

The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland)

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Abstract

During the last two decades, populations of the wild boar *Sus scrofa* in Europe have increased considerably and the species has spread into new areas over the entire continent. Because of the animals' impact on agriculture, livestock and biodiversity, and the resulting necessity of realistic management practices, we were interested in the key environmental factors responsible for this remarkable development. The study was based on data from the canton Thurgau, a region in north-eastern Switzerland. We used data on damage and hunting success to calculate a population density index and related it to eight variables describing ecological conditions, demography and hunting pressure (measured by the number of hunters) over a 25-year period. The analysis shows that the population increase correlates with higher than average winter and spring temperatures and improved food supply through more mast years and an increase in the area of maize cultivation. While favourable temperature conditions mainly reduce juvenile mortality, enhanced food availability is likely to boost reproductive success through younger age at first reproduction, larger litter size and earlier onset of oestrus within a season. Given this link between food and reproduction, supplemental feeding, a management practice recommended and very common all over Europe, should be reconsidered.

Key words: food availability, supplementary feeding, climate, population density, wild boar

INTRODUCTION

Invasion of exotic species and spread of native species into new habitats are natural biological phenomena that have always changed ecological communities. However, due to human activities, such as alterations of the landscape and intentional or inadvertent transport of plants, animals and microbes, the rate at which invasions occur is now many orders of magnitude greater than the natural rate and may pose the most serious threat to ecosystems (Huston, 1994). Among the effects of invasion are increased predation pressure, competitive displacement of native by exotic species, hybridization and spread of diseases, all of which will alter the dynamic equilibrium of communities and change species compositions. This can reduce biodiversity (for overviews see Primack, 1993; Mooney & Hobbs, 2000; Pullin, 2002), although in some cases it may also increase it (Welander, 2000*a,b*). In addition to the ecological effects in natural environments, invasions and spread into areas where species have been previously absent may cause major economic losses in agriculture, animal husbandry and forestry (Pimentel *et al.*, 2001).

A typical example for an animal having such a widespread impact on natural and anthropogenic habitats is the wild boar *Sus scrofa*, the fifth largest ungulate species in Europe (Niethammer & Krapp, 1986). Although today it ranges over the whole continent, it is known from historical sources that populations have fluctuated strongly in the past and that, in some regions, the species was even absent for decades (e.g. Briedermann, 1990; Jedrzejewska *et al.*, 1997). Since the 1980s, wild boar populations have increased remarkably and almost simultaneously over the entire European range. They have also spread naturally into new areas or were accidentally reintroduced through individuals escaping from farms (Macdonald, 2001; Goulding *et al.*, 2003). In some regions numbers killed by hunting increased 10-fold within only a few years (Saez-Royuela & Telleria, 1986). This dramatic increase in hunting numbers within a few years and over the entire European range cannot be explained simply by more intense or more successful hunting. In our study area the number of hunters even decreased over time (Fig. 1*a*). Hence, some major changes of important environmental factors must have occurred, that 'boosted' wild boar population numbers in Europe.

Reaching high population densities within a very short time period is typical for *r*-selected species. Compared

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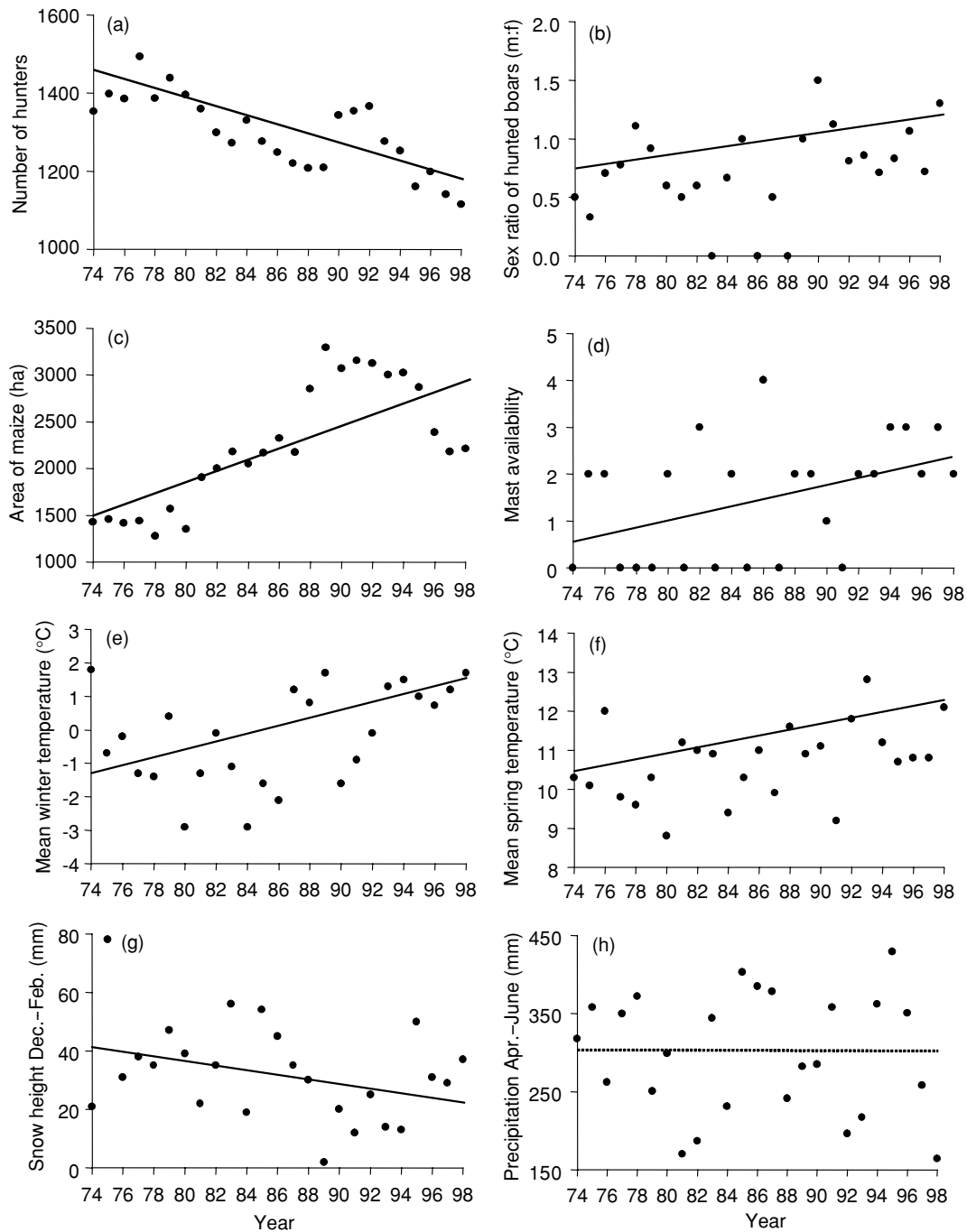


Fig. 1. Development of eight variables (a–h) related to wild boar population dynamics between 1974 and 1998 in the canton Thurgau, Switzerland. Regression lines show the general tendency during the years. Sex ratio, males:females.

to other ungulate species, the wild boar shows several attributes that are typical for *r*-strategists. It has a high ecological plasticity, a very opportunistic feeding behaviour and by far the highest reproductive potential of all ungulate species world-wide in relation to body mass (Boitani *et al.*, 1995; Taylor *et al.*, 1998).

The increase in wild boar numbers in Europe has widespread ecological and economical consequences. In the forest, their natural primary habitat, the population explosion affects plant diversity, vegetation composition and regeneration patterns (Welandner, 2000a,b; Hone,

2002; Kuiters & Slim, 2002). In cultivated areas, the strong population growth causes damage in crop fields and transmission of the swine fever virus and other diseases from wild boar to domestic animals (Geisser, 1998, 2000). This calls for a carefully planned wild boar management plan to reduce the problems. We, therefore, were interested to find key environmental factors that influence wild boar population densities. Our analysis is based on a long-term data set from a region in Switzerland that, until recently, had not been a traditional wild boar habitat. However, following the spread of the species, population size started

to increase in the early 1990s causing increasing problems in agriculture (Geisser & Reyer, 2004).

METHODS

Study area

For our analysis we used data from a 25-year period of the canton Thurgau in the north-east of Switzerland (278°N, 720°E). A canton in Switzerland is a political designation, comparable to a state in the U.S.A. or a county in the U.K. The canton Thurgau is roughly 86 000 ha. Elevation ranges from 400 to 1000 m. The topography is mostly gentle, only the southern areas are of sub-alpine character. The climate is continental with an average annual precipitation between 900 and 1300 mm and average temperatures in January and July of -0.9°C and 18.3°C , respectively, within the study period (1974–1998). Forests, mostly used for wood production, cover 21% of the land area. The forest structure is very patchy and forest areas larger than 250 ha are rare. Agricultural land covers 55% of the area. The agricultural areas are mainly composed of pasture (59% of total agricultural area), wheat (11%) and maize (10%). Natural predators of wild boar are absent, but wild boar hunting is practised throughout the year. Hunters are organized in local hunting groups, where each group leases a hunting area for 8 years (called *Reviersystem*). Supplementary food such as maize, fruits, old bread or industrial food pellets are provided at artificial feeding places throughout the year to bait wild boar for easier shooting or to distract the animals from crop fields. Hunting areas have, on average, 1.05 bait-sites per 100 ha of forest (Geisser, 2000). Immigration of wild boars from other populations was possible from adjacent regions in the west (canton Zurich, Switzerland) and in the north (Baden-Württemberg, Germany), but not from the north-east (where Lake Constance forms a natural barrier) and from the south where wild boars are so far absent.

Data and statistical analysis

Our analysis of the wild boar densities is based on data from 1974 to 1998. Because wild boar are very difficult to count directly (Jedrzejewska *et al.*, 1997) a composite density index was calculated by means of a principal component analysis (PCA) using 3 different data sets: hunting statistics; road kills; damage in agricultural land. The yearly number of damages was extracted from annual statistics kept by the government. Since 1974 the government of the canton Thurgau compensates farmers for wild boar damage, which is an incentive for the farmers to report damage. All damage reported to the Fish and Wildlife Service is assessed by a government agent and information, such as place and time of damage, damage size, type of damage and type of crop being damaged, are collected in a database.

Table 1. Independent variables tested for their potential effects on the population density of wild boar *Sus scrofa* from 1974 to 1998 in the canton Thurgau, Switzerland

Variable	Abbreviation
Hunting	
Number of hunters in the canton Thurgau	HUNT ^a
Demography	
Sex ratio among hunted wild boars (males:females)	SEXR ^b
Food	
Area of maize planted (ha)	MAIZE ^c
Mast availability ⁽¹⁾	MAST ^d
Temperature	
Winter temperature (= average temperature in December, January and February)	TEMPW ^e
Spring temperature (= average temperature in April, May and June)	TEMPS ^e
Precipitation	
mm Snow in December, January and February	SNOW ^e
mm Rain in April, May and June	RAIN ^e

⁽¹⁾ Fruit production of deciduous trees can vary considerably between different years. Years with high fruit production are called *mast years*. In mast years mast availability is high, meaning that food conditions for wild boars are very good. Data on mast availability are based on yearly estimates of forest rangers.

Data sources:

^a Hunting statistics of the Swiss Federal Section for Hunting and Game biology; BUWAL).

^b Hunting statistics of the canton Thurgau.

^c Department of Agriculture of the canton Thurgau.

^d Department of forestry of the canton Thurgau.

^e Meteo Swiss.

Eight variables, 2 describing hunting and demography and 6 quantifying ecological conditions, were available for each year of the study period. The 8 variables are described in Table 1 and their development between 1974 and 1998 is shown in Fig. 1. These variables influence the dynamics of ungulate populations in general (temperature and precipitation: Forchhammer *et al.*, 1998) or of wild boar in particular (number of hunters: Waithmann *et al.*, 1999; sex ratio: Stubbe, 1995; area of maize planted: Massei, Genov & Staines, 1996; mast availability: Jedrzejewska *et al.*, 1997). Other variables that are potentially important for understanding fluctuations in population density were either totally lacking (e.g. immigration rates from neighbouring areas), not available for every year of the study period (e.g. amount of supplemental food) or had previously been shown to have no effect. The latter is true for potential changes in food availability due to field protection with electric fences. In our study area, such fences had no effect, whatsoever, on wild boar feeding, measured by damage (Geisser & Reyer, 2004). Therefore, some variables were not or could not be included in the analyses.

Since the 6 ecological variables (winter and spring temperature, winter and spring precipitation, area of maize planted, mast availability) were likely to be correlated, a PCA with subsequent varimax rotation was performed to reduce them to a smaller number of independent factors

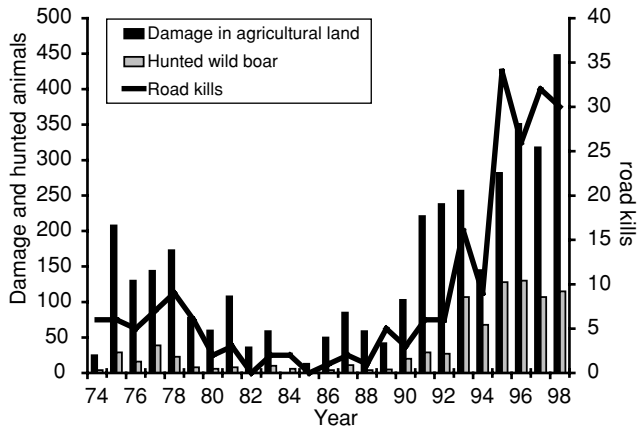


Fig. 2. Number of harvested wild boar *Sus scrofa*, road kills and damage in agricultural land between 1974 and 1998 in the canton Thurgau, Switzerland.

(Sokal & Rohlf, 1995). Following the recommendations of Aspey & Blankenship (1977) and Bauer (1986), for interpretation only factors with eigenvalues ≥ 1 were extracted (so called Kaiser criterion) and only factor loadings $\geq |0.45|$ were considered to be meaningful. In order to test what influences the population density of wild boar, the density-index was related to the 2 ecological factors resulting from the PCA and the 2 hunting variables (HUNT, SEXR) by means of a stepwise multiple regression analysis (SMRA) using the backwards procedure and a p -to-remove threshold of 0.10. Prior to analysis, HUNT and SEXR were $\ln(x + 0.1)$ transformed to achieve better approximation of a normal distribution. All statistical analyses were done with Systat 7.0 for Windows.

RESULTS

Fluctuation in population density

Hunting statistics, number of road kills and number of damage in agricultural land all indicate that the population density fluctuated greatly during the study period (Fig. 2). A first maximum was reached in the late 1970s. During the early 1980s, the density declined to almost zero, but thereafter rose again. The most marked increase occurred in the early 1990s. The number of animals killed by hunters, for instance, jumped from 30 in 1992 to more than 100 in 1993. Thereafter, the number remained above 100 in most years with a maximum of 130 animals killed by hunters in 1996. This strong increase in numbers of hunted boar cannot be the result of changes in hunting pressure because the number of active hunters decreased after 1992 (see Fig. 1a). Road kill and damage patterns differ in details from these hunting figures, but they generally show the same density pattern and are highly correlated with the number of hunted animals (both $r_s > 0.9$, both $P < 0.001$, $n = 25$). This clearly indicates that anthropogenic factors such as changes in the damage compensation system and

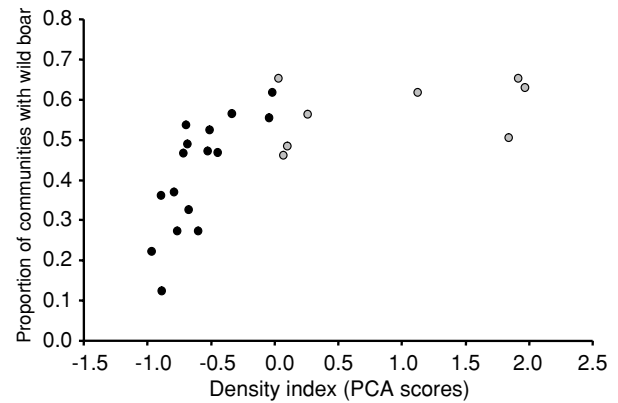


Fig. 3. Proportion of community districts inhabited by wild boar *Sus scrofa* between 1974 and 1998 in relation to the density index, expressed by factor scores from a principal component analysis (PCA) based on harvested wild boar, road kills and damage in agricultural land. Spread into new districts correlates positively when PCA scores are below zero (black circles), but ceases at scores above zero (open circles).

increasing road traffic cannot be held responsible for the observed fluctuations. For road kills, this is supported by the fact, that traffic increased continuously from 1973 to 1997, but number of kills decreased from the 1970s to the mid-1980s (Fig. 2).

The strong correlation between the three population measures is also confirmed by the PCA: all three variables have high positive loadings (≥ 0.946) on the same factor which accounts for 92.8% of the total variance. Hence, the scores of this factor provide an adequate measure for a density index. As this index increased, the number of communities where wild boar were present also went up, but then the range expansion came to an end (Fig. 3). Hence, additional animals probably increased the density in the already inhabited areas rather than caused spread into new areas.

The role of environmental conditions

A further PCA reduced the six ecological variables (MAIZE, MAST, TEMPW, TEMPS, SNOW and RAIN) to two factors. They accounted for 58.7% of the total variation (Table 2). Factor 1 is positively associated with the area of maize under cultivation, extent of annual mast, winter temperature and spring temperature. Hence, this factor expresses the temperature and food conditions for wild boar during the study period and is called *temperature and food*. Factor 2 represents the amount of snow and rainfall during the study period and, hence, is called *precipitation*.

The results of the SMRA relating population density to ecological conditions, demography and hunting are summarized in Table 3. The density index is positively correlated only to factor 1, indicating that population density increased under favourable temperature and

Table 2. Results from a principal component analysis based on data from 1974–98 for the six ecological variables related to wild boar *Sus scrofa* population densities in the canton Thurgau, Switzerland. Shown are loadings of the original variables on the extracted factors and the percentage of total variance explained by each factor. Bold, meaningful loadings

Variable	Factor 1 Food and temperature	Factor 2 Precipitation
MAIZE	0.737	– 0.250
MAST	0.698	0.198
TEMPW	0.621	– 0.188
TEMPS	0.715	– 0.356
SNOW	– 0.245	0.829
RAIN	– 0.031	0.784
Explained variance in %	33.15	25.58

Table 3. Results from the stepwise multiple regression analysis ($n=23$ years) relating the factor scores of the density index (=dependent variable) to the factor scores of the PCA-factors: *food and temperature, precipitation, sex ratio among hunted wild boars (SEXR) and number of hunters in the canton Thurgau (HUNT)* (both ln-transformed). Variables lnSEXR, lnHUNT and precipitation do not appear in the final model. $F=7.411$, $R^2=0.244$, $p=0.012$ for the final model

Variable	Regression coefficient	Standard error	t	p
Constant	– 0.039	0.177	– 0.222	0.826
Food and temperature	0.495	0.182	2.722	0.012

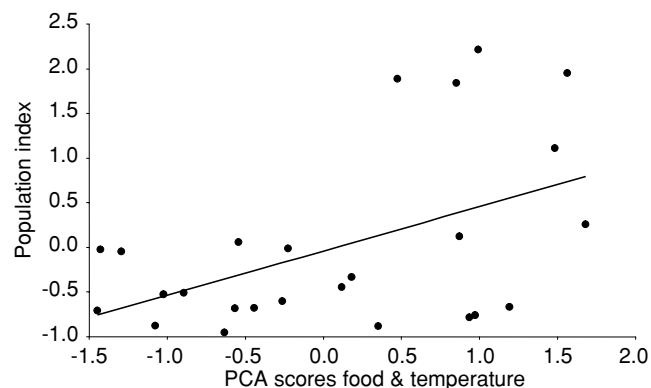


Fig. 4. Relationship between density index and principal component analysis (PCA) scores of factor 1 (food and temperature) from Table 2 according to the results of the multiple regression analysis in Table 3.

food conditions (Fig. 4), but was not related to either precipitation, sex ratio or hunting effort. The same conclusion is reached when a full regression model, including all two-way interactions between the independent variables, is applied. We also tested, by SMRA, if time shifts of 1, 2, 3 or 4 years between the population-index and the ecological variables changed the relationship. In every case, this resulted in less clear

or even non-significant models. Therefore, the population density in a particular year is better explained by food and temperature conditions in that particular year than by conditions in previous years.

DISCUSSION

Our analysis shows that over the last 25 years wild boar densities in the canton Thurgau have fluctuated, but increased markedly overall, and have been at their highest levels in the last few years of the study period (Fig. 2). Although the initial increase was paralleled by a spread into new areas within the range, this expansion came to a standstill (Fig. 3) and the overall distribution is only slightly larger than it was in the 1970s. This means that wild boar are at much higher densities today than 25 years ago. Nevertheless, with 0.75 harvested animals per 100 ha of forest in 1996, density in the canton Thurgau is still low when compared to other European regions, such as Tuscany in Italy with 10.0 (Mazzoni della Santa, Calovi & Burrini, 1995), Arc-en-Barrois in France with 5.0 (Brandt, Vassant & Jullien, 1998) or East Poland with 2.5 harvested animals per 100 ha of Forest (Fruzinski, 1995).

Our study only deals with a single population (for a detailed discussion on this problem see Putman *et al.*, 1996), and the final model explains only 24.4% of the variation in the population-index (Table 3). This indicates that other variables not considered here must have influenced the observed wild boar population dynamics (see Geisser, 2000). Among the potential candidates is migration from neighbouring regions, e.g. from Baden-Württemberg (Germany), where numbers rose by a factor of 5–6 from the early 1970s to the late 1990s (Hahn & Einfeld, 1998). Another candidate is the amount of food provisioning by hunters. However, data for these factors were either not available at all (migration) or not of sufficient precision and completeness (supplemental food) to be included in the statistical analysis. Nevertheless, our analyses clearly show that food and temperature conditions are key factors for the fluctuation in wild boar population density in the canton Thurgau (Fig. 4), while precipitation, sex ratio and hunting had no significant effects.

Food and climate conditions are known to be important factors for the population dynamics of many ungulate species. They affect juvenile survival and strongly influence reproduction (e.g. Putman *et al.*, 1996; Saether, 1997). For wild boar, temperature conditions are essential for the survival of the newborn piglets which are usually born between April and June. Piglets are susceptible to frosts in spring (Howells & Edwards-Jones, 1997) and juvenile mortality can reach up to 90% during the first 2 years of life (Jezierski, 1977; Briedermann, 1990). Hence, increasing winter and spring temperatures are likely to reduce the mortality of wild boar piglets.

Food conditions can influence demography in at least three ways. First, favourable conditions reduce juvenile mortality because they allow the piglets to reach the

minimal body weight until fall that is necessary to survive the cold winter months (Schauss, Coletto & Kutilek, 1990). Second, food availability strongly affects reproductive activity. Several studies have shown that good food conditions result in an earlier onset of oestrus (Baber & Coblentz, 1985; Pepin *et al.*, 1986), increased fertility and larger litter sizes (Howells & Edwards-Jones, 1997; Fernandez-Llario, Carranza & Mateos-Quesada, 1999). Finally, as known for other ungulate species, food availability also influences the age of first reproduction (Saether, 1997). Young wild boar females usually reach the minimal body weight for first reproduction (30–40 kg) in their second year, but under favourable conditions the increase in weight is accelerated (Groot Bruinderink, Hazebroek & van der Voot, 1994), and females first mate at the age of 8–10 months. The proportion of reproducing females can reach up to 90% in good mast years compared to only 20–30% in poor mast years (Massei *et al.*, 1996).

Of course, these food effects are confounded by other factors, e.g. the influence of population structure on synchronization of reproduction or the number of reproducing females in a group (Briedermann, 1990). This, however, does not change the conclusion that optimal food and temperature conditions are very likely to boost reproductive success, decrease juvenile mortality simultaneously and, thereby, increase population density within a short time period. This process has not only occurred in the canton Thurgau, but in several regions of other European countries like Germany (Hahn & Einfeld, 1998), France (Vassant, 1997), Italy (Boitani *et al.*, 1995) and Poland (Jedrzejewska *et al.*, 1997). Such rapid increases are characteristic for *r*-selected species (Boitani *et al.*, 1995).

One reason for the shifting conditions that wild boar have faced over the 25 years investigated in this study are the natural changes in climate and food availability. From 1975 to 1978, and in the early 1990s, winter and spring temperatures were higher than average and the frequency of mast years and the area of maize cultivation increased (Fig. 1c–f). On the other hand, wild boar density strongly decreased during the 1980s when temperature and food conditions were less favourable due to a series of harsh winters and/or poor mast years.

The increase in temperatures and decrease in snow cover (Fig. 1e–g) observed in the canton Thurgau during the 25 years covered by our study are in accordance with corresponding climate changes in the whole of Europe during the same period (Watson, 2001; EEA, 2004; Raisanen *et al.*, 2004). In contrast, the unchanged rain pattern (Fig. 1h) is intermediate between precipitation increases in northern and decreases in southern Europe, as is to be expected from the central geographic location of the Thurgau. The rising productivity of deciduous trees (Fig. 1d) and the increase in the area of planted maize (Fig. 1c) – a crop that is positively affected by higher temperatures – is in line with predictions from several models about the impact of climate changes on productivity and composition of

natural and anthropogenic plant communities (Watson, 2001). Under this scenario, the increase in wild boar numbers with temperature and food availability (Fig. 4) would appear to be related to past climate changes and, hence, might be expected to continue with future global changes over the whole of Europe. This, however, is a much too simplistic interpretation and projection. For developments observed in a small area (such as the canton Thurgau), local conditions and their changes will play a much more important role than global changes. These conditions include farming, logging and hunting policies, housing development and road building, conservation and management practices, plus many small-scale ecological features of a landscape that determine and modify the suitability of an environment for particular species.

One important local factor that has probably contributed to the widely observed increase in wild boar numbers is the fact that most European populations increasingly receive supplementary feeding (mainly maize) often throughout the year (Howells & Edwards-Jones, 1997). Supplementary food is provided either to bait wild boars for easier shooting or to distract the animals from crop fields (Hahn & Einfeld, 1998). In certain areas, this food supply can reach yearly amounts of several tonnes in a hunting area less than 1000 ha (Gaillard *et al.*, 1992; Fernandez-Llario *et al.*, 1998). The impact of such additional food is not yet clear. However, there is some evidence that an artificially increased food availability can, at least locally, advance the period of conception in wild boar females (Fernandez-Llario *et al.*, 1998), trigger exponential population growth (Howells & Edwards-Jones, 1997) and increase, rather than decrease, the damage to agricultural fields (Geisser & Reyer, 2004).

Depending on the relative amounts of supplemental and different types of natural food in any one year and area, the effects on population density and demography can be expected to vary. This may be one reason why Neet (1995), working on data from western Switzerland and from an earlier period (1960–91), found a 2-year time lag between the development of the maize area and the hunting statistics during the study period, whereas we found a synchrony between population size and food availability. Neither Neet's data on maize area nor our food scores may fully account for the precise food availability in any one year, because they both ignore the amount of supplemental food and, Neet's (1995) study also did not take into account the availability of natural mast food in the forest. Another reason for the difference between the two studies may be that the effect of enhanced food conditions differs among areas and/or years, sometimes leading mainly to an improvement of fecundity (and, hence, resulting in a delay) and sometimes leading to a change in adult mortality, juvenile survival and, hence, synchrony.

Whatever the precise mechanism and course of time, given this link between food, density and damage, supplemental feeding should be reconsidered. Depending on whether low, high or intermediate wild boar densities are the goal of management, concerned parties

such as government agencies, farmers, hunters and environmentalists will have differing opinions about the desirability of supplemental feeding.

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