# A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations

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## Summary

**1.** Environmental conditions shape population growth through their impact on demographic parameters. While knowledge has accumulated concerning the effects of population density and climatic conditions, a topical question now concerns how predation and harvest influence demographic parameters and population growth ($\lambda$).

**2.** We performed a comparative demographic analysis based on projection matrix models for female roe deer. Population-specific matrices were parameterized based on longitudinal data from five intensively monitored populations in Norway and France, spanning a large variability in environmental characteristics such as densities of large predators, hunter harvest and seasonality.

**3.** As expected for a large iteroparous vertebrate, temporal variation was invariably higher in recruitment than in adult survival, and the elasticity of adult survival was consistently higher than that of recruitment. However, the relative difference in elasticity of $\lambda$ to recruitment and adult survival varied strongly across populations, and was closely correlated with adult survival.

**4.** Different traits accounted for most of the variance in $\lambda$ in different ecological settings. Adult survival generally contributed more in populations with low mean adult survival and low mean growth rate during the study period. Hunters and predators (Eurasian lynx and red foxes) occurred in two of our study populations and contributed substantially to the variance in $\lambda$, accounting for a total of 35% and 70% in the two populations respectively.

**5.** Across populations, we did not find any evidence that roe deer increased their reproductive output when faced with harsh conditions, resulting in some populations having negative growth rates.

**6.** Generation time, a measure of the speed of the life-history cycle, increased from less than 4 years in the most productive population ('roe deer heaven') to more than 6 years in declining populations facing predation from lynx, red fox and hunters ('roe deer hell'), and was tightly and inversely correlated with $\lambda$. Such a deceleration of the life cycle in declining populations might be a general feature in large herbivores.

**7.** Our results shows that the plethora of environmental conditions faced by populations of large herbivores also induce high intraspecific variation in their ranking along the 'fast–slow' continuum of life-history tactics.

**Key-words:** *Capreolus capreolus*, demographic variation, Eurasian lynx, harvest, life history

## Introduction

To increase our mechanistic understanding of population fluctuations and the evolution of life histories, an important first step is to identify the demographic parameters that are most important for explaining variation in population growth rate. In most taxonomic groups, species' life histories are distributed along a 'fast–slow' continuum (Stearns 1983; Gaillard *et al.* 1989; Harvey, Read & Promislow 1989; Sæther & Bakke 2000; Bielby *et al.* 2007) even after accounting for

differences in body mass. Slow-living species reproduce relatively late in their life span, have low fecundity and long life expectancy, and thereby have long generation times (defined after Leslie 1966 as the weighted mean age of mothers in a population, and typically more than 2 years in slow-living species; Lebreton & Clobert 1991). As the potential impact on λ of a given change in a demographic parameter is closely related to generation time (Gaillard *et al.* 2005), such marked differences in generation time among species might suggest that the functional dependence of λ to changes in adult survival vs. recruitment is species specific. For instance, a given change in adult survival always has a stronger impact on λ in long-lived species than that of any other trait (Gaillard *et al.* 2000). Since life histories partly reflect adaptations to particular environments (Stearns 1992) and temporal variability usually reduces the long-term population growth rate (Tuljapurkar & Orzack 1980), traits that have a large impact on λ should be buffered against temporal variation, as reported for large mammalian herbivores (Gaillard & Yoccoz 2003), birds (Sæther & Bakke 2000) and plants (Pfister 1998). As a result, the observed variation in λ of large herbivores is often attributed to inter-annual variation in recruitment when covariation among demographic rates is not accounted for, despite the stronger functional dependence of λ to variation in adult survival (Gaillard *et al.* 2000).

However, recent analyses have shown that different demographic parameters might account for the observed variation in λ in different populations of the same species (see e.g. Coulson, Gaillard & Festa-Bianchet 2005; Morrison & Hik 2007), and even in different habitats within a population (Ezard *et al.* 2008). Environmental conditions shape λ by their effects on demographic parameters, and empirical evidence shows that age-specific demographic parameters and their covariation are differently affected by environmental variation (Coulson *et al.* 2001). While stressful climatic and nutritional conditions usually affect prime-aged individuals less than pre-prime and post-prime individuals (Gaillard *et al.* 2000; Coulson *et al.* 2001), free-ranging populations might be affected by a plethora of environmental factors acting on different demographic parameters. For instance, while some coursing predators such as wolves (*Canis lupus* L.) are highly selective and mostly focus on young and old individuals within the prey population (Delgiudice *et al.* 2006), ambush predators such as cougars (*Puma concolor* L.) are less selective, and kill a large proportion of prime-aged females (Festa-Bianchet *et al.* 2006). In roe deer (*Capreolus capreolus* L.), fawns are generally not exposed to significant lynx (*Lynx lynx* L.) predation during their first months of life (Panzacchi *et al.* 2008), while older age classes are usually selected over other prey species when present (Jedrzejewski *et al.* 1993; Schmidt 2008). Consequently, when lynx predation varies over time, survival rates at ages other than juveniles are likely to show substantial temporal variation. On the other hand, red fox (*Vulpes vulpes* Say 1823) predation on roe deer is mainly concentrated within the first two months of life (Panzacchi *et al.* 2008). Thus, fluctuations in red fox abundance also cause variation in juvenile survival (Kjellander & Nordstrom 2003). Finally, in human-dominated landscapes, large herbivores are often subject to intensive harvesting (Gordon, Hester & Festa-Bianchet 2004). With harvesting regimes ranging from strongly juvenile biased to trophy harvest of prime age animals (Milner, Nilsen & Andreassen 2007), such human-induced mortality is also likely to create very different patterns in the relationship between λ and demographic parameters than those found in non-hunted populations.

Here we examine the population dynamic responses of a medium-sized ungulate species, the roe deer, to different environmental conditions. More precisely, we use matrix perturbation analysis (Caswell 2001) to investigate the sources of variation in λ in five contrasting European roe deer populations in a total of eight time periods. These populations inhabit widely contrasting environments, spanning gradients in seasonality, predation pressure, harvest levels and population densities. The purpose of this study was (i) to assess the functional dependence of λ on variation in demographic parameters across a wide range of environmental conditions, (ii) to quantify the contribution of changes in demographic parameters to variation in λ, and (iii) to quantify the contribution of predation and harvesting to temporal variation in λ. This latter is particularly important as many of the best-studied populations of temperate ungulates such as red deer (*Cervus elaphus* L., Clutton-Brock, Guinness & Albon 1982), Soay sheep (*Ovis aries* L., Clutton-Brock & Pemberton 2004), roe deer (Gaillard *et al.* 2003) and pronghorn (*Antilocapra americana* Ord 1815, Byers 1997) were not subject to either predation on adults or harvesting, while Festa-Bianchet *et al.* (2006) have demonstrated how dramatic the effect of predation can be when it strikes a previously predator-free population.

## Methods

### STUDY AREAS

We used demographic data from five populations studied in France (Trois Fontaines and Chizé) and Norway (Storfosna, Østerdalen and Akershus/Østfold). These populations span a wide range of environmental conditions (Table 1). The sampling designs that varied among areas are described elsewhere (see e.g. Gaillard *et al.* 1993; Nilsen, Linnell & Andersen 2004).

The study area (7·8 km²) on Storfosna (10·8 km²) is located on a small island 2 km off the coast of central Norway (63°4′ N, 09°3′ E). The island consists of a fine-scaled mosaic of heather-dominated moorland, abandoned meadows, cultivated pasture, and mixed coniferous/deciduous woodland. During the study period, from 1991 to 1994, the population density increased from 10·1 deer km⁻² in spring 1991 to 34·5 deer km⁻² in May 1994 (Andersen & Linnell 2000). Demographic parameters were estimated based on radiocollared roe deer (*n* = 128), mostly marked as fawns (*n* = 94, see Nilsen *et al.* 2004 for further details).

The study area in Østerdalen is located in south-eastern Norway (61°15′ N, 11°30′ W). The topography consists of parallel river valleys running from north to south at about 200–500 m above sea level with hills ranging from 600 to 900 m above sea level. Agricultural land and human settlements are scattered along most valley bottoms. The vegetation is predominantly boreal coniferous forest (Scots pine *Pinus sylvestris*, Norwegian spruce *Picea abies* and birch *Betula* sp.), with 72% of the study area covered with forest. Based on hunter

**Table 1.** The five roe deer populations studied and their main environmental characteristics. Low density is defined as < 5 deer km⁻², medium density is 5–10 deer km⁻², and high density is > 10 deer km⁻². At Chizé, roe deer had a low/medium performance between 1986 and 1992 (high density and density-dependent responses), a high performance between 1994 and 2002 (low density and good climatic conditions during spring–summer), and a very poor performance between 2003 and 2006 (high density and frequent spring–summer droughts). At Trois Fontaines, the population size was weakly variable between 1985 and 2001, whereas population density increased strongly between 2002 and 2006. Red foxes were absent from Storfosna, but present in all other populations

| Population | Predators of adults present | Harvesting | Productivity | Winter climate (temp/snow cover)* | Summer climate (temp/prec.)† | Spring climate (temp/prec.)‡ | Roe deer density | Time span | Comments¶ |
|---|---|---|---|---|---|---|---|---|---|
| Storfosna | No | No | High | 1·2 C 6·5 cm⁻¹ | 12·8 C 85·7 mm⁻¹ | 9·1 C 72·7 mm⁻¹ | High | 1991–94 | Island pop. |
| Østerdalen | Lynx | Yes | Low | −6·1 C 42 cm⁻¹ | 14·7 C 75·1 mm⁻¹ | 10·3 C 81·5 mm⁻¹ | Low | 1995–98 | Open pop. |
| Akershus/Østfold | Lynx (and a few wolves) | Yes | Medium | −2·8 C 13·3 cm⁻¹ | 16·2 C 74·7 mm⁻¹ | 12·4 C 80·8 mm⁻¹ | Medium | 2001–04 | Open pop. |
| Trois Fontaines | No | No§ | High | 4·9 C 0 cm⁻¹ | 19·6 C 70·1 mm⁻¹ | 15·8 C 70·2 mm⁻¹ | Medium | 1985–2001 | Fenced pop. |
| | | | | 5·1 C 0 cm⁻¹ | 20·0 C 69·5 mm⁻¹ | 16·7 C 51·6 mm⁻¹ | High | 2002–06 | |
| Chizé | No | No§ | Low | 6·7 C 0 cm⁻¹ | 20·7 C 44·2 mm⁻¹ | 16·6 C 47·3 mm⁻¹ | High | 1986–92 | Fenced pop. |
| | | | | 5·5 C 0 cm⁻¹ | 20·4 C 56·2 mm⁻¹ | 16·7 C 53·8 mm⁻¹ | Medium | 1994–2002 | |
| | | | | 6·3 C 0 cm⁻¹ | 21·0 C 50·0 mm⁻¹ | 17·5 C 36·4 mm⁻¹ | High | 2003–06 | |

*Mean values for winter, defined as January–March. †Mean values for summer, defined as July–August. Precipitation is mean value/month. ‡Mean values for spring, defined as May–June. Precipitation is mean value/month. §The size of these enclosed populations was controlled by removals during winter, but estimates of demographic parameters are corrected for this management, meaning that the demography reflects the demography of unexploited populations. ¶Open population indicates that the population is not clearly defined spatially, as is the case with the island population (Storfosna) and the fenced populations (Trois Fontaines and Chizé).

records and counts made at supplementary feeding stations, the roe deer density is believed to be extremely low (< 1 per km²). Demographic parameters were estimated based on radiocollared roe deer (*n* = 62) often marked as fawns (*n* = 23, see Panzacchi *et al.* 2008 for further details).

The Akershus/Østfold study area, situated 100 km south of Østerdalen, is also dominated by boreal forest, but includes patches of deciduous forest represented mainly by birch. The landscape is human modified, with the forest fragmented by cultivated land and water bodies, and the altitude is not higher than 300 m above sea level. Roe deer density estimated from hunting records suggest that they occur at moderate densities, and that the density declined slightly during the study period from 2001 to 2005. Demographic parameters were estimated based on radiocollared roe deer (*n* = 116), mostly marked as fawns (*n* = 44, see Panzacchi *et al.* 2008 and Ratikainen *et al.* 2007 for further details).

The study area at Chizé (26·6 km²) in western France (46°05′ N, 0°25′ W) has an oceanic climate with Mediterranean influences, with mild winters and warm often dry summers. This fenced reserve managed by the Office National de la Chasse et de la Faune Sauvage (ONCFS) consists of a forest dominated by oak *Quercus* sp. and beech *Fagus sylvatica*. Overall, the forest is not highly productive because of poor soil quality and of frequent summer droughts. Since 1977, capture–mark–recapture estimates of population size and demographic parameters are available (see Gaillard *et al.* 2003 for further details). High variation in population size (controlled by yearly removals) and climate among years allowed us to define three periods of contrasting roe deer performance (see Table 1). Demographic parameters were estimated based on individually marked (both ear-tags and numbered collar) and known-age roe deer (*n* = 599) often marked as newborns (*n* = 322, see Gaillard *et al.* 2003 for further details).

The study area at Trois Fontaines (13·6 km²) in eastern France (48°43′ N, 54°10′ E) has a continental climate, with quite harsh winters and warm but moist summers. This fenced area managed by the ONCFS consists of a forest dominated by oak and beech. The forest is quite homogeneous at a large spatial scale (> 100 ha) but highly heterogeneous at small spatial scales (< 10 ha). Trois Fontaines is a rich and productive forest (Pettorelli *et al.* 2006) due to high-quality soils and generally high rainfall in spring. Variation in population size (controlled by yearly removals) allowed us to define two periods of contrasting roe deer performance (see Table 1). Demographic parameters were estimated based on individually marked (both ear-tags and numbered collar) and known-age roe deer (*n* = 997) mostly marked as newborns (*n* = 907, see Gaillard *et al.* 2003 for further details).

As well as differing in climate and density, these populations differed with respect to predation. Hunters, Eurasian lynx and red foxes were predators of roe deer in both Norwegian mainland sites, with both hunters and lynx killing all age classes (Andersen *et al.* 2007) and foxes killing fawns during the post-natal period (Panzacchi *et al.* 2008). Although red foxes were present in the two French study sites, there is no evidence of marked predation on fawns in these areas.

ESTIMATION OF DEMOGRAPHIC PARAMETERS

Due to different sampling regimes between study sites, parameter estimation techniques also varied between the study sites. Most importantly, data collection in the three Norwegian populations was based on radiotelemetry studies, whereas the French populations were based on individually marked animals potentially recaptured once every year.
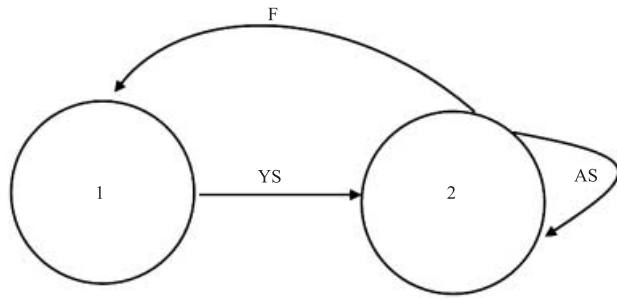
**Fig. 1.** A schematic representation of roe deer life cycle as defined in this study. The stages are yearling (1) and adult (2) respectively, whereas the transitions are given as yearling survival (YS) and adult survival (AS), respectively. Only adult females reproduce (F) in our model and we assume no age dependence in survival and reproduction in the adult stage. See text for justification.

In the Norwegian populations, survival rates were estimated by known-fate capture–mark–recapture (CMR) models well suited to survival analyses of radiotracked animals (White & Burnham 1999). We censored animals with unknown fate (e.g. due to radiocollar failure). Litter size and proportion of females that gave birth were estimated based on direct observations of radiocollared does in the spring close to the birth period (see also Nilsen *et al.* 2004 for further details).

In the French populations, survival rates were estimated using standard CMR methods (Lebreton *et al.* 1992) to account for capture rates being less than 1 (about 0·5 at both Chizé and Trois Fontaines for roe deer older than 1 year of age; Gaillard *et al.* 1993). Age- and sex-specific survival probabilities and their SE were obtained using the software MSURGE 7·1 (Choquet *et al.* 2004). Litter size and proportion of females that gave birth were estimated from ultrasounds performed during winter captures since 1988 and from progesterone assays in the same period before 1988 at Chizé (see Gaillard *et al.* 1992, 2003 for further details). At Trois Fontaines, we assumed that all females older than 1 year of age produced twins, as supported by the empirical evidence (see Gaillard *et al.* 1998). This assumption is likely to lead to a slight overestimation of the reproductive output of females during the high-density period.

ROE DEER LIFE CYCLE

To be able to quantify the relative contribution from different demographic parameters to variation in λ, a life cycle has to be defined. We based our analysis on a pre-breeding life cycle (Fig. 1), assuming that the populations are censused just before the breeding season each year. This implies that the youngest age class present in the population at the census time is the 1-year-olds and that juvenile survival (between birth and 1 year of age) is included in the recruitment rate (see Caswell 2001 for further details). Consequently, we considered the following demographic parameters in our analyses:
• Recruitment rate (F): number of female offspring that enter the population at time *t* + 1 (just before the birth season) per female alive at the beginning of year *t* (just before the birth season). The recruitment is thus given by the product of the proportion of females (≥ 2 years old) that give birth in year *t*, the mean number of females produced in year *t* (litter size divided by 2, i.e. assuming balanced sex ratio at birth), juvenile summer survival (from birth to weaning) and juvenile winter survival (from weaning to 1 year of age).

• Yearling survival (YS): survival probability through the second year of life (i.e. from 1 to 2 years of age).
• Adult survival (AS): annual survival probability for adult females (i.e. aged 2 years or more).

We based our further analysis on perturbation analysis of a transition matrix describing female roe deer population dynamics in five different areas. Although demographic rates of large herbivores show strong age dependency (see e.g. Gaillard *et al.* 1993 for the case of roe deer survival patterns), we pooled all the adult age classes into one adult stage. The reason for this is twofold; first, in our Norwegian populations the time span of the studies were < 5 years, and ages of the individuals were known accurately only for individuals marked during their first year of life. Consequently, an age-structured model would have contained very few individuals in the older age classes. Second, although both survival and reproduction do vary with age in roe deer, it is usually relatively independent of age for prime-aged females (2–8 years) (Gaillard *et al.* 1993; Andersen & Linnell 2000; Festa-Bianchet, Gaillard & Côté 2003). Few individuals would reach senescence, but we are aware that this might cause a slight bias in the estimates of demographic rates and their variance. This happens because the survival of senescent females is lower and more variable than that of prime-aged individuals (Gaillard *et al.* 2000; Festa-Bianchet *et al.* 2003). To assess the robustness of this assumption, we also performed the calculations based on a fully age-structured model for Chizé (see Table S1) where the proportion of old females was the highest. The general patterns did not differ between the two models, but the contribution from adult survival generally decreased slightly when accounting for senescence.

Perturbation analysis of a projection matrix is based on the assumption that the stable age structure and reproductive values are given by the left and right eigenvectors of the projection matrix (see below). However, both age structure and reproductive values might vary for populations in different phases of development. To fully account for this, using a structured demographic account (SDA) would be required, but this method requires complete historical knowledge of all individuals in the population, and in most cases these two methods will give comparable results when covariation between demographic rates is accounted for (Coulson *et al.* 2005). As pointed out by several authors (see e.g. Sæther & Bakke 2000; van Tienderen 2000; Coulson *et al.* 2005), it is important to control for the effect of covariation between demographic rates. In our study, with very short time series from some of the populations and periods (see Table 1), we did not consider covariation between traits. However, the contribution of covariation among parameters accounted for only ~15% of the variation in λ in populations for which we had > 10 years of data (see Table S2).

MATRIX ANALYSIS

*Projection model and analysis – functional relationships*

The demographic rates described above were used to construct a pre-breeding Leslie matrix for the female portion of our roe deer populations. Consider the following population model; $n(t + 1) = An(t)$, where $n(t)$ is a vector giving the abundances of different stages, and $A$ is a projection matrix (Caswell 2001), whose $ij$ entry gives the contribution of an individual in stage $j$ to stage $i$ over one time-step (here, the time-step is taken to be 1 year). The transition matrix ($A$) is given as

$$\mathbf{A} = \begin{bmatrix} 0 & F \\ YS & AS \end{bmatrix} \qquad \text{eqn 1}$$

This matrix (*A*) is a convenient starting point for our analysis, as it has some well-known properties. First, λ is given by the dominant eigenvalue of the matrix. Furthermore, the right and left eigenvectors, *w* and *v* respectively, give the projected stable age distribution and age-specific reproductive values. Although important in their own right, we here use them as a basis for calculating elasticities (e_). In short – a matrix element of which λ has a high elasticity will have a large proportional effect on λ (Caswell 2001).

Based on the demographic data described above, we also calculated generation times ($T_b$, the weighted mean age of mothers in the population *sensu* Leslie 1966) for each of the study populations. Generation time is a reliable measure of the speed of the life history (Gaillard *et al*. 2005), and can be easily obtained as the inverse of e_F, as demonstrated by Brooks & Lebreton (2001).

### Quantifying the contribution of demographic parameters to observed variation in λ

In our analysis, we were interested in the relative contribution of the different demographic parameters on the observed variation in λ estimated from mean and variance of demographic parameters. As mentioned previously, a trait could contribute much to variation in λ if the elasticity is high, if it has a high temporal variability, or if both occur. After Horvitz, Schemske & Caswell (1997), we measured the contribution of a given demographic parameter (T) to the variance in λ by multiplying the square of the elasticity (e_T) with the square of the coefficient of variation (CV_T) for the associated demographic parameter; $(e\_T)^2 \times (CV\_T)^2$ (Horvitz *et al*. 1997).

We also investigated the relative contribution from the different mortality sources within this framework. More precisely, we were interested in the contribution from red fox and lynx predation as well as hunter harvest to the variance in λ. This was carried out by (i) censoring individuals whose mortality was related to the mortality factor of interest and recalculating survival probabilities for the remaining sample. Then (ii) we constructed a new set of elasticity and CV-values, and recalculated the contribution from the trait described above. Then, (iii) the contribution from the mortality factor of interest was calculated by summing the contribution from that factor across all stage-classes – e.g. the square of temporal variation in yearling mortality (CV_YS) from lynx predation was multiplied by the square of e_YS based on the matrix described above. The total contribution from lynx predation and harvesting was calculated as the sum of the contribution from all stage classes.

All matrix calculations were carried out in R 2·4·1 (R Development Team 2006), with elasticities calculated with the package POPBIO.

All correlations are Pearson's correlations, and *n* = 8 in all cases. We report coefficients and *P* values for each correlation, and a visual display of each relationship is provided in Fig. S1.

## Results

### FUNCTIONAL RELATIONSHIPS AND TEMPORAL VARIABILITY

The basic metrics describing the projection matrices for roe deer populations facing different environmental conditions are given in Table 2. Most notably, the population growth rates varied widely, with a strong negative growth in the two inland populations in Norway, and a very rapid positive population growth rate on Storfosna (Table 2). The French populations showed intermediate values.

As expected in long-lived species, e_AS was higher than e_F in all eight cases (sign test, *P* = 0·004). However, looking at the elasticity ratios (e_AS/e_F), it is noticeable that, although the value for adult survival was always higher, the elasticity ratio varied broadly across populations experiencing different environmental conditions and with different population trajectories (Table 2). A similar relationship was found for generation time ($T_b$; Table 2).

Across populations and periods, mean adult survival covaried positively with mean recruitment (*r* = 0·77, *P* = 0·027) and λ (*r* = 0·97, *P* < 0·001), and negatively with e_AS (*r* = –0·87, *P* = 0·004). This led to a strong negative relationship between λ and e_AS (*r* = –0·96, *P* < 0·001). Consequently, the functional relationship between λ and adult survival was even stronger when conditions became worse. The positive correlation between recruitment and adult survival also resulted in a negative correlation between generation time ($T_b$) and λ (*r* = –0·97, *P* < 0·001; Fig. 2), meaning that the roe deer life cycle 'slowed down' under harsh conditions.

As also expected, recruitment rates were more variable than adult survival in all our populations and periods (sign test, *P* = 0·004). If the life histories observed here represented differential trade offs caused by local conditions, one would also expect (i) a negative relationship between the temporal variation in one trait in a given situation and the elasticity of λ to that trait, and (ii) a negative relationship between the
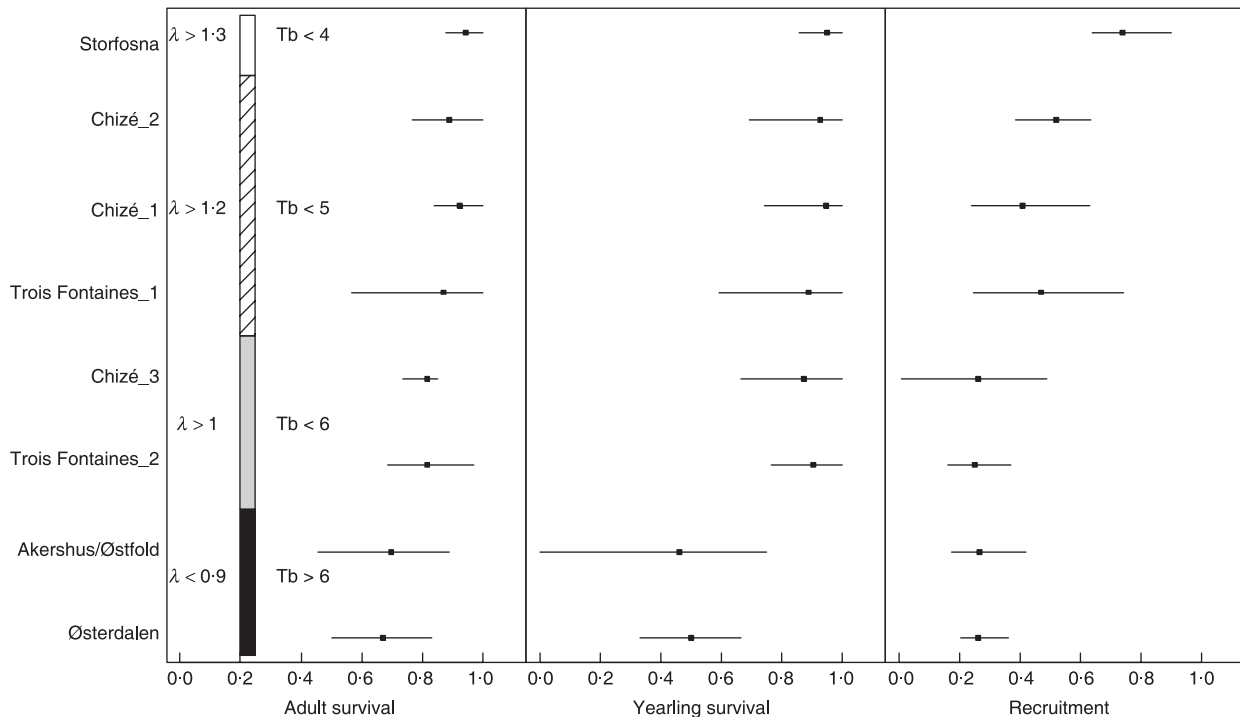
**Table 2.** Summary of λ (SE), generation time ($T_b$) and elasticity of λ to recruitment (e_F) and adult survival (e_AS) for roe deer populations under contrasting environmental conditions and different phases in population development. For further details about periods in Chizé and Trois Fontaines, see legend to Table 1

| Area | λ (SE)* | e_F† | e_AS | Elasticity ratio‡ | $T_b$ | Variance ratio§ |
|---|---|---|---|---|---|---|
| Storfosna | 1·44 (0·062) | 0·25 | 0·49 | 1·93 | 3·93 | 0·34 |
| Østerdalen | 0·83 (0·222) | 0·16 | 0·68 | 4·26 | 6·25 | 0·93 |
| Akershus/Østfold | 0·84 (0·184) | 0·15 | 0·71 | 4·80 | 6·80 | 0·61 |
| Chizé, medium performance | 1·24 (0·087) | 0·20 | 0·60 | 2·96 | 4·96 | 0·18 |
| Chizé, high performance | 1·27 (0·067) | 0·23 | 0·54 | 2·33 | 4·33 | 0·51 |
| Chizé, low performance | 1·04 (0·162) | 0·18 | 0·65 | 3·68 | 5·68 | 0·08 |
| Trois Fontaines, low density | 1·21 (0·110) | 0·22 | 0·56 | 2·52 | 4·53 | 0·51 |
| Trois Fontaines, high density | 1·03 (0·124) | 0·18 | 0·65 | 3·71 | 5·71 | 0·45 |

*Standard errors (SE) calculated based on Tuljapurkar (1982); †e_F is equal to e_YS. ‡Calculated as e_AS/e_F; §Calculated as CV_AS/CV_F.

**Fig. 2.** Relationship between demographic rates, λ and generation time ($T_b$) for eight roe deer 'populations' in Norway and France. Black dots represent estimated demographic rates (mean and range). The colour key represents a range of observed speeds of the life-history cycle as measured by generation time from the fastest in the colonizing population of Storfosna to the slowest ones in the declining populations of Akershus/Østfold and Østerdalen. Chizé_1 is the medium performance period (1986–92), Chizé_2 is the high performance period (1994–2002) and Chizé_3 (2003–06) is the low performance period, Trois Fontaines_1 is the low-density period (1985–2001) and Trois Fontaines_2 is the high-density period (2002–06).

amount of possible variation and the adult elasticity ratio (environmental canalization; see Gaillard & Yoccoz, 2003; buffering effects; see Pfister 1998 and Morris & Doak, 2004). However, when plotting the elasticity ratio (e_AS/e_F) against the relative variability of the adult survival and recruitment rate (CV_AS/CV_F) across populations, there was a weak tendency for an increasing variance ratio with increasing elasticity ratio ($r = 0.37$, $P = 0.363$). Similarly, in our sample populations there was a slight positive tendency between the amount of total variation (measured as the ratio between observed and maximum binomial variance; see Gaillard & Yoccoz 2003 and Morris & Doak 2004 for further details) and the elasticity ratio ($r = 0.41$, $P = 0.313$). This suggests that the observed life histories are direct consequences of local mortality regimes rather than local trade offs. In declining populations of roe deer, adult survival was generally low and variable (i.e. a strong negative relationship existed between adult survival and CV_AS; $r = -0.89$, $P = 0.003$).

### QUANTIFYING THE CONTRIBUTION FROM DIFFERENT DEMOGRAPHIC TRAITS

Recruitment was more variable and this increased the contribution of recruitment to the variance of λ in most populations (Table 3). In contrast to the analysis presented above, there was a large difference between the populations in the ranking of the demographic traits when quantifying their contribution

**Table 3.** Amount of variance (rescaled to percentage) in λ that could be attributed to recruitment (F), yearling survival (YS), and adult survival (AS). For further details about periods in Chizé and Trois Fontaines, see legend to Table 1

| Trait | F | YS | AS |
|---|---|---|---|
| Storfosna | 61% | 13% | 26% |
| Østerdalen | 6% | 8% | 86% |
| Akershus/Østfold | 8% | 22% | 70% |
| Chizé, medium performance | 74% | 5% | 21% |
| Chizé, high performance | 32% | 22% | 46% |
| Chizé, low performance | 88% | 4% | 8% |
| Trois Fontaines, low density | 35% | 9% | 56% |
| Trois Fontaines, high density | 26% | 3% | 71% |

to the variance in λ (Table 3). There was, however, a clear tendency towards a negative relationship among populations between adult survival and the contribution from adult survival to variance in λ ($r = -0.70$, $P = 0.054$). Also, there was a tendency towards a negative relationship among populations between λ and the contribution of adult survival to the variance in λ ($r = -0.62$, $P = 0.103$), and a positive tendency for recruitment ($r = 0.56$, $P = 0.147$). This indicates that for our declining populations, the variance in λ was mostly driven by the temporal variation in adult survival, which also had a low mean in these populations.

In our two inland populations from Norway where two predators (foxes and lynx) and human harvesting were present, we further decomposed the variance in λ into contributions from lynx and red fox predation and harvest. The between-year variation in harvest levels accounted for 15% (Akershus/Østfold) and 16% (Østerdalen) of the variance in λ, respectively. Furthermore, lynx predation explained an additional 25% (Akershus/Østfold) and 43% (Østerdalen). Finally, red fox predation on the fawns during the first summer only accounted for ~2% of the variance in λ in both areas. This was partly because in both populations, variation in recruitment contributed relatively little to variance in λ (Table 3). Assuming full additivity of predation and harvesting, these factors accounted for 70% and 35% of the variance in λ in Østerdalen and Østfold/Akershus, respectively.

## Discussion

A thorough understanding of the dynamics of free-ranging populations requires both the identification of the demographic parameters that are most important for variation in λ and the environmental variables responsible for variation in these (Morrison & Hik 2007). In accordance with previous studies on large herbivores (e.g. Gaillard *et al.* 2000), the functional relationship between λ and adult survival was always stronger than that of any other trait, and recruitment was consistently more variable than adult survival. Our analysis of demographic patterns in roe deer population dynamics across a wide range of environmental conditions highlights however the complex interactions between the environment and population dynamics. Not only did demographic parameters such as survival and recruitment vary among populations in relation to contrasting environmental conditions, but also the relative importance of adult survival and recruitment varied among populations (see Coulson *et al.* 2005 for similar conclusions). Finally and most importantly, we identified for the first time a clear pattern of variation in the speed of life history according to the harshness of environmental conditions: roe deer life history slowed down when faced with adverse environmental conditions.

While hunting and predation often play a fundamental role in shaping the dynamics of populations (Sinclair, Mduma & Brashares 2003; Festa-Bianchet *et al.* 2006) and the evolution of life histories (Stearns 1992), the best-studied populations of large herbivores in temperate areas are subject to no, or limited, hunting and predation pressure on adults (e.g. Coulson *et al.* 2001). Here we report how predation and harvesting caused relationships between λ and demographic parameters that were very different from those found in non-hunted populations not subject to predation on adults. The top-down

impact of predation and hunting on ungulate population dynamics is, however, not only contingent on the number of individuals removed by predators and hunters, but also on the age-class distribution of the kills (Sinclair *et al.* 2003; Nilsen *et al.* 2005). While prime-aged adults of the largest herbivores are in general less vulnerable to predation (Sinclair *et al.* 2003), they are also more sensitive to increased adult mortality should it occur, due to the strong allometric constraints that large body size imposes (i.e., a decrease of litter size, Allainé *et al.* 1987 and an increase of interbirth intervals, Owen-Smith 1988). Thus, as soon as a high level of predation (Owen-Smith & Mason 2005) or hunting (Nilsen *et al.* 2005) occurs on adults, populations of very large herbivores should decline. As roe deer are medium-sized herbivores with a relatively high reproductive potential, we could have expected a different outcome. However, both lynx predation and harvest act on all age classes (Andersen *et al.* 2007) while foxes only prey on juveniles in the months following birth (Panzacchi *et al.* 2008). Consequently, both recruitment and adult survival were affected by predation and harvest, which caused the positive correlation observed here between these parameters. Despite the higher maximal growth rates (*r* max sensu Caughley 1977) of small and medium sized herbivores than larger ones (e.g. Sinclair 1996), the top-down force of predation is thus likely to be more dominant for the former because adult females are also targeted (see also Sinclair *et al.* 2003; Andersen *et al.* 2007). In two of our study areas with predators and hunters permanently present, adult survival rates were very low for a long-lived species such as roe deer (Fig. 2; compare with Table 3 in Gaillard & Yoccoz 2003), and could largely be attributed to high predation and harvest rates. In both study sites, variation in adult survival accounted for a large part of the variance in λ (Table 3), and much of this variation was attributed to variation in predation and harvest levels (see results). When subject to harvest and predation, these two factors can thus have an overwhelming effect on the population dynamics (see also Festa-Bianchet *et al.* 2006; Owen-Smith & Mills 2006), and the demography might be dramatically different from non-hunted populations or populations not subject to predation on adults.

It is no surprise that the elasticity of λ to changes in adult survival was consistently higher than that of recruitment in roe deer (Gaillard *et al.* 2000). Phylogeny and body mass account for much of the variation between mammalian species in demographic tactics (Gaillard *et al.* 2005; Dobson & Oli 2007); thus there are limits to the range of variation one might expect to occur within species-specific demography. Nevertheless, it is instructive to note how much the elasticity ratios (i.e. $e\_AS/e\_F$) varied between different environmental settings (Table 2). In fact, the range of elasticity ratios reported here for roe deer populations facing very different environmental conditions approaches the between-species range reported in Gaillard & Yoccoz (2003) for 22 species of

large herbivores (disregarding the much larger-sized feral horses, with a ratio of 17·54).

Life histories have evolved to partition resources between survival and recruitment, under the constraints of phylogeny and environmental conditions (Stearns 1992). The demographic patterns observed here for five roe deer populations undergoing different phases of population development would thus imply very different selection gradients between populations (see e.g. Table 1 in van Tienderen 2000 for selection gradients). The current mortality regime in our declining populations is of quite recent origin (Andersen *et al.* 2004), so any evolutionary response to the current environmental conditions should thus not be expected. However, if the different life histories observed in our study populations were shaped by differential energy allocation rules caused by observed environmental conditions, one might have expected to find evidence of trade-off's between recruitment and adult survival (Stearns 1992). Our results do not, however, provide any sign of differential trade-offs at the interpopulation level, but rather suggest fitness differences that are direct consequences of the mortality regimes. Contrary to Tasmanian devils (*Sarcophilus harrisii* Boitard 1841), for instance, which responded to a high mortality generated by facial tumour disease by increasing reproductive effort early in life (Jones *et al.* 2008), our results therefore suggest that roe deer are not able to re-allocate resources in order to compensate for a low survival in highly risky environments. In total, these results imply that the life history of roe deer does not allow them to cope with the conditions faced in our hunted populations (with the existing quotas) while simultaneously subject to predation at the observed rates (see also Owen-Smith & Mason 2005). Given the fact that two of our populations subject to harvest and predation had $\lambda$ well below 1 (Table 2; Fig. 2), their very existence in the long run apparently depends on immigration. The very rapid population growth under favourable conditions at Storfosna (Table 2) and the high speed of range expansion reported for roe deer in Scandinavia (Andersen *et al.* 2004) suggest that roe deer are able to rapidly recolonize areas when conditions are good.

INTRASPECIFIC VARIATION IN LIFE-HISTORY TIME-SCALES: FROM A FAST LIFE IN HEAVEN TO A SLOW LIFE IN HELL?

Generation time has been used to rank species along the 'fast–slow' continuum (Gaillard *et al.* 2005). In our intraspecific comparison, we reported unexpectedly large variation in generation times, ranging from 3·9 in the colonizing population of Storfosna to 6·8 in the declining population of Østerdalen. Using the allometric relationship reported in Gaillard *et al.* (2008), these generation times would correspond to large herbivores species with a browser type ecology weighing 12·6 kg at Storfosna and 145·8 kg in Østerdalen. We therefore provide clear evidence that harsh environmental conditions generated by the co-occurrence of high hunting pressure and lynx predation lead to a deceleration in the life-history cycle of roe deer. Note that the 'slow pace of life' observed in declining populations of roe deer did not involve any delayed reproduction as expected from life-history theory (Stearns 1992) and reported empirically to account for increased generation times in high-density vs. low-density populations (see Crampe *et al.* 2006 for a case study on isard *Rupicapra pyrenaica* Bonaparte 1845). This raises the question whether such time-scale changes at the intraspecific level and thereby independently of a shift in body size are a specific feature of roe deer or correspond to a widespread process among large herbivores. The following process can be postulated. When the focal population can respond to increased overall mortality by increasing litter size or reproductive effort at early ages (as reported for Tasmanian devils, Jones *et al.* 2008), a speeding up of the life cycle should occur. On the other hand, when the focal population cannot counterbalance an increase of overall mortality by increasing reproductive effort in early life (as reported here for roe deer, on bighorn sheep by Festa-Bianchet *et al.* 2006, and on woodland caribou by Wittmer *et al.* 2005), a slower life history and a decrease in $\lambda$ should occur. Due to strong constraints on reproductive output (Allainé *et al.* 1987), we would speculate that the latter would be the most common pattern among large herbivores.

The demographic basis underlying variation in $\lambda$ is a central issue in population ecology. The plethora of causes of demographic variation affect different parameters, and many of them can also induce temporal variation in adult survival. Here we have described how two of them, namely predation and hunting, can result in cases where temporal variation in adult survival drives the dynamics of a temperate large herbivore. Such case studies underline how predation, especially when combined with harvest, can potentially have dramatic effects on population dynamics of long-lived species, which in turn could trigger a range of cascading effects through the ecosystem (Andersen, Linnell & Solberg 2006). It will be interesting to test the generality of these results for other predator–prey combinations, especially when considering that different age and sex classes of prey may have widely differing vulnerabilities to different predators (Linnell, Aanes & Andersen 1995).

## Acknowledgements

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Fig. S1.** Relationships between different parameters used to characterize five different roe deer populations in a total of eight time periods, spanning a wide range of environmental conditions.

**Table S1.** Based on the data from Chizé (1986–2006), we conducted an analysis of the contribution of main effects from a complete age-structured matrix model, to investigate the potential bias in the analysis presented in the main document caused by the simplified age structure, and more particularly by neglecting senescence (see Festa-Bianchet *et al.* 2003 for justification)

**Table S2.** Based on the data from Chizé (1986–2006) (a) and Trois Fontaines (1985–2006) (b), we conducted an analysis of the contribution of the main effects and the covariation among demographic rates to assess the assumption that the exclusion of covariation did not severely bias our results