with respect to temperature in spring ($F_{25,636}$=12.26, p<0.001), late summer/autumn ($F_{25,636}$=9.13, p<0.001) and winter ($F_{25,636}$=12.29, p<0.001) and precipitation in spring ($F_{25,636}$=5.11, p<0.001), late summer/autumn ($F_{25,636}$=7.55, p<0.001) and winter ($F_{25,636}$=7.13, p<0.001). Furthermore, the average range spans (max–min) of the different weather variables provided by the different meteorological stations within different counties were lower than the range spans calculated among the averaged values of the counties. Exemplarily shown here for the year 2000, this could be observed with respect to temperatures in spring (averaged $\Delta T_{\text{within counties}}$=1.1 °C±0.2 SE; $\Delta T_{\text{among counties}}$=3.2 °C), late summer/autumn (averaged $\Delta T_{\text{within counties}}$=1.0 °C±0.2 SE; $\Delta T_{\text{among counties}}$=3.1 °C) and winter (averaged $\Delta T_{\text{within counties}}$=1.4 °C±0.2 SE; $\Delta T_{\text{among counties}}$=4.7 °C) and also with respect to precipitation in spring (averaged $\Delta P_{\text{within counties}}$=22.0 mm/month±6.9 SE; $\Delta P_{\text{among counties}}$=59.7 mm/month), late summer/autumn (averaged $\Delta P_{\text{within counties}}$=19.5 mm/month±3.6 SE; $\Delta P_{\text{among counties}}$=49.4 mm/month) and winter (averaged $\Delta P_{\text{within counties}}$=24.6 mm/month±6.0 SE; $\Delta P_{\text{among counties}}$=70.4 mm/month).

Model outline

The aim of the paper was to test the effects of different weather factors on population dynamics of rabbits and hares as assessed by within-county variation of hunting bags. For analysis, we z-transformed the hunting bags within each county, i.e. the number of animals shot per area where hunting was permitted. For this, the mean number of animals shot in each county was set to zero and the deviation from the mean (given as the number of standard deviations within each county) was calculated for every year. For example, a value of 2 (see Fig. 2) means that the hunting bag in this particular year and county was two standard deviations higher with respect to the mean of all hunting bag records from this particular county, averaged over the whole study period. This was done in order to avoid biases caused by the very high differences in hare densities among the different counties.

Weather variables were calculated by first averaging the values of all available weather stations per county (see above) and then by calculating values for each time window as given in Fig. 1. Temperatures represent averaged daily temperature means. Daily measurements of precipitation were summed up over the respective time window and, in order to scale them to a comparable unit, are given as millimetre precipitation per week. Note that we repeated our analyses using data on minimum and maximum temperatures and amounts of precipitation of each time window and obtained similar results.

Statistical analysis

Analyses were done with multivariate models (linear mixed effects models) using the statistic software R version 2.10.1 (R Development Core Team 2011). For this, we used lme4

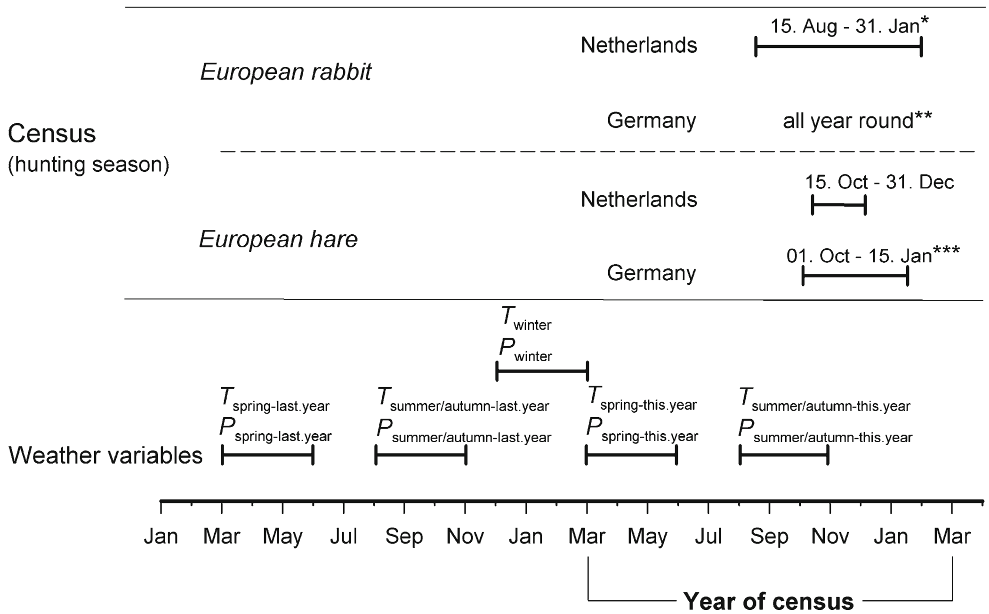

Fig. 1 Schema of the variables used for statistical modelling. *Asterisk*, in case of crop damage, rabbits in the Netherlands can be shot any time during the year. *Two asterisks*, rabbits in Germany can be shot all year round, but in some counties breeding animals must not be hunted during the reproductive season (*three asterisks*). The hunting season of European hares differs slightly among counties in Germany. Hunting of European hares is prohibited in Berlin; however, this county was excluded from the analysis

package (Bates 2005). County was included as a random factor in order to adjust for the repeated measurements. The programme R does not directly provide *p*-values for mixed-effects models calculated with lme4. Thus, for the final models, we extracted the *p*-values and also the parameter estimates by Markov-chain Monte Carlo sampling based on 10,000 simulation runs (Baayen et al. 2008).

For model selection, we first stepwise increased complexity by including higher-order polynomials (including their interactions with the factor country) in order to capture the long-term dynamics of the time series of both species. We stopped when the inclusion of a higher-order polynomial exceeded the level of significance α=0.05 using likelihood ratio tests (Faraway 2006). We then included all weather variables (Fig. 1) and their interactions according to our a priori hypotheses. We considered all two-way interactions between temperature and precipitation within the same season and between weather conditions during the vegetation period and conditions during the following winter. Higher-level interactions were not considered in order to avoid excessive overparameterisation of the models. We also considered optimum curves (quadratic effects) of precipitation in order to test the hypothesis whether medium amounts of precipitation were most advantageous for survival and reproduction of rabbits and hares (Tablado et al. 2012). However, such effects were not significant. We then stepwise reduced all predictors and interaction terms to those with p>0.10. The significance of all higher-order polynomials were re-checked for the final models. In addition, we calculated Nagelkerke's pseudo R^2 based on maximum likelihood estimates (Nagelkerke 1991). This was done for the final models including all significant predictor variables and can be interpreted as the proportion of explained variance.

Normality of the model residuals of the global models as well as of the final models was assured by visually checking normal probability plots and by performing Shapiro–Wilk tests, and we assured the homogeneity of variances and goodness of fit by plotting residuals versus fitted values (Faraway 2006). We also checked for multicollinearities among the different weather variables used in the models. The variation inflation factors calculated for all predictor variables used in the models for rabbits as well as for hares were always smaller than 3, indicating no notable problems with multi-collinearities (Fox and Monette 1992).

Results

European rabbits

Annual variation in European rabbit hunting bags in Germany and The Netherlands was significantly described by a fifth-order polynomial, including an interaction between year and country. Generally, the time course in this species showed a clear decreasing tendency (Fig. 2a).

Given the detected long-term trends in rabbits hunting bags, the number of rabbits shot was lower when precipitation in spring (March to end of May) of the current year was high (Table 1; Fig. 3b). In addition, our results support the longer-term effects of precipitation in spring on rabbit dynamics, but these have a very different effect in interaction with the temperature conditions of the previous winter. The number of rabbits shot was lower after harsh winters with low temperatures but only when the precipitation in spring of the previous year was high (Table 1; Fig. 3a). The variation explained by the final model

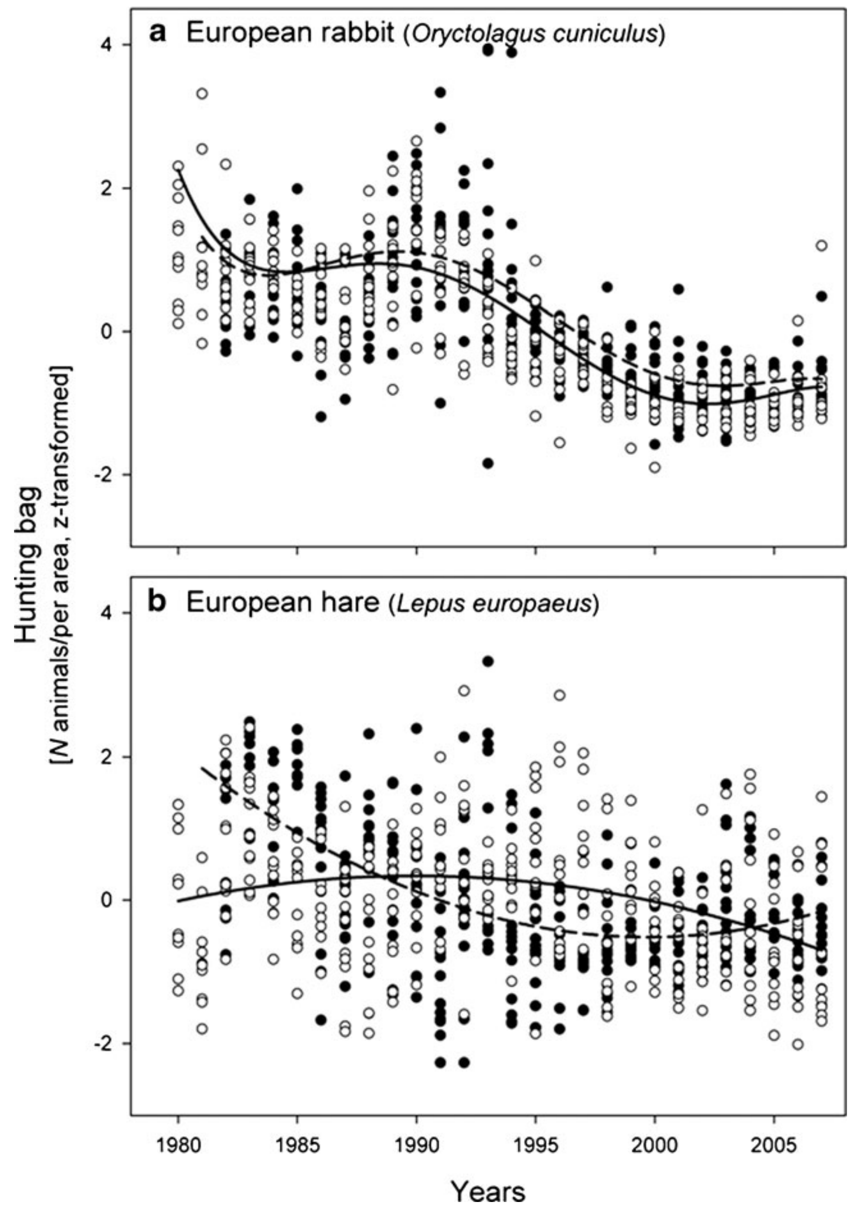

Fig. 2 Time series of the z-transformed hunting bag data (per county) of **a** European rabbits and **b** European hares in the Netherlands (*open circles*, *solid regression line*) and Germany (*filled circles*, *dashed regression line*). For calculation of the regression lines (based on the parameter estimates of the models given in Table 1), all other predictor variables of the respective models were set constant to their means

including all significant predictor variables was $R_{\mathrm{Nagelkerke}}{}^2$= 0.659.

European hares

The temporal variation in European hares shot was significantly explained by a second-order polynomial with a general tendency of a slight decrease during the period of study. For the hare also, the model included an interaction between year and country with a converse U-shaped pattern in the two countries (Fig. 2b). However, the variation explained by the model was rather moderate with $R_{\mathrm{Nagelkerke}}{}^2$=0.247.

The number of hares shot was lower in years with more precipitation in autumn/late summer, i.e. from August until end of October (Table 1; Fig. 3c). Other weather variables or interactions among them were not significant.

Discussion

Our results provide evidence for the impact of weather conditions on the population dynamics of both study species as assessed by hunting bag records. The number of European hares shot was lower in years with higher amounts of precipitation during late summer/autumn, and the number of European rabbits was lower in years with high precipitation in spring of the respective year. In addition, we found support for our third hypothesis concerning potential interactions among weather conditions between different

Table 1 Linear mixed models on the effects of different weather variables on the z-transformed number of (a) European rabbits and (b) European hares shot in 26 different counties (*N* per hunting area and year) of the Netherlands (1980–2007) and Germany (1982–2007). County was included as a random factor. *P*-values and parameter estimates (including 95 % confidence intervals) were calculated by 10,000 Markov-chain Monte Carlo simulation runs. Non-significant interactions and higher-order polynomials ($p_{MCMC} > 0.10$) were omitted before re-calculating the models. A further backward elimination of non-significant predictors (not shown) did not lead to different results than those obtained by calculating *p*-values for the models including all effects shown below

	Predictor variables	Estimate	95 % lower	95 % upper	p_{MCMC}
Rabbit	Country	0.386	−0.042	0.816	0.09
	T_{winter}	−0.077	−0.176	0.018	0.11
	P_{winter}	−0.001	−0.004	0.003	0.75
	$T_{spring—this.year}$	0.038	−0.020	0.096	0.20
	$T_{spring—last.year}$	0.023	−0.027	0.074	0.37
	$P_{spring—this.year}$	−0.004	−0.007	−0.001	0.011
	$P_{spring—last.year}$	−0.006	−0.011	−0.001	0.013
	$P_{summer/autumn—this.year}$	0.001	−0.002	0.003	0.83
	$P_{summer/autumn—last.year}$	−0.001	−0.004	0.001	0.30
	$T_{spring—last.year} \times T_{winter}$	0.002	0.001	0.004	0.016
	Year+year^2+year^3+year^4+year^5				<0.001
	(Year+year^2) × country				0.026
Hare	Country	−2.456	−3.038	−1.862	<0.001
	T_{winter}	−0.001	−0.053	0.053	0.98
	P_{winter}	0.001	−0.004	0.004	0.97
	$T_{spring—this.year}$	0.017	−0.064	0.099	0.70
	$T_{spring—last.year}$	−0.005	−0.075	0.063	0.89
	$P_{spring—this.year}$	−0.001	−0.005	0.004	0.84
	$P_{spring—last.year}$	−0.001	−0.004	0.005	0.95
	$P_{summer/autumn—this.year}$	−0.005	−0.008	−0.001	0.004
	$P_{summer/autumn—last.year}$	−0.002	−0.005	0.002	0.31
	Year+year^2				<0.001
	(Year+year^2) × country				<0.001

seasons: There was a time-delayed, interactive effect between precipitation in spring and winter weather on European rabbit dynamics. Rabbit numbers were limited by low temperatures of the prior winter season, but only when precipitation during spring of the previous year was high.

These weather effects were detectable when “stripping off” the long-term trends in rabbit and hare hunting bags. Both species showed the tendency of a general decrease in numbers over the study period (Fig. 2). This trend showed a rather high variation in the hare with quite different patterns

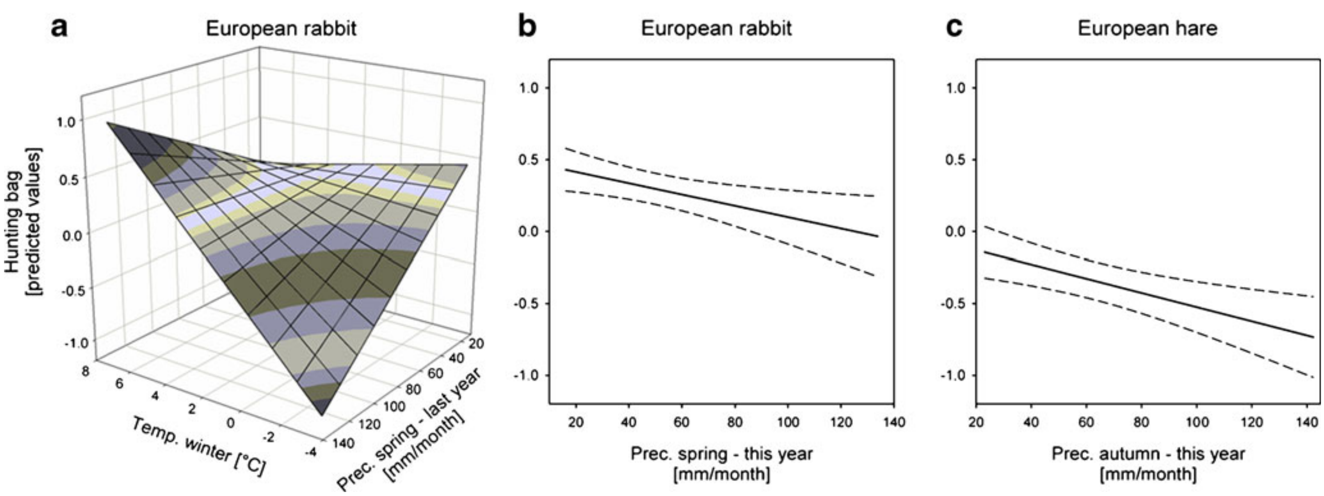

Fig. 3 Model graphs on the effects of different weather variables on the z-transformed hunting bag of European rabbits (**a**, **b**) and European hares (**c**) based on the results of the statistical models given in Table 1. For calculation of the predicted values, all other predictor variables of the respective models were set constant to their means. The *dashed lines* in **b** and **c** show the 95 % confidence intervals of the regression lines

in the two countries studied here, whereas the z-transformed dynamics of rabbits showed a clear and distinct pattern. This might be well explained by the fact that European rabbit dynamics during the last decades was mainly driven by the diseases myxomatosis and RHD (Moreno et al. 2007; Delibes-Mateos et al. 2009) and obviously in a very similar pattern within the different counties of The Netherlands and Germany. Long-term dynamics of the European hare appeared more diffuse, including a much higher variation among the different counties, pointing towards the complex interaction of various factors to be involved here (Smith et al. 2005).

The interactive effect of the amount of precipitation in spring and temperature conditions of the following winter season on European rabbit numbers confirms our hypothesis, mainly inferred from the results of our field enclosure study on European rabbits (see Rödel et al. 2004a). In that study, it has been proposed that young animals, which were exposed to a higher amount of rain, might have to carry higher costs for thermoregulation (cf. Seltmann et al. 2009) and might have a higher chance to get infected with diseases. In particular, rain and humidity are known to favour the spread of endoparasites (e.g. nematodes and coccidia) by increasing the persistence of infective stages outside the body of the host (O'Connor et al. 2006; Stromberg 1997). Especially in younger animals, such infections cause mortality (Broekhuizen and Mulder 1983), but these mechanisms can also together result in lowering the body condition of the animals and thus drive the negative correlation between rainy weather conditions and growth (Rödel and von Holst 2008). In turn, such animals suffering from stunted growth and from high endoparasite burden will then be more susceptible to low winter temperatures since disease-induced mortality can be enhanced by cold stress (Kelley 1980). Furthermore, low winter temperatures do not only have the potential to directly act on body condition and survival of the animals by means of increasing thermal stress and the costs of thermoregulation but can also be considered as a proxy of availability or quality of food (Rödel 2005). We think that it is most likely that these mechanisms were important drivers of the here observed limiting and interacting effects of spring precipitation and winter temperature conditions on rabbit hunting bags.

Nevertheless, other explanations not mutually exclusive might be considered. For example, effects of predation may also contribute in shaping the weather-driven dynamics, as it was apparent in European rabbits. Predators, such as foxes and mustelids, might switch to rabbits as alternative prey to a higher extent when small rodents' densities are low due to cold winters or high amounts of rain in spring, causing flooding and thus high mortality rates in mice and voles. The limiting effects of rain and flooding of breeding burrows on offspring survival are also well known in the European rabbit (Palomares 2003; Rödel et al. 2009a) and might explain the direct negative effect of spring precipitation on rabbit numbers. Another possible explanation for limiting effects of low winter temperatures on rabbit numbers rests on effects on the onset of the annual reproductive season. For example, a delay in the onset of breeding after harsh winters has been reported for several lagomorph species (Rogowitz 1992; Wright and Conaway 1961; European rabbit: Bell and Webb 1991; Rödel et al. 2005). A later onset of breeding limits the number of progeny born early in the season, and early born offspring (at least the ones surviving the early juvenile period) usually have higher chances to survive during the first winter than individuals born later since they enjoy a longer time during the vegetation period for growth prior to the winter (Kraus et al. 2005; Feder et al. 2008; European rabbits: Rödel et al. 2009b). Surely, day length also plays a role in triggering the onset of breeding in the European rabbit (Hudson et al. 1994), but such effects are strongly modified by environmental conditions. On the other hand, and in accordance to our results, the influence of weather conditions on the onset of breeding in the European hare appears to be low, whereas triggering by day length is of significant importance (Frylestam 1980)—although the length of the breeding season has been reported to be extended by mild autumn conditions (Hewson and Taylor 1975).

In our study, weather effects on European hares were only apparent in summer/autumn, indicating the limiting effects of high amounts of rain on hare densities at this time of the year. This result fits very well to the findings of other reports on European hares showing major influences of weather conditions particularly during the summer months (Nyenhuis 1995) and pointing towards a higher importance of rainy weather conditions in comparison to temperatures (Smith et al. 2005; van Wieren et al. 2006). We propose that also here, a higher rate of infection by diseases in areas and years with rainy and wet weather conditions might be the main driver for the observed precipitation effects in summer and autumn. Higher metabolic costs in wet, unfavourable environments, in particular in young animals (Seltmann et al. 2009; Hackländer et al. 2002), may restrict the allocation of energy to other physiological functions such as to the animals' immune defence (Muehlenbein et al. 2010), thus favouring the outbreak of diseases. On the other hand, it cannot be fully ruled out that there might be also a bias caused by the limiting effects of harsh weather conditions (i.e. high precipitation) on hunting effort, thus potentially affecting hunting bag records.

When comparing both study species, there were apparently stronger effects of weather on rabbit than on hare population dynamics (a) by means of the higher number of correlations observed on different levels and (b) due to the higher effect sizes of the observed effects. In the rabbit, the estimated effect size of the interaction model varies by about

1 standard deviation around the population average (Fig. 3a), whereas the slope of the regression line in the hare only varies by around 0.5 standard deviation (Fig. 3c). At first sight, this seems surprising because, in comparison to the precocial hare, rabbits are born and raised in the shelter of a breeding burrows dug by the mother. However, European hares might be better adapted to the climatic conditions of Central Europe's temperate zone habitats (cf. Hackländer et al. 2011) than the European rabbit, which mainly evolved in the climate of the Iberian Peninsular and of which Germany and The Netherlands are in the most northern part of its range (Thompson and King 1994). Furthermore, it remains open whether the here observed effects influence the two study species in a similar way in other climate zones within their distribution range.

It has to be noted that the methodological approach of our study may affect the interpretation of the results. First, drawing conclusions on population dynamics based on hunting bags has been often criticised, and hunting itself might directly affect the population dynamics of a species (Besnarda et al. 2010; Willebrand et al. 2011; Williams et al. 2007). However, some confirmation on the appropriateness of the use of hunting bags as an estimate for population biology studies comes from the fact that hare and rabbit hunting bags of the Netherlands correlate strongly and positively with the (10 years shorter) time series of data collected by systematic visual daylight counts (R^2=0.90 for hare and R^2=0.82 for rabbit; JJAD, unpublished data). Second, we are aware that variation in weather conditions on a local scale was only moderately captured by our method of averaging data from several meteorological stations per county. Thus, we conclude that this study's negative, non-significant results should be interpreted with some caution. We cannot deny that, e.g., winter weather effects may well be involved in the dynamics of European hares (see Marboutin and Hansen (1998); Smith et al. 2005; Tkadlec et al. 2006) as we might have overseen smaller effects with our conservative approach. Therefore, we would have rather underestimated than overestimated the effects of weather conditions on the population dynamics of the two species studied. As a consequence, we propose that the positive results of our study are of significant importance since we managed to detect them despite our conservative approach.

In conclusion, the study clearly shows the impact of weather factors on the dynamics of the two species studied. In particular, the results highlight the importance of the time-delayed interaction between different weather variables acting on the animals during different seasons, and we propose that such effects may also well occur in species other than the European rabbit. Thus, our findings might have important implications for the understanding of the effects of density-independent factors on animal populations and may help to predict potential consequences of climate change.

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