

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

Atle Mysterud · Piotr Tryjanowski · Marek Panek ·
Nathalie Pettorelli · Nils C. Stenseth

Received: 19 May 2006 / Accepted: 11 October 2006 / Published online: 11 November 2006
© Springer-Verlag 2006

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.

Keywords Climate · Crops · NDVI · Poland · Trophic interactions

Communicated by Jean-Michel Gaillard.

Electronic supplementary material Supplementary material is available in the online version of this article at <http://dx.doi.org/10.1007/s00442-006-0584-z> and is accessible for authorized users.

A. Mysterud (✉) · N. Pettorelli · N. C. Stenseth
Centre for Ecological and Evolutionary Synthesis (CEES),
Department of Biology, University of Oslo,
P.O. Box 1066, Blindern, 0316 Oslo, Norway
e-mail: atle.mysterud@bio.uio.no

P. Tryjanowski
CEH Monks Wood, Abbots Ripton,
Huntingdon, Cambs PE28 2LS, UK

P. Tryjanowski
Department of Behavioural Ecology,
Adam Mickiewicz University, Umultowska 89,
61-614 Poznań, Poland

M. Panek
Polish Hunting Association, Research Station,
64-020 Czempin, Poland

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 (Pettoirelli 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*) (Myserud 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 Czempin, 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 Czempin 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; Myserud 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 Czempin 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 , to 31 March y_{+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; Myrsetrud 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 [$\ln(\text{weight})$] 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 ($r^2=0.160$, $INDVI = -55.020 (\pm 35.137) + 0.0336 (\pm 0.0176)$ years, $T=1.905$, $P=0.072$) and to a lesser extent for NDVI in spring ($r^2=0.126$, $NDVI$, 15 April = $-4.495 (\pm 3.050) + 0.0025 (\pm 0.0015)$ 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	0.0114	0.0177	0.647	0.518
December				
November versus	0.0192	0.0199	0.965	0.335
December				
October versus	-0.0194	0.0208	-0.931	0.352
December				
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

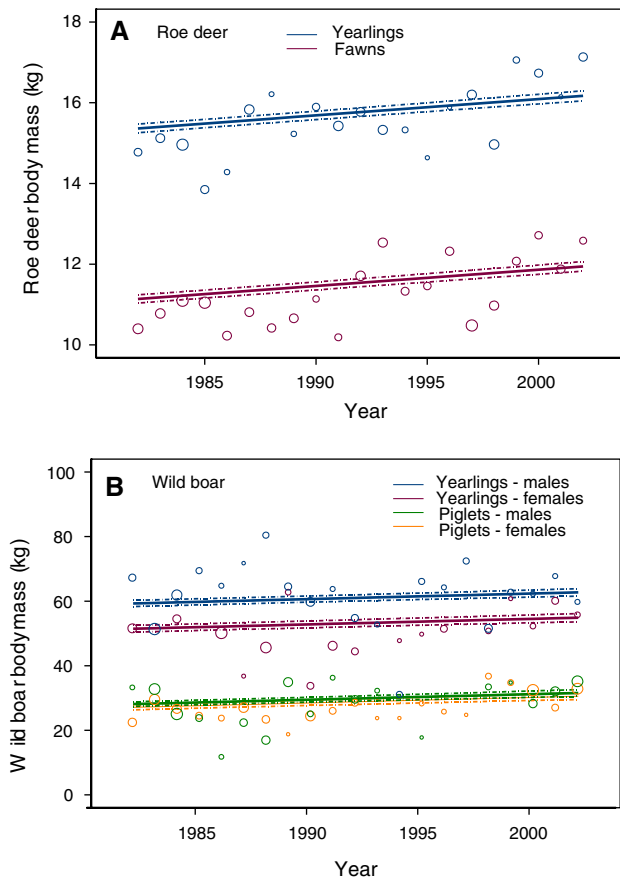


Fig. 1 Temporal development of average body mass of **a** roe deer (*Capreolus capreolus*) and **b** wild boar (*Sus scrofa*) in Poland 1982–2002. Dotted lines indicate 95% confidence intervals. Note that data are unadjusted for monthly variation. Size of circles is directly proportional to the (sqrt) 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 ($\Delta AIC=7.000$). 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 ($\Delta AIC=12.655$) or sex ($\Delta AIC=14.882$) 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 \times age	-0.1647	0.0651	-2.528	0.012
Age \times month				
January versus December	0.0307	0.1036	0.296	0.767
November versus December	-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

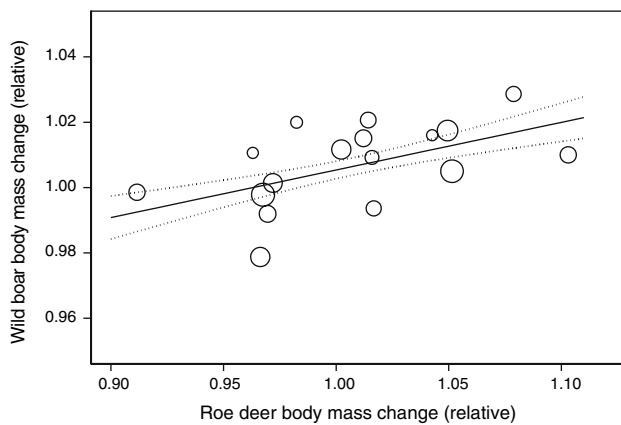


Fig. 2 The relationship between annual autumn body mass change of roe deer and wild boar in Poland for the period 1982–2002. Each circle represent mass change from 1 year to the next [i.e. $(\text{mass year}_t)/(\text{mass year}_{t-1})$]. Size of circles is directly proportional to the (sqrt) sample 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	<i>T</i>	<i>P</i>
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, Fernández-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.

Acknowledgments We gratefully acknowledge the financial support of the Research Council of Norway to A.M. (YFF Project). We are grateful to W. Bresiński, R. Kamiński and many of local hunters for help in collecting field data, J. Karg for assistance with obtaining temperature data. P.T.'s sabbatical at Monks Wood was funded by the Foundation for Polish Science. We

greatly appreciated the comments of Jean-Michel Gaillard, Nicolas Morellet, and one anonymous referee to previous drafts of this paper.

References

- Andersen R, Duncan P, Linnell JDC (1998) The European roe deer: the biology of success. Scandinavian University Press, Oslo
- Andersen R, Gaillard J-M, Linnell JDC, Duncan P (2000) Factors affecting maternal care in an income breeder, the European roe deer. *J Anim Ecol* 69:672–682
- Andrzejewski R, Jezierski J (1978) Management of a wild boar population and its effects on commercial land. *Acta Theriol* 23:309–339
- Berzsenyi Z, Gyorffy B, Lap D (2000) Effect of crop rotation and fertilisation on maize and wheat yields and yield stability in a long-term experiment. *Eur J Agron* 13:225–244
- Bresinski W (1982) Grouping tendencies in roe deer under agrosenosis conditions. *Acta Theriol* 27:427–447
- Bresinski W, Jedryczkowski WB (1999) Situation of hunting game and some protected species in Dezydery Chlapowski landscape park and its surroundings. *Biul Parków Krajozbrazowych Wielkopolski* 5:81–101
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, Berlin Heidelberg New York
- Cederlund G, Sand H, Pehrson Å (1991) Body mass dynamics of moose calves in relation to winter severity. *J Wildl Manage* 55:675–681
- Coulson T, Catchpole EA, Albon SD, Morgan BJT, Pemberton JM, Clutton-Brock TH, Crawley MJ, Grenfell BT (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–1531
- Crawley MJ (2003) Statistical computing. An introduction to data analysis using S-Plus. Wiley, Chichester
- Fernández-Llario P, Mateos-Quesada P, Silvério A, Santos P (2003) Habitat effects and shooting techniques on two wild boar (*Sus scrofa*) populations in Spain and Portugal. *Z Jagdwiss* 49:120–129
- Genov P (1981) Food composition of wild boar in north-eastern and western Poland. *Acta Theriol* 26:185–205
- Grøtan V, Sæther B-E, Engen S, Solberg EJ, Linnell JDC, Andersen R, Brøseth H, Lund E (2005) Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. *Ecology* 86:1472–1482
- Hanski I, Henttonen H (1996) Predation on competing rodent species: a simple explanation of complex patterns. *J Anim Ecol* 65:220–232
- Hastie T, Tibshirani R (1990) Generalized additive models. Chapman & Hall, London
- Hewison AJM, Vincent JP, Angibault JM, Delorme D, Van Laere G, Gaillard J-M (1999) Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. *Can J Zool* 77:58–67
- Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (2003) The North Atlantic Oscillation. Climatic significance and environmental impact. American Geophysical Union, Washington DC
- Jacobson AR, Provenzale A, von Hardenberg A, Bassano B, Festa-Bianchet M (2004) Climate forcing and density dependence in a mountain ungulate population. *Ecology* 85:1598–1610
- Jedrzejska B, Jedrzejski W (1998) Predation in vertebrate communities. The Białowieża Primeval forest as a case study. Springer, Berlin Heidelberg New York
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Justice CO, Townshend JRG, Holben BN, Tucker CJ (1985) Analysis of the phenology of global vegetation using meteorological satellite data. *J Remote Sens* 6:1271–1318
- Kaluzinski J (1982a) Composition of the food of roe deer living in fields and the effects of their feeding on plant production. *Acta Theriol* 27:457–470
- Kaluzinski J (1982b) Dynamics and structure of a field roe deer population. *Acta Theriol* 27:385–408
- Kerr JT, Ostrovsky M (2003) From space to species: ecological applications for remote sensing. *Trends Ecol Evol* 18:299–305
- Klein DR (1965) Ecology of deer range in Alaska. *Ecol Monogr* 35:259–284
- Korpimäki E, Norrdahl K, Huitu O, Klemola T (2005) Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proc R Soc Lond B* 272:193–202
- Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age at first reproduction in a temperate herbivore. *J Anim Ecol* 65:653–670
- Liebold A, Koenig WD, Bjørnstad ON (2004) Spatial synchrony in population dynamics. *Annu Rev Ecol Syst* 35:467–490
- Lindsey JK (1999) Models for repeated measurements. Oxford University Press, Oxford
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- Mysterud A, Østbye E (2006a) Comparing simple methods for ageing roe deer *Capreolus capreolus*: can any of them be useful in management? *Wildl Biol* 12:101–107
- Mysterud A, Østbye E (2006b) The effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes—the Lier valley, Norway. *Wildl Biol* 12:321–329
- Mysterud A, Stenseth NC, Yoccoz NG, Langvatn R, Steinheim G (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* 410:1096–1099
- Mysterud A, Stenseth NC, Yoccoz NG, Ottersen G, Langvatn R (2003) The response of the terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic Oscillation. American Geophysical Union, Washington, pp 235–262
- Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC (2005a) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc R Soc Lond B* 272:2357–2364
- Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker C, Stenseth NC (2005b) Using the satellite-derived normalized difference vegetation index (NDVI) to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510
- Pettorelli N, Weladji RB, Holand Ø, Mysterud A, Breie H, Stenseth NC (2005c) The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer performance. *Biol Lett* 1:24–26
- Pielowski Z, Bresinski W (1982) Population characteristics of roe deer inhabiting a small forest. *Acta Theriol* 27(28):409–425
- Portier C, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Yoccoz NG (1998) Effects of density and weather on survival of big-horn sheep lambs (*Ovis canadensis*). *J Zool* 245:271–278
- Post E, Forchhammer MC (2002) Synchronization of animal population dynamics by large-scale climate. *Nature* 420:168–171
- Ryszkowski L, French NR, Kedziora A (1996) Dynamics of an agricultural landscape. PWRiL, Poznań

- Sæther B-E (1985) Annual variation in carcass weight of Norwegian moose in relation to climate along a latitudinal gradient. *J Wildl Manage* 49:977–983
- Sæther B-E, Heim M (1993) Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *J Anim Ecol* 62:482–489
- Sauer JR, Boyce MS (1983) Density dependence and survival of elk in northwestern Wyoming. *J Wildl Manage* 47:31–37
- Schley L, Roper TJ (2003) Diet of wild boar *Sus scrofa* in Western Europe, with reference to consumption of agricultural crops. *Mammal Rev* 33:43–56
- Stenseth NC, Chan K-S, Tavecchia G, Coulson T, Mysterud A, Clutton-Brock T, Grenfell BT (2004) Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proc R Soc Lond B* 271:1985–1993
- Stenseth NC, Ims RA (1993) The biology of lemmings. Academic Press, London
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan K-S, Lima M (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Stenseth NC, Ottersen G, Hurrell JW, Mysterud A, Lima M, Chan K-S, Yoccoz NG, Ådlandsvik B (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc R Soc Lond B* 270:2087–2096
- Venables WN, Ripley BD (1994) Modern applied statistics with S-plus. Springer, Berlin Heidelberg New York
- Vik JO, Stenseth NC, Tavecchia G, Mysterud A, Lingjerde OC (2004) Living in synchrony on Greenland coasts? *Nature* 427:697–698
- Wallin K, Cederlund G, Pehrson Å (1996) Predicting body mass from chest circumference in moose *Alces alces*. *Wildl Biol* 2:53–58
- Weladji RB, Klein DR, Holand Ø, Mysterud A (2002) Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. *Rangifer* 22:33–50
- Weladji RB, Steinheim G, Holand Ø, Moe SR, Almøy T, Ådnøy T (2003) Temporal patterns of juvenile body weight variability in sympatric reindeer and sheep. *Ann Zool Fenn* 40:17–26