IDEA AND PERSPECTIVE

How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer

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Abstract

How populations respond to climate change depends on the interplay between life history, resource availability, and the intensity of the change. Roe deer are income breeders, with high levels of allocation to reproduction, and are hence strongly constrained by the availability of high quality resources during spring. We investigated how recent climate change has influenced demographic processes in two populations of this widespread species. Spring began increasingly earlier over the study, allowing us to identify 2 periods with contrasting onset of spring. Both populations grew more slowly when spring was early. As expected for a long-lived and iteroparous species, adult survival had the greatest potential impact on population growth. Using perturbation analyses, we measured the relative contribution of the demographic parameters to observed variation in population growth, both within and between periods and populations. Within periods, the identity of the critical parameter depended on the variance in growth rate, but variation in recruitment was the main driver of observed demographic change between periods of contrasting spring earliness. Our results indicate that roe deer in forest habitats cannot currently cope with increasingly early springs. We hypothesise that they should shift their distribution to richer, more heterogeneous landscapes to offset energetic requirements during the critical rearing stage.

Keywords

Age-structured populations, demographic change, income breeding, perturbation analysis, population growth, Recruitment, Stochastic environment, Survival.

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INTRODUCTION

Variation in population abundance is shaped by the interplay between density-dependence, environmental fluctuations, and demographic stochasticity (Lande *et al.* 2003). The relative importance of these processes has been hotly debated (e.g. Nicholson 1933 vs. Andrewartha & Birch 1954) and, for a while, accounting for density-dependence has been privileged over considering stochastic environments. This is well illustrated by the history of demographic analyses. While Leslie included density-dependence in his deterministic model as early as 1948 (Leslie 1948), we had to wait until the late sixties for the first integration of stochastic variation in population growth rate (Lewontin & Cohen 1969) and the early eighties for a full consideration of the stochastic population growth rate (Tuljapurkar & Orzack 1980).

In recent years, the study of the ecological effects of climate change has become a popular research topic (Both *et al.* 2004; Parmesan 2006; Lebreton 2011 for reviews). Evidence is now accumulating that climate change at a global scale affects the geographical distribution of organisms, while topography interacts with climate to influence local weather. This often involves warmer temperatures and earlier springs (i.e. a change in plant phenology such that the

vegetation flush occurs earlier) in temperate areas (Schwartz *et al.* 2006), which markedly influence the population biology of a large range of organisms (Fig. 1). However, these studies have either focussed on climate niche models (Guisan & Zimmermann 2000; Guisan & Thuiller 2005) to quantify the link between local weather and distribution area for predicting the future spatial distribution of a given taxon (e.g. Huntley *et al.* 2006; for a case study on Dartford warbler *Sylvia undata*) or attempted to assess the magnitude of climate-induced variation in demographic parameters (Grosbois *et al.* 2008) or population growth (Hansen *et al.* 2011).

The interactions between demography and climate have not been investigated (Brook *et al.* 2009), although some studies have recently identified demographic responses to climate change (Ozgul *et al.* 2010; Lane *et al.* 2012). In particular, no study has yet assessed the effects of climate change on the demographic processes involved in shaping population growth rate, despite the fact that Andrewartha & Birch (1954) emphasised more than 50 years ago that population growth rate is a dynamic variable influenced by environmental conditions. Moreover, most studies have been performed on single populations, often declining in size (e.g. Barbraud & Weimerskirch 2001 for a case study on Emperor penguin *Aptenodytes forsteri*). As a result, we have very little information on how climate change is
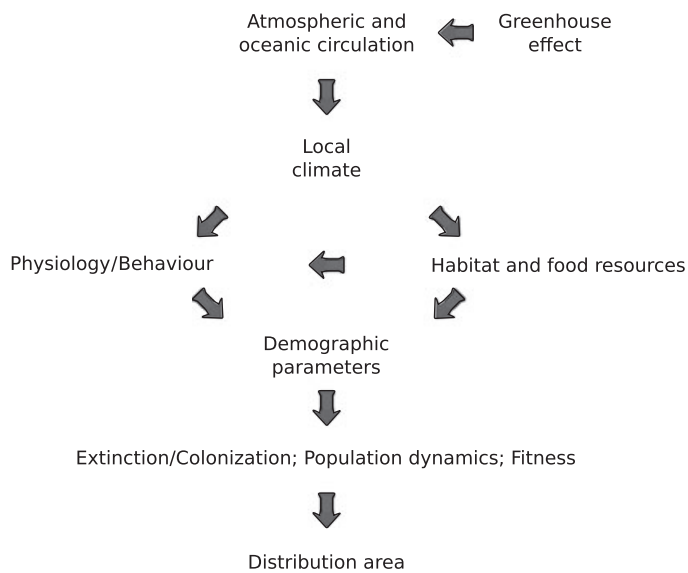
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Atmospheric and ⬅ Greenhouse
oceanic circulation   effect

⬇

Local
climate

↙ ↘

Physiology/Behaviour ⬅ Habitat and food resources

↘ ↙

Demographic
parameters

⬇

Extinction/Colonization; Population dynamics; Fitness

⬇

Distribution area

Figure 1 A general framework for linking climate change and ecology. Free-ranging organisms cope with local climatic conditions (shaped by general atmospheric and oceanic conditions) that are influenced by the greenhouse effect. The local climate influences the ecology of organisms through two pathways: direct influences provoking physiological and behavioural responses, and indirect influences through the modification of habitat conditions and the amount and quality of food resources. Both pathways generate effects on demographic parameters by changing the flow of individuals within (through birth and death) and among (through immigration and emigration) populations, thereby influencing individual fitness and population growth. Spatial heterogeneities in the organisms' responses influence the extinction/colonisation processes which determine the species' range.

influencing demographic processes in populations of abundant and widespread species. Previous studies of climate-induced variation in population dynamics of large herbivores have mostly been performed in mountainous or northern areas and have mainly focussed on the effects of winter conditions (Post & Stenseth 1999), using global measures of climate change such as North Atlantic Oscillation (NAO) as a metric (Hallett et al. 2004). Moreover, most of these studies have looked for relationships between climatic conditions and population growth, but did not evaluate the effects of climate change (e.g. Garrott et al. 2003 on elk Cervus canadensis, Grotan et al. 2008 on ibex Capra ibex). The few studies that have investigated the effects of the timing of spring onset on performance of large herbivores have failed to reveal consistent patterns, either across species or among populations within a given species. Thus, earlier spring was associated with improved individual performance in chamois Rupicapra rupicapra (Garel et al. 2011) and red deer Cervus elaphus (Pettorelli et al. 2005), whereas negative effects of earlier springs on recruitment have been reported in bighorn sheep Ovis canadensis, mountain goat Oreamnos americanus and ibex (Pettorelli et al. 2007). Likewise, reindeer were reported to suffer from the increasing mismatch between the availability of high quality food and the timing of births in Greenland (Post & Forchhammer 2008), whereas they appeared to benefit from earlier springs in Finland (Helle & Kojola 2008). The exact demographic mechanisms through which such contrasting effects of climate change arise remain unknown.

We aimed to fill this gap by analysing the demographic responses of roe deer, Capreolus capreolus, the most abundant and widespread

medium-sized mammalian species in Western Europe (Andersen et al. 1998), to recent climate change using the intensive long-term (> 30 years) monitoring of two contrasted populations. During the last half century, populations of large herbivores have increased substantially over much of the northern hemisphere, both in number and range, due to regulation of hunting and the increased frequency of mild winters (Apollonio et al. 2010). The roe deer is the most successful example of this in a European context (Andersen et al. 1998). Indeed, due to its marked ecological and behavioural plasticity, roe deer could be expected to cope successfully with climate change. To investigate whether this is so, we looked for three possible types of effect of climate change on demographic processes in roe deer using a comparison of contrasting demographic scenarios in terms of population and climatic conditions.

First, we compared how climate change can potentially modify the role of a given demographic parameter (i.e. age-specific survival and fecundity) on population growth across scenarios. This kind of structural change in demography is observed in response to the occurrence of strong perturbations like hunting (Servanty et al. 2011), predation (Nilsen et al. 2009) or disease (Jones et al. 2008). Second, we identified the critical parameter for determining population growth within each demographic scenario. We expected the contribution of a demographic parameter to increase with both its potential demographic impact and its temporal variation (Coulson et al. 2005). Finally, we identified the parameter responsible for driving the observed shift in population growth rate in each demographic scenario.

In temperate areas, climate change involves a co-variation of factors including, for example, earlier spring, higher spring and summer temperatures, a higher peak of plant productivity, a longer vegetative growth season, and an increased frequency of extreme climatic events (IPCC 2007). We focussed on the impact of the timing of the onset of spring on roe deer life history as the effects of climate change are particularly pronounced in this season (Schwartz et al. 2006) and because roe deer females are under substantial energetic stress at this time of year due to the high costs of late gestation and early lactation in large herbivores (Mauget et al. 1997). Moreover, the roe deer can be considered as an income breeder (sensu Jonsson 1997), relying on current resource intake, rather than fat reserves, to offset the costs of reproduction (Andersen et al. 2000). Hence, we assumed that the most evident response of roe deer populations to climate change should be revealed by the link between demography and spring conditions. However, we also discussed possible demographic variation induced by summer conditions, as the expected increase in the frequency of summer drought is also likely to influence roe deer demography at the southernmost limit of its range.

MATERIALS AND METHODS

Roe deer as a biological model

The roe deer is a medium-sized forest-dwelling mammal (about 25 kg, Andersen et al. 1998). This large herbivore occupied lowland forest as its habitat of origin, but since the early eighties has considerably expanded its distribution range northwards and southwards (Andersen et al. 1998), colonising new habitat types including both agricultural landscapes (Kaluzinski 1982) and mountainous areas (Acevedo et al. 2005). Roe deer have low sexual size dimorphism,

with males about 10% larger than females (Hewison *et al.* 2011), and a low level of polygyny (typically less than 3 females mated by a given male in a given year, Vanpé *et al.* 2009). Roe deer females are strongly sedentary, spending their whole life within less than 50 ha in forest habitat (Hewison *et al.* 1998). They are long-lived (up to 18 years of age, Loison *et al.* 1999), iteroparous (one reproductive attempt per year, from 2 years of age onwards, Gaillard *et al.* 1998) and allocate high levels of energy to each breeding attempt, most often producing twins that are born heavy (about 1.6 kg each) and grow quickly (about 150 g^{-1} day) during the weaning period (Gaillard *et al.* 1993a), compared with other large herbivores (Robbins & Robbins 1979). Births are highly synchronised (> 80% of births within less than 25 days) and the mean birth date (15th of May) is remarkably constant over years (Gaillard *et al.* 1993b).

Study sites

We studied two fenced roe deer populations managed by the Office National de la Chasse et de la Faune Sauvage. These populations inhabit deciduous forests managed by the Office National des Forêts. In both forests, oak (*Quercus* sp.) and beech (*Fagus sylvatica*) are the main tree species. At Trois Fontaines, the understorey is made up of hornbeam (*Carpinus betulus*) and brambles (*Rubus* sp.). At Chizé, three different habitats can be identified in relation to the type of timber stand and coppice structure (from richest to poorest: oak with hornbeam, oak with Montpellier maple (*Acer monspessulanum*), and beech with little coppice, Pettorelli *et al.* 2003). Roe deer have been caught every year since 1975 (at Trois Fontaines) and 1977 (at Chizé) using winter drive-netting (over 10 days per year, mostly in January–February) resulting in the capture of roughly half the roe deer present in the forest each year (Gaillard *et al.* 2003). At capture, all animals are weighed, inspected for marks or newly marked (with both leather numbered collars and ear-tags) and, at Chizé only, the reproductive status of females is assessed using ultrasonography (since 1988). Marked known-aged roe deer are then released back to the forest, while a variable number of animals of unknown age (between 0 and 150) are removed to manipulate population size (Fig. 2). As a result, observed variation in population abundance over time was mainly driven by management strategy and was therefore decoupled from the variation in demographic parameters estimated from the monitoring of known-aged and individually recognisable animals (more than 70% of the population during most years).

The two sites are quite contrasted in terms of environmental conditions. Trois Fontaines is a 1360 ha forest located in Eastern France (48°43′ N, 2°61′ W), with a continental climate typified by rather cold winters (mean daily temperature in January of 3.1 °C) and warm but often wet summers (mean daily temperature in July of 19.6 °C with an average total rainfall of 72.4 mm). Trois Fontaines lies on rich and fertile soils, leading to high forest productivity (long-term average wood production of 5.9 m^3 ha^{-1} per year, Pettorelli *et al.* 2006). In contrast, the Réserve Biologique Intégrale of Chizé is a 2614 ha forest located in Western France (46°05′ N, 0°25′ W), with an oceanic climate under some Mediterranean influence, characterised by mild winters (mean daily temperature in January of 5.6 °C) and warm but often dry summers (mean daily temperature in July of 20.5 °C with an average total rainfall of 53.4 mm). Forest productivity at Chizé is quite low (long-term average wood production of 3.8 m^3 ha^{-1} per year, Pettorelli *et al.* 2006). As a direct result of these between-population differences in
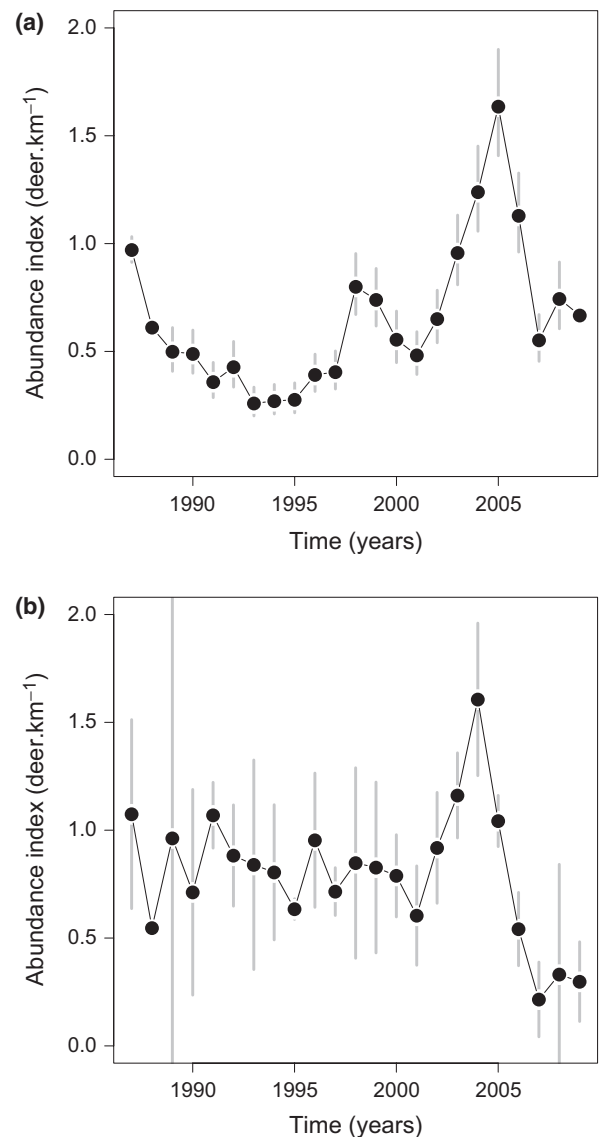
Figure 2 Yearly abundance index of roe deer population size at (a) Chizé and (b) Trois Fontaines. The index corresponds to the average number of roe deer observed per km of standardised transect walked in March–April (see Vincent *et al.* 1991 for further details)

climatic and edaphic conditions, the demographic performance of the roe deer population was substantially higher at Trois Fontaines than at Chizé, especially during the late seventies and early eighties (Nilsen *et al.* 2009), but less so during the period studied here (1988–2009). There are no large predators and no hunting of roe deer on either of the sites, and no epizootic events have been recorded, despite regular epidemiological surveys on the caught roe deer.
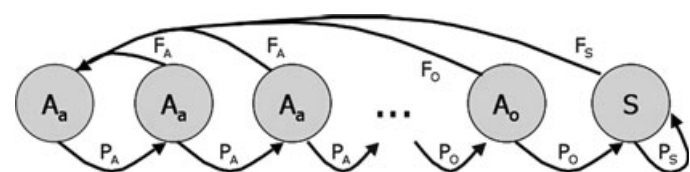
We assessed the magnitude of climate change in both study sites using the number of degree-days higher than 7 °C (°D7) from February to April, when early plant growth occurs in both sites. In temperate areas, this metric is indeed directly related to the phenology of vegetation (plant growth), rather than to plant abundance (Wilson & Barnett 1983). That is, the vegetation flush occurs increasingly earlier as the number of degree-days > 7 °C increases. For the period 1976–2011, annual mean daily temperature and total

rainfall were obtained from Météo-France weather stations located within 5 km of the study areas (Beauvoir-sur-Niort for Chizé and Saint-Dizier for Trois Fontaines). To detect evidence of climate change over the study period, we then regressed the number of degree-days > 7 °C against time (in years).
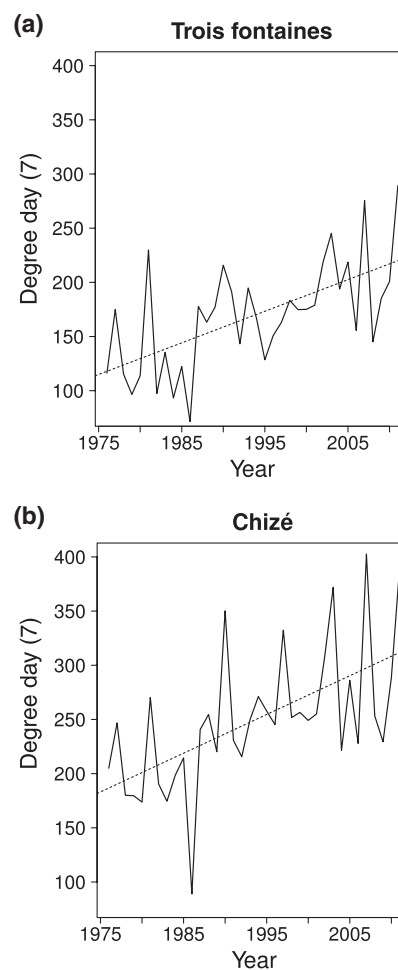
Assessing demographic processes

The intensive Capture-Mark-Recapture monitoring of roe deer in both study sites allowed us to obtain a complete time series of reliable annual estimates of all demographic parameters from 1988 to 2009 (Gaillard et al. 2003; Nilsen et al. 2009). To investigate a possible regime shift of demography in response to climate change, we divided the population-specific time series into two periods of equal duration (i.e. 11 year periods). We expected the spring vegetation flush to occur later on average during the first period (1988–1998) than during the second period (1999–2009). We thus built four demographic scenarios using population- and period-specific parameters. To account for possible confounding effects of density-dependence, we tested for density-dependent responses of all demographic parameters in both populations (see Appendix S1 for further details). As density-dependent responses occurred in most parameters during the study period at Chizé, we replicated the demographic analysis for this site by standardising the yearly estimates to the median density (Appendix S1). We modelled each scenario using a pre-census Leslie matrix model (Caswell 2001). The life cycle graph (Fig. 3) included four age classes and four demographic parameters. Female recruitment in a given age class was defined as the product between the proportion of females that give birth, the number of female offspring produced by those females, and offspring survival between birth and 1 year of age. We obtained yearly estimates of these parameters by updating previous analyses (e.g. Gaillard et al. 2003). As roe deer females reproduce for the first time at 2 years of age (but see Van Laere et al. 1997 for an exceptional case of successful reproduction at 1-year old), recruitment at 1 year old was set to 0. Although female fertility decreases from 12 years of age onwards in roe deer (Gaillard et al. 1998), we assumed a constant recruitment rate with age because we were unable to generate reliable year-specific estimates of recruitment for old females due to the scarcity of data. Following previous analyses (Gaillard et al. 2003), we considered three age classes for survival: a prime-age stage, from 1 to 7 years of age, an old-age stage, from 7 to 12 years of age, and a senescent stage, from 12 years onwards.

For each population- and period-specific matrix, we estimated the deterministic population growth rate (λ) and the elasticity of each demographic parameter (i.e. the proportional change in λ obtained

when changing a given parameter by 1%) using standard matrix calculations (Caswell 2001). To assess the potential impact of a given demographic parameter on λ, we performed a prospective analysis (sensu Caswell 2000) by comparing the ranking and the relative values of elasticities among demographic scenarios. We then measured the contribution of a given demographic parameter to the observed variance in λ by performing a retrospective analysis (sensu Caswell 2000). Using the approximation of variance in λ proposed by Horvitz et al. (1996), we measured the absolute contribution of a given parameter as the product of its squared elasticity and its squared coefficient of variation (CV). The sum of the contributions of all demographic parameters provided a measure of variance in λ. The relative contribution of a given demographic parameter to the observed variance in λ was then obtained as the ratio between the absolute contribution of that parameter and the variance in λ. As co-variations can be important, we also measured the contribution of the two-way interactions between demographic parameters to the observed variance in λ. However, we did not account for possible serial autocorrelations in demographic parameters. Lastly, we performed a Life Table Response Experiment (LTRE, Caswell 2001) to measure the contribution of a given demographic parameter to the observed difference in λ between scenarios. We excluded senescent

Figure 3 Life cycle graph of roe deer. A_a: females in the prime-age stage (from 1 to 7 years of age), A_o: females in the old-age stage (from 7 to 12 years of age), S: females in the senescent stage (from 12 years of age onwards), P: annual survival probability, F: recruitment (measured as the number of female offspring at 1 year of age produced by a female of 2-years old or older).

Figure 4 Yearly changes in the number of degree-days > 7 °C (February to April) between 1976 and 2011 at (a) Trois Fontaines and (b) Chizé. The dotted line corresponds to the best-fit linear increase over time.

Table 1 Potential impact of a proportional change in a given demographic parameter on λ (measured by the elasticity) for the four contrasting scenarios describing roe deer demography for two periods (normal (1988–1998) and early (1999–2009) springs) and two populations (Chizé and Trois Fontaines)
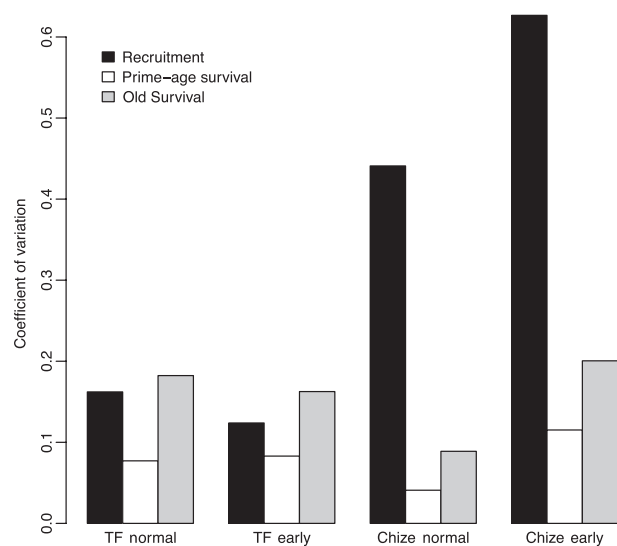
Demographic scenario	Recruitment	Prime-age stage survival	Old-age stage survival	Senescent stage survival
Chizé (Normal springs)	0.230	0.703	0.065	0.002
Chizé (Early springs)	0.215	0.704	0.076	0.005
Trois Fontaines (Normal springs)	0.246	0.705	0.048	0.001
Trois Fontaines (Early springs)	0.217	0.715	0.065	0.003

stage survival from these analyses because of its negligible contribution (i.e. an order of magnitude lower than the smallest contribution of other parameters) to variation in population growth rate.

RESULTS

A strong signal of climate change

In both study sites, the number of degree-days > 7 °C increased markedly over time (yearly increase of 2.91 °D7 ± 0.65, $P < 0.001$ and 3.58 °D7 ± 0.84, $P < 0.001$ at Trois Fontaines and Chizé, respectively, Fig. 4), demonstrating that spring occurred increasingly earlier over years at both locations. From these models, we obtained a clear difference in the timing of the onset of spring between the two 11-year periods (model estimates of 167.49 and 247.46 °D7 for 1988–1998, hereafter denoted 'normal spring period', vs. 199.55 and 286.79 °D7 for 1999–2009, hereafter denoted 'early spring period', for Trois Fontaines and Chizé respectively).

Prospective demographic analysis

The potential impact of a proportional change in a given demographic parameter on λ was remarkably constant across demographic scenarios (Table 1). A given proportional change in prime-age stage survival consistently had the largest impact on growth rate, provoking a modification in λ that was about three times greater than an equivalent change in recruitment and about 10 times greater than an equivalent change in old-age stage survival. In contrast, the impact of an equivalent change in senescent stage survival on λ was negligible (Table 1). Clearly, therefore, the relative potential impact of the different demographic parameters on λ was insensitive to both the difference in the earliness of spring between periods and to the differences in environmental conditions between populations. Accounting for density-dependence (Chizé only) did not influence this general pattern (Table S2).

Retrospective demographic analysis

In all four demographic scenarios, prime-age stage survival was less variable among years than recruitment rate and old-age survival (with a CV of around 0.10 or less, Fig. 5). However, marked between-population differences occurred in both the magnitude of temporal variation in demographic parameters and the sensitivity of this variation to changes in the earliness of spring. At Trois Fontaines, the overall variation in all demographic parameters was quite low (all CVs less than 0.20, Fig. 5) and was not influenced by the between-period difference in the earliness of the onset of spring. In contrast, there was marked temporal variation in recruitment at Chizé, with a CV of more than 0.40 (Fig. 5) [or more than 0.30 (Fig. S1) when accounting for density-dependence] and the observed between-year variation in all parameters was higher during
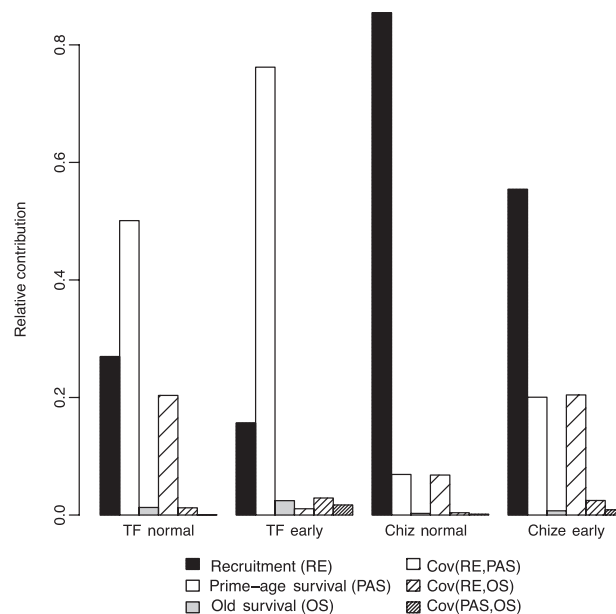

Figure 5 Coefficients of variation for temporal variation in each demographic parameter for the four demographic scenarios. TF Normal: Trois Fontaines population monitored during years with normal springs (1988–1998); TF Early: Trois Fontaines population monitored during years with early springs (1999–2009); Chizé Normal: Chizé population monitored during years with normal springs (1988–1998); Chizé Early: Chizé population monitored during years with early springs (1999–2009).

Figure 6 Relative contribution of the demographic parameters to observed variation in population growth rate in the four demographic scenarios. TF Normal: Trois Fontaines during normal springs (1988–1998); TF Early: Trois Fontaines during early springs (1999–2009); Chizé Normal: Chizé during normal springs (1988–1998); Chizé Early: Chizé during early springs (1999–2009).

the early spring period compared with the normal spring period [0.40 vs. 0.6 (Fig. 5), or 0.30 vs. 0.36 (Fig. S1) when accounting for density-dependence]. These clear differences in the variation of demographic parameters between populations, periods and parameters (Fig. 5) are in marked contrast with the virtually constant patterns of parameter elasticity across demographic scenarios (Table 1). As a consequence, it remains clear that among-scenario differences in demography were driven by differences in the relative amount of temporal variation among demographic parameters. As a result of the above, the variance in λ was one order of magnitude larger at Chizé than at Trois Fontaines, and was largest during the period of early spring in both populations (variance of 0.0328 vs. 0.0119 and of 0.0044 vs. 0.0033 in the period of early spring vs. normal spring at Chizé and Trois Fontaines respectively). This pattern was consistent even when correcting for density-dependence at Chizé (variance of 0.0130 vs. 0.0074).

The marked variation in recruitment rate over years observed at Chizé meant that the observed variation in λ was mostly accounted for by changes in this demographic parameter (Fig. 6). However, although temporal variation in recruitment rate was higher during the early spring period compared with the normal spring period at Chizé, the relative contribution of recruitment rate to variance in λ was lower during the early spring period (Fig. 6 and Fig. S2) because temporal variation in adult survival (when either not accounting for density-dependence or doing so respectively) was also higher during this period (Fig. 5 and Fig. S1). As a result, temporal variation in prime-age stage survival (respectively old stage survival) accounted for about one-fifth (respectively one tenth) of the observed variation in λ in this scenario [compared to about one tenth (respectively one per cent) in normal years, Fig. 6 (respectively Fig. S2)]. At Trois Fontaines, the observed variance in λ was mostly

driven by variation in prime-age stage survival (Fig. 6), despite the fact that temporal variation in both recruitment rate and old-age stage survival was clearly more marked (Fig. 5). This pattern was due to the low absolute variation in all four demographic parameters during both the normal spring and early spring periods (Fig. 5) which limited the degree of variance in λ. As a result, the relative contribution of the three demographic parameters to variance in λ was predominantly shaped by their elasticity values. The co-variation among parameters contributed relatively little to variance in λ (from 5.7 to 23.8%) compared to their main effects (Fig. 6 and Fig. S2). The co-variation between recruitment rate and prime-age stage survival was the most important of the co-variations, but there was no obvious pattern concerning the contribution of this co-variation among scenarios, that is, in relation to the earliness of the onset of spring or between populations (Fig. 6 and Fig. S2).

Life table response analyses (LTRE)

We performed four LTREs to assess the relative contributions of the three demographic parameters to observed differences in population growth rate among scenarios, both between populations for a given period of spring earliness and between periods for a given population (Fig. 7). The between-period difference in λ within a given population was much larger than the between-population difference within a given period. The slightly higher λ at Chizé (1.298) than at Trois Fontaines (1.284) during the normal spring period was due to higher survival at Chizé for both prime-age (0.958 vs. 0.911 at Trois Fontaines) and old-age (0.921 vs. 0.819 at Trois Fontaines) stages, which almost exactly compensated for the lower recruitment rate observed at Chizé (0.48 vs. 0.55 at Trois Fontaines). As a result, recruitment rate and survival had an approximately equivalent influence on the between-population difference in λ. In contrast, during the early spring period, λ was higher at Trois Fontaines than at Chizé, and this was almost entirely due to the between-population difference in prime-age stage survival (0.955 at Trois Fontaines vs. 0.895 at Chizé). When accounting for density-dependence (Chizé only), the between-period difference in λ was weak (1.278 vs. 1.264).

The lower values of λ during the early spring period compared with the normal spring period were mostly driven by a fall in recruitment rate in both populations between periods (from 0.48 to 0.36 at Chizé and from 0.55 to 0.34 at Trois Fontaines). This result held when accounting for density-dependence at Chizé (Fig. S3). However, despite this more marked susceptibility of recruitment rate to earlier springs at Trois Fontaines, the observed λ was slightly higher in this population (1.187) compared with Chizé (1.147) during the early spring period. This was due to an increase in prime-age stage survival at Trois Fontaines during the early spring period (0.955 vs. 0.911 during the normal spring period), which dampened the decrease of λ between periods. Hence, at Trois Fontaines, the lower value λ observed during the early spring period compared to the normal spring period was essentially due to a lower recruitment rate. In contrast, at Chizé, a lower level of prime-age stage survival (respectively old-age stage survival when accounting for density-dependence) during the early spring period [0.895 (respectively 0.874) compared with 0.958 (respectively 0.914) observed during normal springs] acted in concert with the lower level of recruitment to generate the lower value of λ in this demographic scenario.
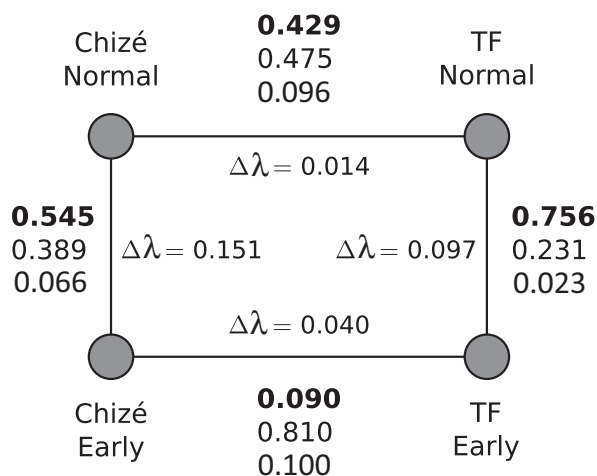
Figure 7 Results of the Life Table Response Experiment analyses performed for four scenarios comprising two populations and two periods of contrasting spring earliness. We report the relative contributions of recruitment rate (in bold), prime-age stage survival (in standard typeface) and old-age stage survival (in italics) to observed differences in λ (Δλ) among scenarios: between populations within a given period (horizontal comparisons) and between periods within a given population (vertical comparisons). TF Normal: Trois Fontaines during normal springs (1988–1998); TF Early: Trois Fontaines during early springs (1999–2009); Chizé Normal: Chizé during normal springs (1988–1998); Chizé Early: Chizé during early springs (1999–2009).

DISCUSSION

Two main outcomes can be identified from our comparative analyses of contrasted populations of roe deer. First, there is a clear evidence for a strong signature of climate change involving increasingly earlier springs over time in both study sites. This is in line with previous studies that have identified similar trends across the whole Northern hemisphere (e.g. Schwartz *et al.* 2006). However, it is noteworthy that the signature of climate change was almost identical in both study sites (with a linear increase of about 3 degree-days > 7 °C per year) despite the fact that they are 600 km apart. Interestingly, a remarkably similar signature of climate change was observed in a third site (Aurignac in South France, 43°13′ N, 0°52′ E) where the roe deer population has been intensively monitored for about 12 years (Hewison *et al.* 2009). In this site, composed of forest patches interspersed within a matrix of agricultural land and subject to an Aquitanian climatic type (a warmer and drier variant of an oceanic climate), the number of degree-days > 7 °C also increased by about 3 units per year (slope of 3.396 ± 0.786). This suggests the existence of a rather constant speed of change in the earliness of spring across the lowlands of Western Europe.

Second, the population growth rate for roe deer at both study sites was lower during the more recent period with early springs compared to the preceding period with normal springs (Fig. 7). This demographic shift involved several demographic processes which differed in relation to the environmental conditions of the focal population. The relative potential role of the different demographic parameters did not vary, either in response to earlier springs or between populations experiencing contrasting environmental conditions. This indicates, irrespective of whether density-dependence occurred, that the continuous and regular increase in the earliness of spring did not markedly affect the functional dependence of population growth rates on given demographic parameters. This contrasts with the demographic response to sudden and strong perturbations generated by disease (Jones *et al.* 2008), heavy hunting (Proaktor *et al.* 2007; Servanty *et al.* 2011) or strong predation pressure (Wittmer *et al.* 2005; Festa-Bianchet *et al.* 2006). This has practical consequences, as it means that the demographic signature of climate change is potentially much harder to detect than that of other types of perturbation and requires long-term and detailed monitoring to be assessed. Indeed, obtaining accurate estimates of demographic parameters across climatic gradients is an important priority for future data collection (Brook *et al.* 2009). Likewise, the critical demographic parameter that contributed most strongly to the observed variance in growth rate among years of a given population did not differ between the period with normal springs and the period with early springs, but this critical parameter did differ between populations. At Chizé, recruitment rate had the highest contribution to observed variance in population growth rate in both periods, whereas prime-age stage survival was the critical parameter for both periods at Trois Fontaines. This supports the view that the identity of the critical demographic parameter is context-dependent (Coulson *et al.* 2005). We tentatively propose that the amount of variation observed in population growth rate could determine which parameter is critical. When this variance is low, we expect demographic parameters with the highest potential demographic impact to drive variation in population growth, whereas when it is high, demographic parameters with the highest temporal variation should contribute the most.

In contrast, in both populations, the lower growth observed during the early spring period was mainly due to a marked decline in recruitment. This reinforces our inference that spring is the critical period for roe deer, with early fawn mortality in relation to maternal condition and climatic conditions during late gestation and early lactation driving roe deer recruitment (Gaillard *et al.* 1997). This also provides some of the first evidence that the demographic parameters that are responsible for most of the variation in population growth rate among years may not necessarily be the same as those that drive changes in mean growth rate between periods of contrasting environmental conditions. It is also noteworthy that at Chizé, where roe deer suffered most from early springs, adult survival also decreased in the period of early springs and partly accounted for the observed decline in population growth rate. The marked increase in adult prime-age survival between periods when accounting for density-dependence (from 0.895 to 0.934) indicates that both high density and climate change must occur simultaneously to influence prime-age adult survival markedly. As adult survival is generally buffered against environmental variation in long-lived mammals (Gaillard & Yoccoz 2003), the low values of this parameter that we observed in recent years at Chizé during high density might indicate severe energetic stress in this population. This was supported recently by biochemical and immunological analyses (Gilot-Fromont *et al.* 2012). This observation suggests that, in addition to spring earliness, summer climatic conditions might also limit population growth in water-stressed environments. Severe summer droughts such as that in 2003 at Chizé have indeed been linked to increased female mortality in roe deer (Bonenfant *et al.* unpublished data).

The identification of recruitment as the key parameter in the observed decline of population growth rate in response to increasingly earlier springs in both populations suggests the existence of a general explanation related to the life history of the focal species. In temperate regions, we can consider three possible ways for organisms of a given species to cope with climate change involving increasingly earlier springs. The simplest way involves resisting this change, maintaining invariant timing of life history events and constant demographic performance. To be efficient, this (absence of) response requires some degree of decoupling between vegetation phenology and the resource acquisition process needed for meeting the energy requirements of reproduction. Previously accumulated body reserves (i.e. capital breeding tactic, Jonsson 1997) or a diet based on food items which are not directly dependent on the vegetation might provide potential pathways to acquire resources independently of the timing of the vegetation flush. These pathways are clearly not available to a medium-sized herbivore feeding on plants which are available in forest coppice and displaying an income breeder tactic such as the roe deer. As a result, the roe deer is unable to resist the energetic constraints imposed by increasingly early springs and the increasing frequency of summer droughts, likely because of its strong dependence on high quality vegetation (Latham *et al.* 1999). This resulted in a marked decline in demographic performance in both our study populations.

A second way to deal successfully with increasingly early springs involves adapting the timing of life history events to track changes in the phenology of vegetation. This has been reported to occur in several vertebrate species (Visser 2008; Carey 2009), including large herbivores (Moyes *et al.* 2011 on red deer). The lower population growth that we observed in both populations during the period of

early springs indicates that roe deer are unable to adjust the timing of their reproductive cycle to maintain constant demographic performance. In particular, contrary to other large mammalian herbivores such as red deer (Coulson *et al.* 2003) or wild boar (Gamelon *et al.* 2011), roe deer females have inflexible birth dates (Plard *et al.* unpublished data), leading to an increasingly marked mismatch between the earlier vegetation flush and the birth peak which has remained constant over years. For an income breeder which allocates substantially to reproduction, a decrease in resource availability during late gestation-early lactation, when energy expenditure peaks in large herbivores (Oftedal 1985), is likely to lead to increased early mortality of offspring. In both populations, a decrease in recruitment was responsible for most of the observed decline in population growth, involving a marked decrease in early survival of fawns when shifting from normal to early springs (from 0.75 to 0.64 and from 0.60 to 0.42 at Chizé and Trois Fontaines respectively). The ability, or lack of it, to match the phenology of reproductive events to earlier springs might thus be the critical factor determining which organisms can and cannot adapt to climate change in seasonal environments (Coppack & Both 2002). For instance, Salido *et al.* (2012) recently showed that increased flexibility of laying date positively correlated with population growth rate among UK passerine bird species. Likewise, Pau *et al.* (2011) predicted that the phenology of plant species of temperate areas should shift in time in response to earlier springs. Although data from a larger range of populations would be required, our findings strongly suggest that the inflexibility of birth date in roe deer leads to the observed decline of population growth in early spring years through increased early offspring mortality because roe deer females are unable to track temporal changes in the phenology of the vegetation flush.

The last way to cope with changing spring conditions involves escaping this change by moving. For instance, seasonal migration has been observed in a large range of organisms and has been interpreted as a tactic for tracking spatio-temporal variation in resources (Swingland & Greenwood 1983; Fryxell & Sinclair 1988). Shifting spatial distribution is also predicted to be the response of tropical plant species to climate change (Pau *et al.* 2011). However, in a context of global change, moving through space is unlikely to enable populations or species to directly escape increasingly early springs, as this is a general phenomenon across temperate areas. However, individuals may successfully cope with earlier springs by moving into secondary habitats that provide alternative food resources during the critical mismatch period. Agricultural landscapes, which include forest patches disseminated within open habitats of differing nature and containing a variety of food resources, might provide such a suitable habitat for roe deer. Interestingly, roe deer began to colonise agricultural landscapes in the late seventies and now occupy most of this habitat type throughout Western Europe. Moreover, roe deer appear to perform better in these open agroecosystems than in forest blocks. Indeed, by obtaining access to higher quality diets, especially in terms of nitrogen and phosphorous content, roe deer in open areas are able to attain larger body mass than in strict forest habitat (Hewison *et al.* 2009). As fast early body development is positively associated with increased early survival (Da Silva *et al.* 2009), we might expect roe deer in agricultural landscapes to cope with ongoing climate change, and in particular increasingly earlier springs, without adjusting the timing of their reproductive cycle.

Our demographic analysis suggests that the roe deer, following a very rapid increase in abundance over the eighties-nineties through-

out Western Europe, could be now confronting the adverse effects of increasingly early springs. This seems to be a general pattern throughout its geographical range. Indeed, hunting statistics show that the previously marked increase in the number of roe deer shot annually has reached a ceiling, or may even be decreasing, in most European countries since the early part of this century (Apollonio *et al.* 2010). We suggest that these are the first signs that the 'success story' of forest roe deer that began in the second half of the last century (Andersen *et al.* 1998) might be nearing its end due to climate change. Indeed, given the current level of hunting pressure that is exerted on this economically important game species, roe deer populations in strict forest habitat may soon decline markedly as spring becomes increasingly early. In contrast, because the breeding phenology of sympatric large herbivores such as red deer and wild boar appears more flexible (Gamelon *et al.* 2011; Moyes *et al.* 2011), these species may cope more efficiently with ongoing climate change. This predicted interspecific asynchrony in the effects climate change among sympatric large herbivores (but see Mysterud *et al.* 2007) is likely to impact on interspecific relationships within multi-herbivore communities. We suggest that the only way roe deer can escape the adverse effects of climate change is by increasingly shifting their distribution to open landscapes which offer richer food resources during spring, enabling females to successfully offset their energetic requirements during the critical rearing stage. This testable prediction is a promising avenue for future investigation.

REFERENCES

Acevedo, P., Delibes-Mateos, M., Escudero, M.A., Vicente, J., Marco, J. & Gortazar, C. (2005). Environmental constraints in the colonization sequence of roe deer (*Capreolus capreolus* Linnaeus, 1758) across the Iberian Mountains, Spain. *J. Biogeogr.*, 32, 1671–1680.

Andersen, R., Duncan, P. & Linnell, J.D.C. (1998). *The European Roe Deer: the Biology of Success.* Scandinavian University Press, Oslo, Norway.

Andersen, R., Gaillard, J.-M., Linnell, J.D.C. & Duncan, P. (2000). Factors affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.*, 69, 672–682.

Andrewartha, H.G. & Birch, L.C. (1954). *The Distribution and Abundance of Animals.* Chicago University Press, Chicago, Illinois, USA.

Apollonio, M., Andersen, R. & Putman, R. (2010). *European Ungulates and their Management in the 21st Century.* Cambridge University Press, Cambridge, UK.

Barbraud, C. & Weimerskirch, H. (2001). Emperor penguins and climate change. *Nature*, 411, 183–186.

Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T. et al. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. Lond. B.*, 271, 1657–1662.

Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. & Araujo, M.B. (2009). Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biol. Lett.*, 5, 723–725.

Carey, C. (2009). The impacts of climate change on the annual cycles of birds. *Phil. Trans. R. Soc. B.*, 364, 3321–3330.

Caswell, H. (2000). Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, 81, 619–627.

Caswell, H. (2001). *Matrix Population Models: construction, Analysis and Interpretation*, 2nd edn.. Sinauer Associates, Sunderland, Massachusetts, USA.

Coppack, T. & Both, C. (2002). Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea*, 90, 369–378.

Coulson, T., Kruuk, L.E.B., Tavecchia, G., Pemberton, J.M. & Clutton-Brock, T.H. (2003). Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*, 57, 2879–2892.

Coulson, T., Gaillard, J.-M. & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *J. Anim. Ecol.*, 74, 789–801.

Da Silva, A., Gaillard, J.-M., Yoccoz, N.G., Hewison, A.J.M., Galan, M., Coulson, T. et al. (2009). Heterozygosity-fitness correlations revealed by neutral and candidate gene markers in roe deer from a long-term study. *Evolution*, 63, 403–417.

Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T. & Pelletier, F. (2006). Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc. B.*, 273, 1537–1543.

Fryxell, J.M. & Sinclair, A.R.E. (1988). Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.*, 3, 237–241.

Gaillard, J.-M. & Yoccoz, N.G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, 84, 3294–3306.

Gaillard, J.-M., Delorme, D. & Jullien, J.-M. (1993a). Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia*, 94, 57–61.

Gaillard, J.-M., Delorme, D., Jullien, J.-M. & Tatin, D. (1993b). Timing and synchrony of births in roe deer. *J. Mamm.*, 74, 738–744.

Gaillard, J.-M., Boutin, J.M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.D. (1997). Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, 112, 502–513.

Gaillard, J.-M., Liberg, O., Andersen, R., Hewison, A.J.M. & Cederlund, G. (1998). Population dynamics of roe deer. In *The European Roe Deer: the Biology of Success*. (eds Andersen, R., Duncan, P. & Linnell, J.D.C.). Scandinavian University Press, Oslo, Norway, pp. 309–335.

Gaillard, J.-M., Duncan, P., Delorme, D., Van Laere, G., Pettorelli, N., Maillard, D. et al. (2003). Effects of hurricane Lothar on the population dynamics of European roe deer. *J. Wildl. Manage.*, 67, 767–773.

Gamelon, M., Besnard, A., Gaillard, J.-M., Servanty, S., Baubet, E., Brandt, S. et al. (2011). High hunting pressure selects for earlier birth date: wild boar as a case study. *Evolution*, 65, 3100–3112.

Garel, M., Gaillard, J.-M., Jullien, J.M., Dubray, D., Maillard, D. & Loison, A. (2011). Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *J. Mamm.*, 92, 1112–1117.

Garrott, R.A., Eberhardt, L.L., White, P.J. & Rotella, J. (2003). Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology*, 81, 33–45.

Gilot-Fromont, E., Jégo, M., Bonenfant, C., Gibert, P., Rannou, B., Klein, F. et al. (2012). Immune phenotype and body condition in roe deer: individuals with high body condition have different, not stronger immunity. *PLoS ONE*, 7, e45576.

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J. et al. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.*, 83, 357–399.

Grotan, V., Saether, B.E., Filli, F. & Engen, S. (2008). Effects of climate on population fluctuations of ibex. *Global Change Biol.*, 14, 218–228.

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, 8, 993–1009.

Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.*, 135, 147–186.

Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B.T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430, 71–75.

Hansen, B.B., Aanes, R., Herfindal, I., Kohler, J. & Saether, B.E. (2011). Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology*, 92, 1917–1923.

Helle, T. & Kojola, I. (2008). Demographics in an alpine reindeer herd: effects of density and winter weather. *Ecography*, 31, 221–230.

Hewison, A.J.M., Vincent, J.-P. & Reby, D. (1998). Social organisation of European roe deer In: *The European Roe Deer: the Biology of Success* (ed. Andersen, R., Duncan, P. & Linnell, J.D.C.). Scandinavian University Press, Oslo, Norway, pp. 189–219.

Hewison, A.J.M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J.M., Cargnelutti, B. et al. (2009). Landscape fragmentation influences winter body mass of roe deer. *Ecography*, 32, 1062–1070.

Hewison, A.J.M., Gaillard, J.M., Delorme, D., Van Laere, G., Amblard, T. & Klein, F. (2011). Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size allometry in roe deer. *Oikos*, 120, 1217–1226.

Horvitz, C., Schemske, D.W. & Caswell, H. (1996). The relative "importance" of life-history stages to population growth: prospective and retrospective analyses In: *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (ed. Tuljapurkar, S. & Caswell, H.). Chapman & Hall, New York, New York, USA, pp. 247–271.

Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006). Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, 148, 8–28.

IPCC (2007). *Intergovernmental Panel on Climate Change: fourth Assessment Report*. (http://www.ipcc.ch).

Jones, M.E., Cockburn, A., Hamede, R., Hawkins, C., Hesterman, H., Lachish, S. et al. (2008). Life-history change in disease-ravaged Tasmanian devil populations. *PNAS*, 105, 10023–10027.

Jonsson, K.I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78, 57–66.

Kaluzinski, J. (1982). Dynamics and structure of a field roe deer population. *Acta Theriol.*, 27, 385–408.

Lande, R., Engen, S. & Sæther, B.-E. (2003). *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, UK.

Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O. & Dobson, F.S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature*, 489, 554–557.

Latham, J., Staines, B.W. & Gorman, M.L. (1999). Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. *J. Zool.*, 247, 409–418.

Lebreton, J.-D. (2011). The impact of global change on terrestrial vertebrates. *Comptes Rendus Biologies*, 334, 360–369.

Leslie, P.H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, 35, 213–245.

Lewontin, R.C. & Cohen, D. (1969). On population growth in a randomly varying environment. *PNAS*, 62, 1056–1060.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Jullien, J.M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, 80, 2539–2554.

Mauget, C., Mauget, R. & Sempéré, A. (1997). Metabolic rate in female European roe deer (*Capreolus capreolus*): incidence of reproduction. *Can. J. Zool.*, 75, 731–739.

Moyes, K., Nussey, D.H., Clements, M.N., Guinness, F.E., Morris, A., Morris, S. et al. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biol.*, 17, 2455–2469.

Mysterud, A., Tryjanowski, P., Panek, M., Pettorelli, N. & Stenseth, N.C. (2007). Inter-specific synchrony of two contrasting ungulates: wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*). *Oecologia*, 151, 232–239.

Nicholson, A.J. (1933). The balance of animal populations. *J. Anim. Ecol.*, 2, 132–178.

Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., Van Laere, G. et al. (2009). A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *J. Anim. Ecol.*, 78, 585–594.

Oftedal, O.T. (1985). Pregnancy and lactation In: *Bioenergetics of Wild Herbivores* (ed. Hudson, R.J. & White, R.G.). CRC Press, Florida, USA, pp. 215–238.

Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T. & Olson, L.E. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466, 482–485.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Evol. Syst.*, 37, 637–669.

Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K. *et al.* (2011). Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biol.*, 17, 3633–3643.

Pettorelli, N., Dray, S., Gaillard, J.-M., Chessel, D., Duncan, P., Illius, A. *et al.* (2003). Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia*, 137, 363–369.

Pettorelli, N., Mysterud, A., Yoccoz, N.G., Langvatn, R. & Stenseth, N.C. (2005). Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc. R. Soc. B*, 272, 2357–2364.

Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Stenseth, N.C., Delorme, D. *et al.* (2006). Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos*, 112, 565–572.

Pettorelli, N., Pelletier, F., von Hardenberg, A., Festa-Bianchet, M. & Côté, S.D. (2007). Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology*, 88, 381–390.

Post, E. & Forchhammer, M.C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Phil. Trans. R. Soc. B*, 363, 2369–2375.

Post, E. & Stenseth, N.C. (1999). Climatic variability, plant phenology, and northern ungulates. *Ecology*, 80, 1322–1339.

Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007). Evolutionary responses to harvesting in ungulates. *J. Anim. Ecol.*, 76, 669–678.

Robbins, C.T. & Robbins, B.L. (1979). Fetal and neonatal growth- Patterns and maternal reproductive effort in ungulates and sub-ungulates. *Am. Nat.*, 114, 101–116.

Salido, L., Purse, B.V., Marrs, R., Chamberlain, D.E. & Shultz, S. (2012). Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. *Ecography*, 35, 604–613.

Schwartz, M.D., Ahas, R. & Aasa, A. (2006). Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biol.*, 12, 343–351.

Servanty, S., Gaillard, J.-M., Ronchi, F., Focardi, S., Baubet, E. & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: implications for wildlife management. *J. Appl. Ecol.*, 48, 835–843.

Swingland, I.R. & Greenwood, P.J. (1983). *The Ecology of Animal Movements*. Oxford University Press, Oxford, UK.

Tuljapurkar, S. & Orzack, S.H. (1980). Population dynamics in variable environments. 1. Long-run growth rates and extinction. *Theor. Pop. Biol.*, 18, 314–342.

Van Laere, G., Renaud, G. & Gaillard, J.-M. (1997). Observation d'un cas de reproduction réussie chez un chevreuil (*Capreolus capreolus*) de moins de 12 mois. *Mammalia*, 61, 267–270.

Vanpé, C., Gaillard, J.-M., Morellet, N., Kjellander, P., Liberg, O., Delorme, D. *et al.* (2009). Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J. Mamm.*, 90, 661–665.

Vincent, J.-P., Gaillard, J.-M. & Bideau, E. (1991). Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theriol.*, 36, 315–328.

Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B*, 275, 649–659.

Wilson, L.T. & Barnett, W.W. (1983). Degree days: an aid in crops and pest management. *Calif. Agric.*, 37, 4–7.

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S. *et al.* (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. *Canada. Can. J. Zool.*, 83, 407–418.

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