Inter-specific synchrony of two contrasting ungulates: wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*)

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Abstract Very few studies on ungulates address issues of inter-specific synchrony in population responses to environmental variation such as climate. Depending on whether annual variation in performance of ungulate populations is driven by direct or indirect (trophic) interactions, very different predictions regarding the pattern of inter-specific synchrony can be derived. We compared annual autumn body mass variation in roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) from Poland over the period 1982–2002, and related this to variation in winter and summer climate and plant phenological development [the Normalized Difference Vegetation Index (NDVI), derived from satellites]. Roe deer fawns (~1.3 kg increase from year 1982 to 2002) and yearlings both increased markedly in mass over years. There was also an increase for wild boar mass over years (~4.2 kg increase for piglets from 1982 to 2002). Despite our failure to link annual body mass to spring or winter conditions or the NDVI, the body mass of roe deer and wild boar fluctuated in synchrony. As this was a field roe deer population, and since wild boar is an omnivore, we suggest this may be linked to annual variation and trends in crop structure (mainly rye). We urge future studies to take advantage of studying multiple species in order to gain further insight into processes of how climate affect ungulate populations.

Communicated by Jean-Michel Gaillard.

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Introduction

Climate influence dynamics of ungulate populations both directly and indirectly through trophic interactions (reviews in Weladji et al. 2002; Mysterud et al. 2003). Population sizes of northern ungulates typically decline after severe winters with much snow (e.g. Jacobson et al. 2004; Grøtan et al. 2005; Mysterud and Østbye 2006b), and there may also be negative effects of severe winter conditions on body mass (Cederlund et al. 1991). Early summer conditions (temperature and precipitation) are regarded as particularly important for individual growth and operate through climate effects on plants (Klein 1965; Sæther and Heim 1993; Langvatn et al. 1996; Mysterud et al. 2001). This has recently been verified directly through the use of satellite-derived vegetation indices [Normalized Difference

Vegetation Index (NDVI)] at large spatial scales (Pettorelli et al. 2005a, c).

In the literature on rodents, inter-specific patterns of synchrony have been a main theme to separate hypotheses related to predation and food (e.g. Stenseth and Ims 1993; Hanski and Henttonen 1996; Korpimäki et al. 2005). However, very few studies on ungulates address issues of inter-specific synchrony in population responses to climate. In Norway, body mass of domestic sheep (*Ovis aries*) has been shown to vary annually in synchrony with mass of red deer (*Cervus elaphus*) (Mysterud et al. 2001), moose (*Alces alces*) (Sæther 1985) and semi-domestic reindeer (*Rangifer tarandus*) (Weladji et al. 2003), while on Greenland, some evidence has suggested population synchrony between muskox (*Ovibos moschatus*) and reindeer (e.g. Post and Forchhammer 2002, but see also Vik et al. 2004).

Depending on whether annual variation in performance of ungulate populations is driven by direct or indirect (trophic) interactions, very different predictions regarding the pattern of inter-specific synchrony can be derived. If ungulates are affected directly by factors such as snow depth, patterns of annual variation in performance should be irrespective of ungulate diet (and dietary overlap). However, we would expect large-sized species to be less strongly affected and, possibly, grazers to be more strongly affected than browsers since the field layer is more restricted by snow than deciduous browse. In contrast, if annual variation in performance is driven by climate operating through plants, we would expect synchrony only among species with a similar diet, unless different forage plants are synchronous as well.

In this study, we compare patterns of annual variation in body mass of two very different ungulates, the wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*), using a long-term data set (1982–2002) from Poland. Wild boar is a medium-sized (~80–150 kg) omnivore (Jedrzejewska and Jedrzejewski 1998), while the roe deer is a small (~20–30 kg) browser (Andersen et al. 1998). We aim to test whether these species are affected directly by conditions during winter (duration of snow cover and temperature) and/or early summer (temperature and precipitation, as well as the satellite derived NDVI), and to test whether there is inter-specific synchrony in annual body mass variation. Our prediction is that both species may be affected by snow, but that roe deer should be more influenced by plants (NDVI) being a strict herbivore. We predict inter-specific synchrony in annual variation if body mass of both species is driven by direct effects of climate (through snow depth), but not if they are affected indirectly through plants.

Materials and methods

Study area

The study was carried out in the experimental area, approximately 150 km² in extent, of the Polish Hunting Association Research Station at Czempiń, western Poland (52°08′N, 16°44′E). This is a typical farmland region, with arable fields occupying nearly 70% of the area. The climate of the region is typical for central Europe, where oceanic and continental climate types meet. The mean annual temperature is ca. 8°C (sub-zero mean monthly temperatures occur in December–February) with mean annual precipitation ca. 550 mm (Ryszkowski et al. 1996). The two study species are the most common and most numerous large mammal species both in the study area, and in western Poland in general (Bresinski and Jedryczkowski 1999). While both species in the past were mainly connected with forests, roe deer in the 1930s and wild boar in the 1970s started to establish local field populations in this area of Poland (Andrzejewski and Jezierski 1978; Pielowski and Bresinski 1982; Kaluzinski 1982b). Roe deer live here mainly on arable fields, sporadically using small woodland patches as resting sites (Pielowski and Bresinski 1982; Bresinski 1982; Kaluzinski 1982a, b). Food of roe deer in the study area consists mainly of crops and grasses (over 75%), while in some years, big flocks of deer foraged on oil-seed rape fields (Kaluzinski 1982a).

Roe deer data

Data on roe deer derive from hunting in the Czempiń area of Poland. We obtained data on carcass mass (i.e., live mass minus viscera, bleedable blood and metapodials), hereafter referred to as body mass. Carcass mass correlates closely with total body mass (Wallin et al. 1996, for moose). Roe deer were aged by tooth wear (e.g. Hewison et al. 1999; Mysterud and Østbye 2006a). As this method is not highly reliable especially for older ages, we considered only fawns (~0.5 year) and yearlings (~1.5 years). We restricted the analysis to data from October through January. From this period, there was limited data on males, and we therefore limited the analysis to data on females. Sample size was therefore 444 individuals from 1982 to 2002 (Appendix).

Wild boar data

Data on wild boar also derive from hunting in the Czempiń area of Poland. In Poland, wild boar are shot

not only for trophies but also as a farmland pest (Andrzejewski and Jezierski 1978). Body mass data are carcass mass as for roe deer (see above). In this area, wild boar only have one litter each year. Age groups can be classified to (1) piglets, which are individuals less than 1 year (from 1 April y_t to 31 March y_{t+1}), (2) yearlings, which are between 1 and 2 years of age, and (3) adults that are more than 2 years of age. Due to low sample sizes from parts of the year, we restricted the analysis to data from September through January. Further, as body mass is not stable from 2 years onwards, we excluded adults and analysed variation in mass of piglets and yearlings. Sample size was therefore 311 individuals from 1982 to 2002 (Appendix). For wild boar, there were also available data on counts during drive hunts in spring each year. We used this as an index for density, though we have no assessment of how well this tracks actual population size, therefore results must be interpreted with some caution. The trend in counts over time was marked. There was a decrease from the first half of 1980s (~150 counted annually), until mid-1990 (~50 counted annually), and then an increase again until 2002 (~150 counted annually).

Hunting in the area is done using three methods: drive hunts, stalking and posting (i.e. waiting for prey in one location). There have been no special preferences for different methods over the study period nor are we aware of any changes over the study period. The problem in most cases working with hunters' data are that no independent data are available, so that hunter selectivity cannot be addressed. However, as we work only with wild boar piglets and yearlings and roe deer females, it is highly unlikely that hunter selectivity is important. The methods of eviscerating roe deer and wild boar have not changed over time.

Climate data

We obtained monthly averages of snow depth, temperature and precipitation from a local weather station at Turew, in the western sector of the study area.

We also used the seasonal indices of the North Atlantic Oscillations (NAO) (Hurrell et al. 2003; available from http://www.cgd.ucar.edu/~jhurrell/nao.pc.html) (winter, December–February; spring, March–May; summer, June–August; autumn, September–November). The best indices are regarded as those based on principal component analysis (Hurrell et al. 2003), and they were therefore used in addition to the station-based winter index, which is the one most commonly used (Stenseth et al. 2003). In general, high NAO values are correlated with much precipitation and high temperatures in the study area in Poland, in particular during

winter. A more detailed description of these indices is given elsewhere (Hurrell et al. 2003), and also concerning their major impact on ecological systems (Stenseth et al. 2002; Mysterud et al. 2003).

NDVI data

We used the NDVI from the pathfinder Advanced Very High Resolution Radiometer (AVHRR) collected by the National Oceanic and Atmospheric Administration (NOAA). We used NDVI data from the GIMMS group (kindly provided by Compton Tucker) at a spatial scale of 8×8 km and aggregated for every second week. The NDVI is regarded as the most robust index and correlates strongly with aboveground net primary productivity and absorbed photosynthetically active radiation (Myneni et al. 1997; Kerr and Ostrovsky 2003; review in Pettorelli et al. 2005b). The NDVI index is derived from the ratio of red to near-infrared reflectance [NDVI = (NIR − RED)/(NIR + RED)], where NIR and RED are the amounts of near-infrared and red light reflected by the vegetation. This corresponds to the absorption of red light by chlorophyll and the scattering of near-infrared light by mesophyll leaf structure. NDVI values typically range from −0.2 to 1 (theoretically from −1 to +1, but values less than −0.2 correspond to water), negative values corresponding to an absence of vegetation (Justice et al. 1985; Pettorelli et al. 2005b). Data on the NDVI was available from 1982 to 2002. The seasonal and annual pattern of variation in the NDVI is given in appendix Fig. 1. We also used the integrated NDVI value (INDVI), which corresponds to the sum of the NDVI values over the growing season (Pettorelli et al. 2005b).

Statistical analyses

We explored the correlation between environmental covariates with simple Pearson correlation coefficients, and trends over years with simple linear regressions.

To analyse variation in body mass, we used mainly linear models (LM) after some initial use of additive models (AM; Hastie and Tibshirani 1990) with smoothing splines to ensure that predictors were linearly related to response variables. We used the standard logarithmic transformation [ln(weight)] of body mass to get residuals with constant variance. We also used linear-mixed effects (LME) models with year as a random effect (Lindsey 1999), which is a more conservative approach than using each year as the level of replication (rather than number of individuals).

As we had a fairly high number of climatic variables potentially influencing the dynamics, we used the

Akaike Information Criterion (AIC; Burnham and Anderson 1998; Johnson and Omland 2004) for selecting an appropriate model for hypothesis testing. The model with the lowest AIC value is regarded as the best compromise between explaining most of the variation and simultaneously using as few parameters as possible. We used the small-sample correction $AIC_c=AIC + 2K(K + 1)/(N − K + 1)$, where N is the number of observations and K is the number of regression coefficients including intercept. The detailed strategy when selecting models is given in tables (see Appendix). Model selection was always done on LM and not LME (cf. Crawley 2003).

Separate models were run for roe deer and wild boar. When comparing the pattern of synchrony, we used a simpler model without any environmental variables, but with "cohort year" entered as a categorical term so as to estimate body mass for each year. We then calculated mass change from 1 year to the next and used linear regression, with predicted values for mass change of wild boar (most common category, i.e. male piglets in November) regressed on predicted values for mass change of roe deer (female fawns in November) with the (square root) number of observations for wild boar as "weights" (but years with $n<5$ were excluded).

All analyses were done in S-Plus versus 6.2 (Venables and Ripley 1994; Crawley 2003).

Results

Temporal trends and correlations in environmental variables

There was no trend in April temperature ($r^2=0.007$, $T=0.355$, $P=0.726$), May temperature ($r^2=0.002$, $T=−0.181$, $P=0.858$), number of snow days ($r^2=0.031$, $T=0.776$, $P=0.447$) or in the winter index of the NAO ($r^2=0.022$, $T=−0.658$, $P=0.518$) over the study period. There tended to be a positive trend in the NDVI over time, as seen for the INDVI ($r^2=0.160$, INDVI= $−55.020$ (±35.137) + 0.0336 (±0.0176) years, $T=1.905$, $P=0.072$) and to a lesser extent for NDVI in spring ($r^2=0.126$, NDVI, 15 April$=−4.495$ (±3.050) + 0.0025 (±0.0015) years, $T=1.653$, $P=0.115$). There was no correlation between NDVI and temperature in April (NDVI, 15 April $r=0.055$; INDVI $r=−0.145$). The NAO in winter was positively correlated with temperature (January $r=0.642$; February $r=0.453$; March $r=0.703$), but not with precipitation (January $r=0.259$; February $r=0.296$; March $r=0.269$) or duration of snow cover ($r=0.298$).
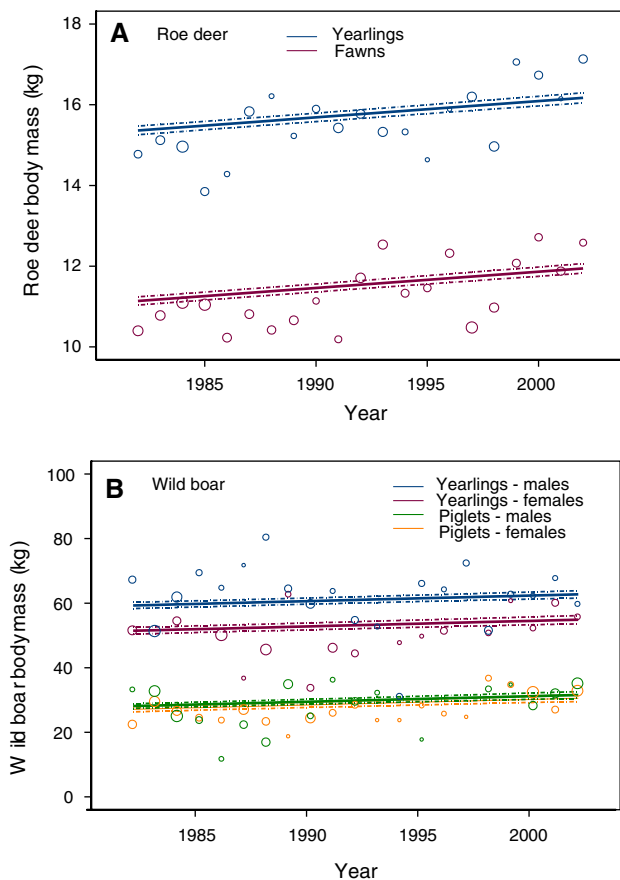
Roe deer

Carcass mass of fawns averaged 11.3 kg (from 7.0 to 16.0) and yearlings 15.7 kg (from 10.2 to 20.2) over the whole period 1982–2002. The most parsimonious model as assessed with the AICc explained 62.7% of the variation in female roe deer body mass (slaughtered) between October and January (Table 1). As would be expected, fawns were smaller than yearlings. Body masses were smaller in October than from November to January, especially for fawns. Body mass increased over years (Fig. 1). A fawn in October had a mass of 10.25 kg in 1982 and 11.55 kg in year 2002. Temperature in April entered the most parsimonious model being marginally significant (Table 1). In a more restrictive LME with year as a random variable, the effect of temperature in April was not significant (l.s. estimate=0.00906, SE=0.00615, df=19, T=1.474, P=0.157). The different indices based on the NDVI did not enter the most parsimonious model.

Wild boar

There was huge variation in body mass of wild boar, ranging from 7 to 51 kg in piglets and from 27 to 86 kg in yearlings. The most parsimonious model as assessed with the AICc explained 68.6% of the variation in body mass (slaughtered) of piglets and yearlings between September and January (Table 2). Naturally, piglets were smaller than yearlings, and males were larger than females, and the difference between males and females was larger for yearlings than for piglets. There was also some variation in mass due to month, and this interacted with age. There was a positive trend in body mass over years (Table 2); piglets and yearlings weighed on average, respectively, 27.1 and 55.8 kg in 1982 and 31.3 and 64.5 kg in 2002 (Fig. 1). There was also a positive effect of population density as indexed

Table 1 Results from the most parsimonious model for annual variation in (ln) body mass (kg) of roe deer (*Capreolus capreolus*) from 1982 to 2002 in Poland

Variable	L.s. estimate	SE	T	P
Intercept	−9.1562	2.2745	−4.026	0.000
Month				
January versus December	0.0114	0.0177	0.647	0.518
November versus December	0.0192	0.0199	0.965	0.335
October versus December	−0.0194	0.0208	−0.931	0.352
Age (1.5 vs 0.5 year)	0.3362	0.0128	26.266	0.000
Cohort year	0.0058	0.0011	5.036	0.000
Temperature, April	0.0089	0.0049	1.835	0.067

Fig. 1 Temporal development of average body mass of **a** roe deer (*Capreolus capreolus*) and **b** wild boar (*Sus scrofa*) in Poland 1982–2002. *Dotted lines* indicate 95% confidence intervals. Note that data are unadjusted for monthly variation. Size of *circles* is directly proportional to the (sqrt) sample size (within species), but overall sample sizes are smaller for wild boar than for roe deer

from the spring counts (Table 2), which also remained when running a more conservative LME with year as a random effect (l.s. mean=0.00209, SE=0.000608, *df*=20,

T=3.431, *P*=0.003). Temperature in May entered the most parsimonious model, but was not significant (Table 2).

Inter-specific synchrony

Based on estimated body mass separately for both species (read out for wild boar piglets and yearling roe deer), there was significant correlation between body mass change of roe deer and wild boar from one year to the next (r^2=0.412, Fig. 2). This result was similar when using bootstrap (bootstrap estimate=0.130, 95% CI=0.0296, 0.232), and remained when adding a linear year term to remove possible trends (Table 3). This result was robust to the choice of age class. For roe deer, when restricting analysis to years with data on both age classes (Appendix), adding an interaction term between age and cohort year (categorical) resulted in a less parsimonious model (ΔAIC=7.000). For wild boar, when restricting analysis to years with data on both age and sex classes (Appendix), adding an interaction term between cohort year (categorical) and age (ΔAIC=12.655) or sex (ΔAIC=14.882) resulted in less parsimonious models.

Discussion

For both roe deer and wild boar, body mass increased considerably over years (Fig. 1). There tended to be a parallel increase in the NDVI. However, we failed to link variation in NDVI to body mass of either roe deer or wild boar, and if this non-significant term was nevertheless added to the model, the estimate of the NDVI effect was positive in roe deer and negative in wild boar. Therefore, the rather strong trend in mass of

Table 2 Results from the most parsimonious model for annual variation in (ln) body mass (kg) of wild boar from 1982 to 2002 in Poland

Variable	L.s. estimate	SE	T	P
Intercept	−19.9221	5.3726	−3.708	0.000
Sex (male vs female)	0.1789	0.0511	3.503	0.001
Age (piglets vs yearlings)	−0.5369	0.0913	−5.881	0.000
Month				
January versus December	−0.0659	0.0861	−0.766	0.445
November versus December	−0.0465	0.0861	−0.540	0.590
October versus December	0.0221	0.0917	0.241	0.810
September versus December	−0.1263	0.0869	−1.453	0.147
Cohort year	0.0120	0.0027	4.452	0.000
Density (harvest size)	0.0020	0.0005	3.718	0.000
Temperature, May	−0.0177	0.0114	−1.550	0.122
Sex × age	−0.1647	0.0651	−2.528	0.012
Age × month				
January versus December	0.0307	0.1036	0.296	0.767
November versus Decembr	−0.0517	0.1062	−0.487	0.627
October versus December	−0.2715	0.1188	−2.285	0.023
September versus December	−0.4039	0.1079	−3.744	0.000
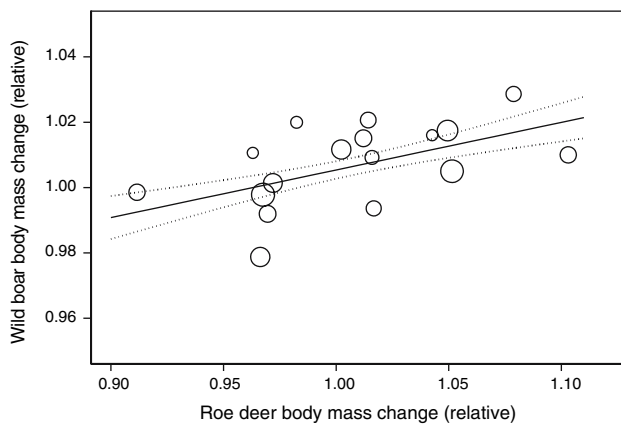
Fig. 2 The relationship between annual autumn body mass change of roe deer and wild boar in Poland for the period 1982–2002. Each *circle* represent mass change from 1 year to the next [i.e. (mass year$_t$)/(mass year$_{t-1}$)]. Size of *circles* is directly proportional to the (sqrt) sample size for wild boar (more data were available for roe deer). *Dotted lines* indicate 95% confidence intervals

Table 3 Results from the linear model for annual change in (ln) body mass (kg) of wild boar as a function of annual change in roe deer mass and cohort year as a continuous term (to remove trends)

Variable	L.s. estimate	SE	T	P
Intercept	−0.3713	0.7853	−0.473	0.644
Ln (roe deer mass change)	0.1359	0.0542	2.510	0.025
Cohort year (continuous)	0.0006	0.0004	1.571	0.139

both species may likely be caused by some other factor in the environment. As there was no effect of winter conditions in either wild boar or roe deer, it was surprising that annual body mass variation of the two species was synchronous, as we predicted synchronous pattern only if direct effects of climate operating through plants were present.

The lack of strong responses of climatic variation on performance of roe deer and wild boar may be either biological or methodological in origin. Litter size was unknown neither in roe deer nor in wild boar. Although heavier animals might be born in smaller litters (wild boar, Fernándex-Llario et al. 2003; roe deer, Andersen et al. 2000), whether the difference persists over time is unclear. Further, we also did not have data on population density of roe deer, and only the spring counts as a measure of density in wild boar. Lack of data on density for roe deer may also have made it more difficult to find effects of variation in climate, especially if the effect of population density interacts with the climate effect (Sauer and Boyce 1983; Portier

et al. 1998; Coulson et al. 2001; Stenseth et al. 2004). The effect of density on wild boar body mass was small and positive, suggesting no competition within the density range experienced. The general impression is that population density for both species has increased during the study period (Bresinski and Jedryczkowski 1999), thus we would have predicted decreased body mass over time. As there was both a common trend and inter-specific synchrony in body mass, and since for both species we would have predicted decreasing rather than increasing body mass if density increased over time, there is likely some other factor that we have not measured that is responsible for these patterns.

The causes of inter-specific synchrony have been highlighted as complex and difficult to identify (Liebhold et al. 2004). In our case, we can only provide implicit evidence for a mechanism, by excluding both direct effects of winter weather and indirect effects of plants (NDVI). A possible explanation is that both the trend and synchrony is related to crop structure, which may be important for both species. While rye, lucerne and oil-seed rape are the most important food sources for roe deer (over 60% of diet except in spring; Kaluzinski 1982a), cereals, potatoes and maize are the most important food sources for the wild boar (for our area, Genov 1981; general review in Schley and Roper 2003). Even though wild boar seem to prefer maize, they also eat rye as do roe deer. In the study area (around 1995), agricultural crops were 50% cereals (mainly rye), 20% row crops (including oil-seed rape), 10% perennial fodder crops and 20% others (Ryszkowski et al. 1996). Both maize and cereals may be links between the two species, and crop rotation is similar to the Norfolk system (cf. Berzsenyi et al. 2000), therefore cover structure changes annually and likely may show a trend as well.

We suggest further studies comparing sympatric populations of ungulates to be rewarding—both inter-specific synchrony and lack of such will help us understand better the mechanisms by which climate impacts on ungulates (Mysterud et al. 2001). Part of the lack of such studies likely arises due to data limitations. Most monitoring is focussed on single species, and data from different species are often gathered by different people or institutions not usually collaborating. A better overview of the rewards of such cooperation may indeed facilitate more interspecific comparisons in the future.

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